

Dear Dr. Bricaud,

Thank you for accepting this manuscript for publication in Biogeosciences.

We appreciate time and effort, yours as well as the one dedicated by the reviewers. You will find final version of our manuscript uploaded, and below you will find our answer to the reviewer's comments (**in bold**) with references to appropriate parts of the text (***in bold italic***), as well as a marked up (**red**) version of the final manuscript.

Sincerely,

Ivona Cetinić

### ***Answer to Reviewer's comments***

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The authors changed the text according to my comments (where necessary), and I am happy as a reviewer to accept the manuscript to be published, but only if the following minor points are further revised.

(1) Please provide statistical result for Fig. 5B (e.g. regression analysis), since this plot is actually the one which "directly" translates the authors' conclusion (i.e. the "direct" evidence that the optical index, ChlF/bbp, varies with diatom fraction), hence the most important result/plot for the authors' conclusion.

**In this paper, we are saying that the higher values of optical index (higher than 80 Vm) are associated with higher concentrations of diatoms, not that those two parameters are covariant in linear manner, hence calculating a regression would go against our claims. What we are offering in return, as a proof of statistical strength of our claim, are the results of a t-test that are now part of the text, demonstrating that average diatom fraction in the <80 mV group is significantly smaller than the one in > 80 mV group (one tailed t-test,  $p < 0.001$ ) [line 7, pg 12].**

(2) The authors responded to one of my major comments (as to the necessity of patchiness discussion for drawing the authors' final conclusion) by mentioning:

"This is, to our knowledge, the first analysis of this kind, where the distribution of the phytoplankton community was assessed for a two-month period with such high spatial and temporal resolution. Without the patchiness study, this is just a methods paper".

I personally interpreted that this is a methodology paper according to what was originally written in this manuscript (and nothing is wrong with it) but I respect this authors' answer. Then I would suggest that the authors more emphasize, in the manuscript, such a "selling point" of patchiness discussion (i.e. originality, etc).

**We have changed the text throughout the manuscript to reflect the reviewer's suggestion:**

**[In 5, pg 2] ....provides a unique tool...**

**[In 20, pg 3] *This is, to our knowledge, first attempt of its kind to use such approach to construct a spatial time series of the evolution of phytoplankton community structure and to document its spatial heterogeneity.***

**[In 11, pg 18] *This is, to our knowledge, the first analysis of this kind, where the distribution of the phytoplankton community was assessed for a two-month period with such high spatial and temporal resolution.***

**[In 14, pg 19] *The application of the optical index demonstrated, for the first time on appropriate spatial and temporal scales....***

Other:

Title (pp.1) To be more precise, I suggest that the authors change the term "plankton community composition" to "phytoplankton community composition".

**Changed**

L13(pp.6)  $K_D$  is usually denoted as  $K_d$ .

**Changed**

L22(pp.7) Use italic font only for "Synechococcus" rather than for "Synechococcus spp."

**Changed**

1 **A simple optical index shows spatial and temporal**  
2 **heterogeneity in planktonphytoplankton community**  
3 **composition during the 2008 North Atlantic Bloom**

4  
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14  
15 **Abstract**

16 The ratio of two *in situ* optical measurements, chlorophyll fluorescence (*Chl F*) and optical  
17 particulate backscattering ( $b_{bp}$ ), varied with changes in phytoplankton community composition  
18 during the North Atlantic Bloom experiment in the Iceland Basin in 2008. Using ship-based  
19 measurements of *Chl F*,  $b_{bp}$ , chlorophyll *a* (*Chl*), HPLC pigments, phytoplankton composition  
20 and carbon biomass, we found that oscillations in the ratio varied with changes in plankton  
21 community composition; hence we refer to  $Chl F/b_{bp}$  as an “optical community index”. The  
22 index varied by more than a factor of two, with low values associated with pico- and  
23 nanophytoplankton and high values associated with diatom dominated phytoplankton  
24 communities. Observed changes in optical index were driven by taxa-specific chlorophyll-to-  
25 autotrophic carbon ratios and by physiological changes in *Chl F* driven by the silica limitation. A  
26 Lagrangian mixed-layer float and four Seagliders, operating continuously for two months, made  
27 similar measurements of the optical community index and followed the evolution and later

1 demise of the diatom spring bloom. Temporal changes in optical community index and, by  
2 implication the transition in community composition from diatom to post-diatom bloom  
3 communities, were not simultaneous over the spatial domain surveyed by the ship, float and  
4 gliders. The ratio of simple optical properties measured from autonomous platforms, when  
5 | carefully validated, provides a unique tool for studying phytoplankton patchiness on extended  
6 temporal scales and ecological relevant spatial scales, and should offer new insights into the  
7 processes regulating patchiness.

8

## 9 **1 Introduction**

10 Autonomous observations of phytoplankton are becoming increasingly ubiquitous, including *in*  
11 *situ* optical sensing from Argo-type and Lagrangian floats, gliders, and moorings, as well as  
12 remote sensing from space. Phytoplankton biomass is assessed through several different optical  
13 proxies including *in situ* chlorophyll *a* fluorescence (*Chl F*; Lorenzen, 1966), phytoplankton  
14 absorption coefficient ( $a_{phy}(\lambda)$ ) or particulate absorption coefficient in waters dominated by  
15 phytoplankton (Bricaud et al., 1995; Roesler and Barnard, 2014), and chlorophyll derived from  
16 *in situ* or remotely-sensed ocean reflectance at visible wavelengths (O'Reilly et al., 1998). High-  
17 frequency optical measurements are ideal for detecting temporal change and spatial patchiness,  
18 and in improving understanding of the role of meso- and submeso-scale physics on the  
19 distribution of phytoplankton in the ocean (Denman and Platt, 1976; Yoder et al., 1987; Munk,  
20 2000). Autonomous optical observations have enabled advances in understanding the timing of  
21 and mechanisms responsible for initiating blooms (Perry et al., 2008; Boss and Behrenfeld, 2010;  
22 Ryan et al., 2011; Mahadevan et al., 2012; Matrai et al., 2013).

23 Less common, more challenging, but increasingly important are autonomous measurements of  
24 phytoplankton community composition. Knowledge of the community composition is critical to  
25 understanding and predicting vital ecosystem functions such as carbon flux and efficiency of  
26 carbon transfer to higher trophic levels (biomass is not enough), particularly as the oceans  
27 change in response to climate change and ocean acidification. A few direct autonomous  
28 measurements of phytoplankton community composition have been made, but only on moorings  
29 due to the high power consumption of the flow or imaging-in-flow cytometric sensors (Olson  
30 and Sosik, 2007; Sosik and Olson, 2007; Campbell et al., 2013). A diversity of satellite-based

1 algorithms for determining phytoplankton functional types from ocean color reflectance has been  
2 developed in the last decade (see review of Moisan et al., 2012), although without community  
3 consensus as to robustness. Nencioli et al. (2010) implied that changes in the ratio of *Chl*-to-  
4 particulate beam attenuation coefficient ( $c_p$ ) and the backscattering ratio ( $b_{bp}/b_p$ , where  $b_{bp}$  is total  
5 particulate scattering coefficient and  $b_p$  is backscattering coefficient) are associated with changes  
6 in phytoplankton composition and physiological (light) adaptation in eddies off Hawaii. In a  
7 mooring study of the spring bloom in the Labrador Sea, change in phytoplankton species  
8 composition is offered as the explanation for the observed variability in  $Chl\ F/c_p$ , although this  
9 suggestion is unconfirmed by *in situ* measurement of species composition (Strutton et al., 2011).

10 In this study we define an “optical community index” as the ratio *Chl F*-to- $b_{bp}$  and connect it to  
11 plankton community composition using ship-based measurements of *Chl F*,  $b_{bp}$ , HPLC pigments,  
12 phytoplankton composition, and carbon biomass during two cruises to the Iceland Basin. For two  
13 months during the 2008 North Atlantic Bloom experiment (NAB 2008), we used a Lagrangian  
14 float as the reference frame to track the initiation of the diatom bloom in mid-April, through  
15 depletion of silicic acid and bloom termination in mid-May. The optical index,  $Chl\ F/b_{bp}$ , varied  
16 as a function of plankton community composition, decreasing by a factor of two as the early  
17 diatom spring bloom community transitioned into a recycling community dominated by smaller  
18 pico- and nanophytoplankton (Cetinić et al., 2012). Rigorous cross-calibration of optical sensors  
19 amongst all platforms enabled us to project the optical community index to data collected by four  
20 Seagliders. [This is, to our knowledge, first attempt of its kind to use such approach](#) to construct a  
21 spatial time series of the evolution of phytoplankton community structure and to document its  
22 spatial heterogeneity. This approach, of using simple optical measurements validated with more  
23 expensive ship-based measurements, allows projection of the ship measurements to broader  
24 temporal and spatial scales.

25

## 26 **2 Material and methods**

### 27 **2.1 Study site and platforms**

28 A Lagrangian float and four Seagliders were deployed near the JGOFS NABE 60°N site  
29 (Ducklow and Harris, 1993) from the *R/S Bjarni Saemundsson* on yearday, YD, 95 (4 April

1 2008; Fig. 1; (Briggs et al., 2011; Alkire et al., 2012; Mahadevan et al., 2012). The float tracked  
2 the horizontal motion of the mixed layer for almost two months, until the end of its mission on  
3 YD 146 (25 May 2008). An extensive discussion of the evolution of the bloom in the patch  
4 tracked by the float is provided in Alkire et al. (2012). The gliders were piloted to survey an  
5 approximately 50 km region around the float. Depending on currents and eddies, they  
6 occasionally swept further away (up to 175 km from the float). By the end of the float  
7 deployment in late May, they operated within 50 km of the float. A water sampling and sensor  
8 inter-calibration cruise on the *R/V Knorr* occurred between YD 123 –142 (2 – 21 May 2008),  
9 when the ship surveyed waters in proximity of the float and gliders.

10 The Lagrangian float, designed and built at the University of Washington Applied Physics  
11 Laboratory, was similar to the MLFII model described in D'Asaro (2003). The float's deployment  
12 and sampling strategy, detailed in Alkire et al. (2012), were designed to mimic the motion of  
13 plankton, drifting within the mixed layer; once per day (~ 15 UTC) it profiled from the surface to  
14 a depth of ~ 230 m, returning thereafter to the mixed-layer drift mode. The float measured  
15 temperature and conductivity with two CTD sensors (Sea-Bird Electronics, Inc., SBE 41), one  
16 near the top and another near the bottom of the platform (see list of measured parameters and  
17 associated methods in the Table 1). A WET Labs FLNTU mounted at the bottom of the float  
18 measured *Chl F* ( $\lambda_{\text{ex}}=470$  nm,  $\lambda_{\text{em}}=700$  nm) and optical backscattering ( $\lambda=700$  nm) at an angle,  $\theta$ ,  
19 of 140°. Photosynthetically active radiation, PAR (400 – 700 nm), was measured by a  
20 downwelling cosine PAR sensor (LI-COR 192-SA) mounted at the top of the float.

21 Seagliders, autonomous underwater vehicles designed for long ocean deployments, move  
22 forward horizontally while gliding vertically in a sawtooth pattern (Eriksen et al., 2001). Four  
23 Seagliders (SG140, SG141, SG142 and SG143) were deployed during this experiment, with an  
24 adaptive mission to follow the Lagrangian float on its path and provide measurements on larger  
25 spatial scales and to depths of 1,000 m. All gliders were equipped with an unpumped custom  
26 Sea-Bird Electronics, Inc., CT sensor that measured conductivity and temperature and carried a  
27 WET Labs BB2F that measured backscattering at two wavelengths (470 and 700 nm;  $\theta=124^\circ$ )  
28 and *Chl F* ( $\lambda_{\text{ex}}=470$  nm,  $\lambda_{\text{em}}=700$  nm).

29 Extensive surveys around the float and glider deployment area were carried out during a three-  
30 week process cruise aboard the *R/V Knorr*, with 134 CTD profiles. The CTD rosette was

1 equipped with a Sea-Bird Electronics, Inc., SBE 911*plus* CTD. A WET Labs FLNTU (similar to  
2 that on the float) was mounted on the bottom of the frame. A Biospherical QSP2300 sensor  
3 mounted on the top of the CTD rosette frame measured scalar underwater PAR. The same set of  
4 optical sensors was used during the short, six-day deployment cruise aboard the *R/S Bjarni*  
5 *Saemundsson*; fewer profiles and samples were collected during this cruise (9 CTD profiles).

6 All data used in this paper and the cited calibration reports are available under the project name  
7 NAB 2008 from the Biological and Chemical Oceanography Data Management Office (BCO-  
8 DMO, at <http://osprey.bcodmo.org/project.cfm?flag=view&id=102&sortby=project>).

## 9 **2.2 In situ optical measurements and sensor inter-calibration procedure**

10 *Chl F* and  $b_{bp}$  were measured on the float, four gliders and ship, with a total of six sensors (two  
11 FLNTUs and four BB2Fs). The ship's FLNTU was used as the primary reference sensor to  
12 which the autonomous sensors were brought into alignment via *in situ* inter-calibrations. All  
13 sensors were factory calibrated before and after the cruise *en masse* (with the exception of  
14 sensors on SG142, which was not retrieved). Dark readings (voltage) for both channels of the  
15 ship's FLNTU sensor were measured *in situ* by covering the detector window with black  
16 electrical tape on two profiles to 600 m, as suggested by Twardowski et al. (2007); these *in situ*  
17 dark measurements agreed with the mean factory dark volts. Prior to inter-calibration, mean pre-  
18 and post-deployment factory calibrations were applied to all sensors to convert *Chl F* into  
19 nominal *Chl* concentration and scattering measurements to the volume scattering function,  $\beta_{total}$   
20  $(\theta, 700 \text{ nm})$ , which was converted to  $b_{bp}$  as follows. The volume scattering function of seawater,  
21  $\beta_{sw}(\theta, 700 \text{ nm})$ , calculated following Zhang et al. (2009), was subtracted from  $\beta_{total}(\theta, 700 \text{ nm})$  to  
22 yield the volume scattering function of particles,  $\beta_p(\theta, 700 \text{ nm})$ , which was then converted to  $b_{bp}$   
23 by multiplying  $\beta_p(\theta, 700 \text{ nm})$  by  $2\pi\chi$ , using  $\chi$  factors of 1.132 for FLNTU and 1.077 for BB2F  
24 (Sullivan et al., 2013).

25 Offsets were applied to the factory calibrated glider data to bring the pre-bloom deep values for  
26 all gliders into alignment. The autonomous sensors were further aligned with ship sensors using  
27 matchups from intentional calibration stations, in which the float or glider was brought to the  
28 surface within close proximity to the ship and a CTD cast made as the vehicle descended. A total  
29 of 11 float casts and 2-3 casts per glider were made. Profiles were aligned in density coordinate  
30 space and ship profiles were interpolated to match the densities of the more sparse autonomous

1 measurements, creating a ship-autonomous sensor matchup for every autonomous measurement  
2 from each of the inter-calibration casts. Matchups from float inter-calibration casts were pooled  
3 to calculate a single linear regression for each sensor type (*Chl F* and  $b_{pp}$ ), which were used to  
4 align float sensors to the ship. Matchups were insufficient to align each glider to the ship  
5 independently, so matchups from all four gliders (already aligned at depth) were pooled to  
6 calculate a single regression per sensor type, aligning all gliders with the ship as well. Finally,  
7 *Chl F* for all sensors was converted to volts, V (referenced to the ship's FLNTU). More details  
8 on the inter-calibration procedures are available in (Briggs et al., 2011) and in the reports  
9 available on BCO-DMO (Briggs, 2011).

10 PAR was measured with a LI-COR cosine PAR on the float and a Biospherical scalar PAR on  
11 the ship's CTD Rosette frame. Both instruments were factory calibrated prior to the experiment,  
12 with NIST traceable calibration lamps; the data reported here are based on factory calibrations  
13 only. The float made a single daily vertical profile (~ noon/early afternoon); PAR from this  
14 profile was used to derive the diffuse attenuation coefficient,  $K_d$ , using all data  $> 10 \mu\text{mol}$   
15 photons  $\text{m}^{-2} \text{s}^{-1}$ .  $K_d$  was applied to all measurements of PAR acquired during the float's  
16 mixed-layer drift mode and extrapolated to the surface to produce hourly subsurface PAR fields  
17 from which daily isolumes were computed. The isolume of  $0.415 \text{ mol photons m}^{-2} \text{ d}^{-1}$  is taken as  
18 the radiation level below which net photosynthesis does not occur (Letelier et al., 2004; Boss and  
19 Behrenfeld, 2010), and is hereafter referred to as the 0.415 isolume.

### 20 **2.3 Water samples and laboratory analyses**

21 Water samples were collected from the CTD upcast with 10 L Niskin bottles mounted on the  
22 CTD Rosette. Samples for nitrate plus nitrite, hereafter referred as to nitrate, and silicic acid, Si,  
23 were collected directly from Niskin bottles into acid-washed LDPE bottles, pre-rinsed three  
24 times with sample (Kallin et al., 2011). Unfiltered water samples were frozen immediately after  
25 collection and stored at  $-20^\circ \text{C}$  for up to 8 mo. Samples were thawed in the dark prior to analysis  
26 and vigorously vortexed (Gordon et al., 1992) prior to absorptiometric analysis on a Lachat  
27 Quickchem 8000 Flow Injection Analysis System (Lachat, 1996, 1999). In addition to quality  
28 control of the Lachat output spectra, profiles of Si and nitrate concentrations were examined  
29 following the recommendation of the IODE workshop on quality control of chemical  
30 oceanographic data (IOC, 2010).

1 Water samples for pigments and spectral absorption coefficients were filtered through Whatman  
2 GF/F filters. Samples for fluorometric analysis of *Chl* were extracted in 5 mL of 90% acetone at  
3  $-20^{\circ}$  C for 24 h and analyzed on a Turner Designs Model 10-AU digital fluorometer that was  
4 calibrated before and after the field experiment with Turner Designs *Chl* standards. *Chl*  
5 concentrations were calculated following JGOFS protocol (Knap et al., 1996). Filters collected  
6 for HPLC pigment analysis were stored in liquid nitrogen until analysis (up to 5 mo). Horn Point  
7 Laboratories performed HPLC pigment analyses, using a methanol-based reversed-phase  
8 gradient C8 chromatography column system and appropriate standards (Van Heukelem and  
9 Thomas, 2001; Hooker et al., 2009).  $Chl_{HPLC}$  is the sum of *Chl* plus chlorophyllide *a*, with the  
10 latter adjusted to *Chl* equivalent mass ( $\times 893.5/614$  molecular mass ratio); the ratio of  
11 chlorophyllide-to- $Chl_{HPLC}$  is also reported in *Chl* mass equivalents. Filters collected for  
12 particulate spectral absorption coefficients were scanned at sea on a Varian Cary 50 UV-Visible  
13 spectrophotometer with a xenon flash lamp and a 1.5 nm slit width, following the Mitchell and  
14 Kiefer (1988) method. The filters were extracted in hot methanol and re-scanned to measure  
15 residual detrital particulate absorption (Kishino et al., 1985). The difference between the total  
16 particulate and detrital absorption coefficients was attributed to the phytoplankton absorption  
17 coefficient ( $a_{phy}(\lambda)$ ).

18 Microbial plankton cell size and numerical concentrations were determined on fresh samples at  
19 sea during the May cruise (Sieracki and Poulton, 2011). Cells smaller than 20  $\mu$ m were analyzed  
20 with a flow cytometer (FACScan, BD Biosciences), using *Chl* and phycoerythrin fluorescence as  
21 discriminators for three groups of phytoplankton: eukaryotic pico- and nanophytoplankton,  
22 | cryptophytes, and prokaryotic *Synechococcus* spp. (*Prochlorococcus* was not observed).  
23 Heterotrophic microbes were analyzed on separate subsamples and detected using fluorescent  
24 stains; heterotrophic bacteria were stained with PicoGreen – Life Technologies Inc. (Veldhuis et  
25 al., 1997) and heterotrophic nanoprotoists were stained with LysoTracker Green – Life  
26 Technologies Inc. (Rose et al., 2004). Cell size for all these groups was determined from forward  
27 scatter, where size and scatter relationships were established with microbead size standards and  
28 algal cultures of known cell size (Sieracki and Poulton, 2011). Phytoplankton cell carbon was  
29 estimated from cell size following the algorithm of Verity et al. (1992). Cells larger than 20  $\mu$ m  
30 were analyzed using a Fluid Imaging Technologies FlowCAM, with image collection triggered  
31 by *Chl F*. Four major sub-groups were identified: diatoms, dinoflagellates (autotrophic and

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1 mixotrophic), ciliates, and ‘other’ microphytoplankton. Biovolume estimates were determined  
2 following the method of Sieracki et al. (1989), where particle boundary points were found using  
3 the Connected Component Labeling algorithm of Chang et al. (2004), as implemented in Burger  
4 and Berge (2008). Cell carbon was calculated from derived biovolumes using the algorithms of  
5 Menden-Deuer and Lessard (2000). Heterotrophic microprotists were not enumerated with the  
6 FlowCAM, and hence estimates of their carbon biomass missing from analyses of heterotrophic  
7 carbon. Total particulate organic carbon (POC) was analyzed as reported in (Cetinić et al., 2012).

#### 8 **2.4 Data analysis and derivation of proxies**

9 Optical data were median filtered (7 point running median) to remove spikes associated with  
10 aggregates and other larger particles in the water column (Briggs et al., 2011). Water samples  
11 were collected on the upcast, with the CTD held at a constant depth for 60 s before the Niskin  
12 bottle closed; only data recorded during the last 30 s before bottle closure were used for analysis.  
13 *Chl* samples collected during the *R/V Knorr* cruise were used to convert the ship’s FLNTU *Chl F*  
14 voltage to *Chl* ( $\mu\text{g L}^{-1}$ ) using a non-linear best-fit function of temperature, PAR, depth and YD  
15 (Figs. 2A, B;  $n=835$ ; D’Asaro, 2011); this algorithm mostly removed the effects of solar  
16 quenching (Fig. 2C) and Si limitation (Section 3.4) on *Chl F*. The resulting *Chl* product  
17 converted *Chl F* to *Chl* within an error of 30 – 50% (Figs. 2A, B). This uncertainty, and the lack  
18 of PAR sensors on the gliders, caused us to use *Chl F* rather than *Chl* in the subsequent analysis.  
19 Glider *Chl F* in digital counts was converted to V, referenced to the ship’s FLNTU, based on the  
20 inter-calibration procedures; *Chl F* is therefore reported as V for all platforms and the optical  
21 community index,  $Chl F/b_{bp}$ , is reported in units of V m.

22 In this paper, we focus on properties of the upper water column, i.e., 50 m and shallower.  
23 Daytime fluorescence quenching is a ubiquitous phenomenon in surface layers of the ocean, with  
24 decreases in *Chl F* caused by photo-inhibitory and/or energy-dependent quenching (Sackmann et  
25 al., 2008). *Chl F* normalized to fluorometrically measured *Chl* declined at values of PAR > 100  
26  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$  (Fig. 2C). Since 92 % of all PAR values > 100  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$  were  
27 measured within the top 10 m by both ship and float, we omitted *Chl F* and  $b_{bp}$  data collected at  
28 depths shallower than 10 m from further analysis for all platforms to avoid potential bias  
29 associated with solar quenching of *Chl F*. However, data from water samples (nutrients, HPLC  
30 pigments, etc.) collected at all depths shallower than 50 m are included in the analyses.

1 Principal component analysis (PCA) for assessing potential sources of variability in *Chl F/b<sub>bp</sub>*  
2 was performed on data from 38 CTD profiles from the May cruise. Input parameters for PCA  
3 were temperature, mixed layer depth (calculated as the depth at which density differed from the  
4 mean density in the top 10 m by  $< 0.05 \text{ kg m}^{-3}$ ), depth of the 0.415 isolume, nitrate, Si, *Chl F/b<sub>bp</sub>*  
5 and a term representing diatom dominance of phytoplankton biomass (defined in Section 3.3). A  
6 single median value for the upper 50 m was assigned to each parameter for each profile, except  
7 for *Chl F/b<sub>bp</sub>* for which median values were calculated for 10 – 50 m (as explained above). The  
8 0.415 isolume for a given day was derived from float data and assigned to a CTD profile based  
9 on YD. Prior to analysis, data were standardized by subtracting the mean and dividing by the  
10 standard deviation. Scores of individual data points were scaled by the maximal absolute value  
11 of the sample scores and maximal coefficient vector length (Matlab code *biplot.m*).

12 A “heterogeneity index” for similarity of plankton community composition was calculated based  
13 on similarity/dissimilarity of *Chl F/b<sub>bp</sub>* between pairs of autonomous platforms. The six-hour  
14 median value of *Chl F/b<sub>bp</sub>* between 10 and 50 m was determined for each platform and assigned  
15 to one of three optical community groups (as described in Results). These assignments were then  
16 compared for each platform pair (total of 10 comparisons). A value of 0 was assigned if the  
17 community groups were identical (low heterogeneity) and a value of 1 (high heterogeneity) if  
18 they were different. The final heterogeneity index reported for a given time is the average of the  
19 10 comparisons.

20

## 21 **3 Results**

### 22 **3.1 The evolution of the spring bloom observed from the Lagrangian float**

23 The evolution and community succession of the spring bloom was measured by the Lagrangian  
24 float. Alkire et al. (2012) divided the evolution into six periods based on measured physical and  
25 biogeochemical parameters. The float was deployed into a deep wintertime mixed layer with *Chl*  
26  $< 0.5 \mu\text{g L}^{-1}$  (the period of *Deep Mixing*, Fig. 3A). During the *Early Bloom* (YD 114 – 119) the  
27 mixed layer shoaled from  $> 100 \text{ m}$  to  $\sim 50 \text{ m}$ , approximately the depth of the 0.415 isolume (Fig.  
28 3B); during this period *Chl* exponentially increased to  $\sim 2 \mu\text{g L}^{-1}$ . Surface phytoplankton  
29 concentration was diluted and net growth was slowed by a storm (*Storm*) which deepened the

1 mixed layer to  $\sim 100$  m between YD 119 and 123, slightly decreasing near-surface *Chl*.  
2 Following the storm, the upper ocean quickly restratified and the mixed layer shoaled above the  
3 0.415 isolume. *Chl* continued to increase during the *Main Bloom* (YD 124 – 134). Beginning  
4 around YD 126, spikes below 200 m in *Chl F* and  $b_{bp}$  were observed in ship and glider data, as  
5 well as in ship  $c_p$  data, indicating the onset of a flux event of sinking diatom aggregates (Briggs  
6 et al., 2011). *Chl* reached a maximal value of  $4.6 \mu\text{g L}^{-1}$  on YD 133 and shortly thereafter  
7 abruptly declined to a quarter of the peak bloom value,  $\sim 1 \mu\text{g L}^{-1}$ , by YD 137. Bloom  
8 termination continued into the *Eddy* period; *Chl* remained relatively unchanged during the *Post*  
9 *Bloom* period and until the end of the float mission on YD 146.

### 10 **3.2 Diel and longer temporal patterns in the optical community index**

11 The optical community index at the location of the float varied over time on both diel and longer  
12 time scales; the observed diel variability was due mostly to *Chl F*, with the peak consistently  
13 occurring around midnight (Fig. 3A, C, D). Similar diel patterns have been previously observed  
14 for both *Chl F* and  $b_{bp}$  (Marra, 1997; Loisel et al., 2011). Although the effects of solar quenching  
15 on daytime values of *Chl F* (Sackmann et al., 2008) were minimized by removing data from the  
16 upper 10 m (Fig. 2C), a small daytime quenching signal remained. The longer term variations in  
17  $Chl F/b_{bp}$  were considerably larger than the diel and, as shown below, were associated either  
18 with shifts in the phytoplankton community composition, i.e., diatom vs. pico and  
19 nanophytoplankton dominance, or a physiological response of diatoms to Si limitation between  
20 YD 133 – 136.

21 During the *Deep Mixing* period, the optical community index was low and variable (Fig. 3D).  
22 Part of this variability may have been due to instrumental noise since both *Chl F* and  $b_{bp}$  were  
23 small (Fig. 3C). There is insufficient ship data during this period to determine whether the  
24 variability was due to real fluctuations in community composition. Starting mid-way into the  
25 *Early Bloom*, the optical community index increased and remained high until the end of the *Main*  
26 *Bloom* period. As Si concentrations measured from ship samples dropped below  $1 \text{ mmol m}^{-3}$   
27 (YD 133 – 136), the optical community index increased to its highest values. It then abruptly  
28 decreased by more than a factor of two (end of *Main Bloom*) and remained low (*Eddy* and *Post*  
29 *Bloom*) through the end of the float mission.

1 Figure 4A shows a scatter plot of *Chl F* vs.  $b_{bp}$ ; three groupings are evident. Within Groups 1 and  
2 2, *Chl F* and  $b_{bp}$  covaried linearly but with different slopes; Group 1:  $Chl F = 53.63 b_{bp} + 0.01$ ;  
3 Group 2:  $Chl F = 105.34 b_{bp} - 0.02$ . The range in  $b_{bp}$  was equivalent, indicating that the  
4 relationship was not driven by the changes in magnitude of  $b_{bp}$ . Group 1 is characteristic of the  
5 *Eddy* and *Post Bloom* periods; Group 2 of the *Early* through *Main Bloom* periods. Groups 2 and  
6 3 reflect a biphasic relationship, with a break in the slope at higher values of  $b_{bp}$ . The regression  
7 intercept for the third group is non-linear and does not pass near zero (regression not shown).  
8 Group 3 occurred only in the latter part of *Main Bloom* period.

9 The frequency histogram in Fig. 4B also illustrates these patterns, with two clearly defined  
10 groupings of the optical community index: low (Group 1 is centered on 58 V m) and  
11 intermediate (Group 2 is centered on 98 V m). Group 3 is more diffuse. As a way to more clearly  
12 separate Groups 2 and 3, a frequency distribution was constructed for YDs 120 – 127, a period  
13 when diatoms were clearly dominant and Si was not limiting. The results of this analysis (shown  
14 as a dashed gray line in Fig. 4B) confirmed the upper limit of the optical community index for  
15 Group 2 as 120 V m. Indices in excess of 120 V m were classified as Group 3. Cetinić et al.  
16 (2012) refers to Group 1 as a ‘recycling community’ comprised primarily of pico- and  
17 nanophytoplankton and Groups 2 and 3 as a ‘diatom community’; in Section 3.3 we present the  
18 justification for these designations, which are used henceforth.

### 19 **3.3 Optical community index is a proxy for phytoplankton community** 20 **composition**

21 Ship-based measurements of phytoplankton cell carbon allowed us to establish that changes in  
22  $Chl F/b_{bp}$  corresponded to changes in phytoplankton community composition. In May, the  
23 fraction of diatom cell carbon as a percentage of total autotrophic cell carbon, % *diatom<sub>C</sub>*, was  
24 calculated from flow cytometer and FlowCAM samples. The diatoms were primarily chain  
25 formers, belonging to the genera *Chaetoceros*, *Thalassionema* and *Pseudo-nitzschia* (K.  
26 Richardson, *pers. comm.*). Coincident measurements of flow cytometer, FlowCAM and HPLC  
27 pigments (n=16) were used to create a proxy that converted the mass ratio of fucoxanthin-to-*Chl*  
28 ( $Fuco/Chl$ , g/g) to the fraction of diatom cell carbon. This relationship, shown in Fig. 5A (Type  
29 II regression,  $r^2=0.78$ ,  $p<0.01$ ), allowed us to include all HPLC samples in the analysis of  
30 community composition:

1  $\% \text{ diatom}_C = 77.36(\pm 9.87) \times \text{Fuco}/\text{Chl} - 11.31(\pm 4.85) .$  (1)

2 The combined data set, including both the direct  $\% \text{ diatom}_C$  measurements and those derived  
3 from (1), was designated as  $\% \text{ diatom}_C \text{ product}$  and provided information for a total of 94  
4 individual samples from 42 stations, of which 4 were from early April and 38 from May.

5 Figure 5B used the  $\% \text{ diatom}_C \text{ product}$  to show that the optical community index was low when  
6 pico and nanoplankton dominated (Group 1) and high when diatoms dominated (Groups 2 and  
7 | 3), with a transition at about 80 V m, as in Figs. 3D and 4B- (one-tail t-test,  $p < 0.001$ ). There was  
8 no clear distinction between Groups 2 and 3 in terms of percent diatom domination. An  
9 alternative visualization of the optical community index also shows that the highest values were  
10 associated with diatoms (Fig. 6A). Changes in  $\text{Chl } F$  or  $b_{bp}$  were not strongly correlated with  
11 variability of  $\% \text{ diatom}_C$  (respective  $r^2$  of 0.21 and 0.16, and  $p$  of  $< 0.01$  and  $p < 0.1$ ). During May,  
12 the ratio of  $\text{Chl}$ -to-autotrophic carbon showed a moderate trend of higher ratios associated with  
13 diatom-dominated communities (Fig. 5C; Type II regression,  $r^2 = 0.55$ ,  $p < 0.01$ ). Here  $\% \text{ diatom}_C$   
14 is used rather than the  $\% \text{ diatom}_C \text{ product}$ , since total autotrophic carbon is available only from  
15 flow cytometer and FlowCAM samples. Samples from periods when mixed layers were deeper  
16 than 70 m were excluded to avoid confounding effects of low light photo-adaption on the  $\text{Chl}$ -to-  
17 carbon ratio.

18 The absolute magnitude of heterotrophic carbon (sum of heterotrophic bacteria and  
19 nanoflagellate carbon) varied between 15 and 30  $\mu\text{g L}^{-1}$ . The corresponding percentage of  
20 heterotrophic carbon-to-POC varied between ~10 – 25% and was not correlated with the  
21 variability observed in the optical community index (Fig. 5D,  $n = 74$ , Type II regression,  $r^2 = 0.07$ ,  
22  $p > 0.01$ ). Thus, the optical community index  $\text{Chl } F/b_{bp}$  varies with the fraction of the planktonic  
23 carbon due to diatoms.

#### 24 **3.4 Principal component analysis**

25 PCA of  $R/V$  Knorr CTD profiles (Fig. 7,  $n = 38$ ) also show a separation between recycling and  
26 diatom dominated communities. Principal component one (PC 1; 38.5% of variance) is  
27 dominated by an inverse relationship of surface temperature with mixed layer depth and nutrient  
28 concentrations. However, PC 2, explaining nearly as much of the variance (30.2 %), is nearly  
29 parallel to  $\text{Chl } F/b_{bp}$  (i.e., the  $\text{Chl } F/b_{bp}$  vector is nearly vertical in Fig. 7). Most stations with a

1 recycling community (low optical community index) had lower loadings on PC 2, while stations  
2 with a diatom community (high optical community index) had higher loadings. The analysis  
3 confirmed that trends observed in  $Chl\ F/b_{bp}$  are associated with the proportion of diatoms, as the  
4 % *diatom*<sub>C</sub> *product* had the largest loading on the second component (0.66).

5 Although PC 2 shows no significant difference in the % *diatom*<sub>C</sub> *product* among stations for the  
6 two types of diatom communities, i.e., Groups 2 and 3 (n=27; two tailed t-test,  $p > 0.05$ ), PC 1  
7 separated them as a function of nutrient concentration, as shown by the high loadings on Si  
8 (0.57). Nitrate was not a limiting factor for phytoplankton growth, decreasing from an initial  
9 concentration of  $> 12\ \text{mmol m}^{-3}$  in early April to a minimal value of  $\sim 8\ \text{mmol m}^{-3}$  in late May  
10 (Alkire et al., 2012). In contrast, Si was likely limiting to diatoms by the peak of the bloom,  
11 decreasing from initial surface concentrations of  $> 4\ \text{mmol m}^{-3}$  in early April to  $< 1\ \text{mmol m}^{-3}$   
12 towards the end of the *R/V Knorr* cruise (Fig. 6B).

### 13 3.5 Ancillary analyses

14 Ancillary analyses of chlorophyllide and phytoplankton UV absorption spectra are also  
15 indicative of differences between diatoms vs. pico and nanophytoplankton. The highest ratios of  
16 chlorophyllide-to- $Chl_{HPLC}$  were measured at CTD stations with high values of  $Chl\ F/b_{bp}$  (Fig.  
17 8A). Unfortunately, no HPLC samples were collected next to the float during the period when  
18  $Chl\ F/b_{bp}$  was highest. In May some of the phytoplankton absorption spectra exhibited unusual  
19 spectra. UV peaks with a ratio of  $a_{phy}(\lambda\text{-UV peak})/a_{phy}(676)$  in excess of 2 were correlated with a  
20 high optical index, i.e., in excess of 80  $V\ m$  (Fig. 8B); 18 out of 63 spectra fit this criterion.  
21 While most UV peaks were centered between 325 – 330 nm, four samples associated with Group  
22 3 had up to seven-fold higher peak heights with maxima shifted to lower wavelengths (310 – 320  
23 nm), increased absorption at 412 nm and reduced absorption at 437 and 467 nm peaks.

### 24 3.6 Patchiness of phytoplankton communities

25 The evolution of the diatom spring bloom, its demise and transition to a pico- and  
26 nanophytoplankton community was assessed over a two-month period for the float and four  
27 gliders. Both the optical community index and mixed layer depths showed some spatial  
28 variability (Figs. 9A, B), likely reflecting submesoscale variability as well as variability in the  
29 timing of the diatom bloom initiation and termination. During the bloom peak in May, the *R/V*

1 *Knorr* carried out a series of bow-tie sampling patterns and the optical community index varied  
2 between some of the lowest and highest values as the ship moved in and out of different patches  
3 (Fig. 6, YD 130 – 135). The period of greatest heterogeneity in phytoplankton community  
4 composition occurred between YD 115 – 137 (Fig. 9C). The strong salinity component in PC 2  
5 (Fig. 7) also reflects this patchiness; the float patch had an anomalously high value of salinity in  
6 addition to a high value of the optical community index.

7

## 8 **4 Discussion**

### 9 **4.1 Why does the *Chl F*/*b<sub>bp</sub>* ratio vary?**

10 High and low values of the optical community index were correlated with diatom-, and pico- and  
11 nanophytoplankton-dominated communities, respectively (Figs. 5, 6 and 7). The direct  
12 measurement of HPLC pigments and phytoplankton from the flow cytometer and FlowCAM  
13 allowed us to create an optical proxy for phytoplankton community composition for this specific  
14 period and to apply it to glider and float data to assess community composition over a broader  
15 spatial scale (Fig. 9). The question remains, why does this optical index vary as a function of  
16 phytoplankton type? Is it strictly taxonomical, or is it based on physiology, or combination of  
17 both?

18 Ratios must be interpreted with caution, as changes could be due either to the numerator,  
19 denominator, or both. *Chl F* is a proxy for *Chl*, but with physiological variability associated with  
20 solar quenching (Sackmann et al., 2008; Roesler and Barnard, 2014) and nutrient stress  
21 (Cleveland and Perry, 1987). However, neither solar quenching nor Si limitation appears to be  
22 responsible for the difference in optical community index between Groups 1 and 2. The  
23 influence of the former was minimized by the deliberate exclusion of depths less than 10 m.  
24 Nitrogen limitation was unlikely, but indications of Si limitation were correlated only with the  
25 highest values of *Chl F*/*b<sub>bp</sub>* (see Section 4.2, and Figs. 6B and 7). The denominator, *b<sub>bp</sub>*, is a  
26 function of particle concentration. Although *b<sub>bp</sub>* is also influenced by particle size and refractive  
27 index (Stramski et al., 2004), the relationship between POC and *b<sub>bp</sub>* within the mixed layer  
28 during the May NAB 2008 cruise did not vary as a function of plankton community composition  
29 (Cetinić et al., 2012), making a change in particle optics an unlikely explanation.

1 We examined two hypotheses for the observed patterns of the optical community index. First, the  
2 relative contribution of heterotrophic carbon to POC and  $b_{bp}$  could vary systematically between  
3 the different communities. If the contribution of heterotrophs was consistently greater for Group  
4 1,  $Chl\ F/b_{bp}$  would be lower. However, heterotrophic (bacteria and nanoprotist) carbon as a  
5 percentage of POC was not correlated with the optical community index (Fig. 5D), making it  
6 unlikely that heterotrophic carbon was responsible for changes in the ratio. Although  
7 heterotrophic protists  $> 20\ \mu\text{m}$  were not analyzed, their carbon is less than 30% of the  
8 heterotrophic nanoprotist carbon at this time of year (Verity et al., 1993) and inclusion of these  
9 larger protists would not change the observed trend.

10 Second, the  $Chl$ -to-carbon ratio of diatoms could be larger than that of pico and  
11 nanophytoplankton, thereby increasing  $Chl\ F/b_{bp}$  in the diatom community. In laboratory  
12 cultures for the same irradiance,  $Chl$  per cell volume scales inversely with cell size (cf. Fujiki  
13 and Taguchi, 2002), resulting in higher  $Chl$ -to-carbon ratios for larger cells. Field studies where  
14 cell carbon was determined from measurements of cell volume show higher  $Chl$ -to-carbon ratios  
15 for diatom dominated communities in contrast to communities dominated by small  
16 phytoplankton (Llewellyn et al., 2005; Putland and Iverson, 2007). In the California Current,  
17 observations supported by models also find higher  $Chl$ -to-carbon ratios for diatoms than  
18 picoplankton for similar environmental conditions (Li et al., 2010). Our data revealed the same  
19 trend, approximately a factor of two higher ratios of  $Chl$ -to-autotrophic carbon for samples  
20 dominated by diatoms, although with considerable scatter (Fig. 5C). We conclude that  
21 differences observed in  $Chl\ F/b_{bp}$  between Groups 1 and 2 are primarily due to taxa specific  
22 differences in the cellular  $Chl$ -to-autotrophic carbon ratios and that the optical community index  
23  $Chl\ F/b_{bp}$  varies as a function of the fraction of the planktonic carbon due to diatoms. While  
24 changes in the  $Chl$ -to-carbon ratio of individual species do occur in response to changing light,  
25 nutrient, and temperature conditions (e.g. Geider, 1987), species succession offers an alternative  
26 hypothesis to that of physiological change as the sole explanation for change in phytoplankton  
27  $Chl$ -to-carbon and hence ratios of  $Chl\ F/b_{bp}$  in the field (cf. Behrenfeld et al. 2005).

#### 28 **4.2 Evidence of Si limitation**

29 Analysis by Egge and Aksnes (1992) indicates that diatoms are unlikely to do well in waters with  
30 Si concentrations  $< 2\ \text{mmol}\ \text{m}^{-3}$ . In their review of silicon metabolism in diatoms, Martin-

1 Jezequel et al. (2000) compiled data for the Michaelis-Menten half saturation constant for Si-  
2 dependent growth rate; the median half saturation constant for 17 studies was  $1.0 \text{ mmol m}^{-3}$ .  
3 Concentrations of Si at highest values of  $Chl F/b_{bp}$  were  $< 1 \text{ mmol m}^{-3}$  (Fig. 6B), leading us to  
4 suggest that Group 3 represented diatoms whose photosynthetic physiology was limited by Si.

5 Does Si limitation affect photosynthetic efficiency and  $Chl F$ ? Reduced photosynthetic  
6 efficiency is a typical response to limitation by nitrogen, phosphorous and iron due to the  
7 structural and functional roles of these elements in photosynthesis. For most species,  $Chl$   
8 concentration per cell volume decreases with nutrient limitation, while fluorescence normalized  
9 to  $Chl$  concentration increases when nutrients are limiting (Kruskopf and Flynn, 2006). The  
10 increase in fluorescence is due in part to an increase in the  $Chl$ -specific absorption coefficient  
11 due to reduced pigmentation and in part to reduced photochemical quenching due to nutrient  
12 limitation (Cleveland and Perry, 1987). While Si itself is not directly associated with  
13 photosynthesis and relatively few papers report the effect of Si limitation on fluorescence  
14 efficiency in diatoms, the available results suggest that Si limitation does reduce photosynthetic  
15 efficiency. For Si-limited cultures of the diatom *Thalassiosira weissflogii*, (Lippemeier et al.,  
16 1999; Bucciarelli and Sunda, 2003) report a decrease in photosynthetic efficiency (equivalent to  
17  $F_v/F_m$ ). In a field study in the Iceland Basin and Rockall Trough in May and June 2001, Moore et  
18 al. (2005) found  $F_v/F_m$  to be correlated with Si concentration, suggesting reduction in  
19 photosynthetic capacity in response to Si stress (note, N concentrations in that study were always  
20  $> 3 \text{ }\mu\text{M}$ , but Si concentrations were often  $< 1 \text{ }\mu\text{M}$ ). They also found  $\sim 2 \text{ x}$  higher values of  $F_0/Chl$   
21 associated with low Si concentrations. During the *Main Bloom* period in NAB 2008, enhanced  
22  $Chl F$  normalized to both  $b_{bp}$  (i.e., optical community index) and extracted  $Chl$  coincided with Si  
23 depletion (Figs. 2D, 4A, 6B, 7). During this period Briggs and Gudmundsson (*pers. comm.*)  
24 found that rates of net primary productivity based on float diel cycles of optics and oxygen could  
25 only be reconciled with photosynthesis vs. irradiance (P-E)-based estimates of productivity if the  
26 P-E parameters were reduced with a Michaelis-Menten-like function and a  $K_s$  of  $1 \text{ }\mu\text{M}$ . Hence,  
27 we propose that the highest values of  $Chl F/b_{bp}$  are indicative of diatom Si limitation.

28 Two other measurements are also suggestive of physiological effects of Si limitation at the end  
29 of the diatom bloom. Chlorophyllide is a pigment linked with diatom senescence (Lorenzen,  
30 1967; Jeffrey, 1980; Llewellyn et al., 2008). Although chlorophyllide is noted as a potential  
31 extraction artifact (Jeffrey and Hallegraeff, 1987), this pigment has often been used as a marker

1 for senescent diatoms at the end of diatom blooms in coastal, open ocean, and high latitude  
2 environments (Ridout and Morris, 1985; Head and Horne, 1993; Sigleo et al., 2000; Llewellyn et  
3 al., 2008). High relative concentrations of chlorophyllide were associated with both Groups 2  
4 and 3, suggesting that diatoms were in transition to senescence. Unusual features in  
5 phytoplankton absorption spectra were only found for samples with high optical community  
6 indices, including peaks in the UV typically suggestion of MAAs (mycosporine-like amino  
7 acids; Fig. 8B). While such UV peaks are often interpreted as MAAs, Llewellyn and Airs (2010)  
8 caution that for diatoms, UV absorption peaks can be associated with derivatives of  
9 photosynthetic pigments. Since no direct chemical analyses of MAAs were made, the UV peaks  
10 may be another indicator of diatom senescence. *In toto*, these observations suggest that as Si  
11 became limiting to diatoms, Si limitation was responsible for the highest values of  $Chl F/b_{bp}$ , as  
12 well as the termination of the Main Bloom, leading to subsequent dominance of pico- and  
13 nanophytoplankton that do not require Si in the post-bloom community

#### 14 **4.3 Patchiness of phytoplankton communities**

15 The ship, float and gliders carried sensors for  $Chl F$  and  $b_{bp}$  that had been rigorously inter-  
16 calibrated, allowing us to directly compare optical measurements across all platforms. The float  
17 tracked a parcel of water, within the constraints discussed by Alkire et al. (2012). The gliders  
18 tracked the float, typically operating within 50 km of the float, although at the beginning of the  
19 experiment strong currents and eddies occasionally swept them further away. The timeline  
20 within the float patch showed a steady progression of increasing phytoplankton biomass  
21 beginning about YD 110 and continuing through the *Main Bloom* (Fig. 3A). The increase in  
22 biomass was accompanied by an increase in the optical community index, reflecting the  
23 beginning of the transition from wintertime pico- and nanophytoplankton to spring bloom  
24 diatoms (Fig. 3D); within the float patch, the optical index was relatively constant between YD  
25 118 – 132.

26 Initially, a similar pattern of low biomass was observed in data from all four gliders, but as the  
27 bloom progressed more than a five-fold variation was observed on any given day (Mahadevan et  
28 al., 2012). Not only was biomass patchy, but the optical community index was also patchy as the  
29 gliders (and ship during the May cruise) moved in and out of water parcels with different  
30 phytoplankton communities (Figs. 6A, 9A).

1 Through analysis of glider and model data, Mahadevan et al. (2012), showed that the springtime  
2 stratification is due to the action of submesoscale mixed layer eddies that drive a net horizontal  
3 transfer of lighter water above heavier water, thereby stratifying the mixed layer. This  
4 mechanism generates patches of shallower mixed layers as seen in Fig. 9B, resulting in patchy  
5 blooms. They speculated that different species might dominate in different patches, but they  
6 referenced patchiness only as biomass. Here we show patchiness in community composition,  
7 with the period of highest heterogeneity occurring after YD 115 and persisting for ~ 20 d (Fig.  
8 9C). Our observation is similar to that of d'Ovidio et al. (2010), who used satellite data to  
9 determine that submesoscale patches are short-lived (O(weeks)) ecological niches that allow  
10 different phytoplankton taxa to bloom.

11 This is, to our knowledge, the first analysis of this kind, where the distribution of the  
12 phytoplankton community was assessed for a two-month period with such high spatial and  
13 temporal resolution. Our observations raise the question as to the mechanism(s) of the observed  
14 patchiness in phytoplankton community composition. Is it a product of temporal offsets in bloom  
15 evolution in the various patches, related to restratification by submesoscale mixed layer eddies,  
16 or potential nutrient injection (Levy et al., 2012)? Or to a lack of diatom bloom development in  
17 some water parcels, perhaps due to zooplankton patchiness or insufficient diatom seed  
18 populations? Or a combination of controlling factors? The float patch appeared to have persisted  
19 for the longest time period as a diatom community, although at least one glider briefly observed  
20 a diatom patch after the bloom terminated at the float (yellow dots on YD 147-148). The  
21 mechanism for diatom bloom termination might also differ among the different patches,  
22 controlled by patch-specific abiotic and biotic factors. One mechanisms of diatom bloom  
23 termination observed on board the ship was resting spore formation and sinking (Rynearson et  
24 al., 2013). This appeared to be widespread as judged by the dominance of these spores in  
25 sediment traps at depth. Regardless, from YD 140 to the end of the float mission 5 days later, all  
26 five autonomous platforms observed only the single phytoplankton community, i.e., Group 1.

27

## 28 **5 Conclusions**

29 Simple optical measurements made from autonomous platforms allow us to follow the variability  
30 in phytoplankton biomass (*Chl F*) and POC concentration ( $b_{bp}$ ) on highly resolved spatial and

1 temporal scales. The ratio of these optical measurements provides additional, more qualitative  
2 information about the plankton community composition. The interpretation of these ratios must  
3 be based on *in situ* validation and used within a limited set of conditions, at least until a better  
4 mechanistic understanding is developed. In late April the increase in the ratio  $Chl F/b_{bp}$  signaled  
5 a transition from a winter phytoplankton community dominated by pico- and nanophytoplankton  
6 to an early spring community dominated by diatoms. The observed shift in the optical index was  
7 primarily driven by the change in phytoplankton composition and distribution of biomass,  
8 reflecting differences in taxa-specific chlorophyll-to-autotrophic carbon ratios. Furthermore, the  
9 optical index allowed us to observe changes in the physiological status of the community as well,  
10 clearly isolating the senescent, Si-limited, termination stage of the diatom bloom from  
11 surrounding patches of diatoms not yet in senescence. However, the changes in  $Chl F/b_{bp}$ , and by  
12 implication the transition in community composition, was not simultaneous over the spatial  
13 domain surveyed by the ship and gliders. The application of the optical index demonstrated, for  
14 the first time on appropriate spatial and temporal scales, that mesoscale and submesoscale  
15 variability in physical structures is reflected not only in total biomass, but in community  
16 composition as well. Although our analysis did not manage to resolve the primary drivers of the  
17 observed spatial patchiness in community composition, the optical ratio approach offers a new  
18 tool set to study plankton patchiness *in-situ* on temporal and spatial scales relevant to ecosystem  
19 and biogeochemical research.

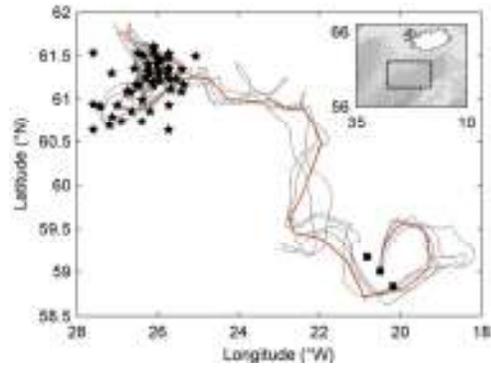
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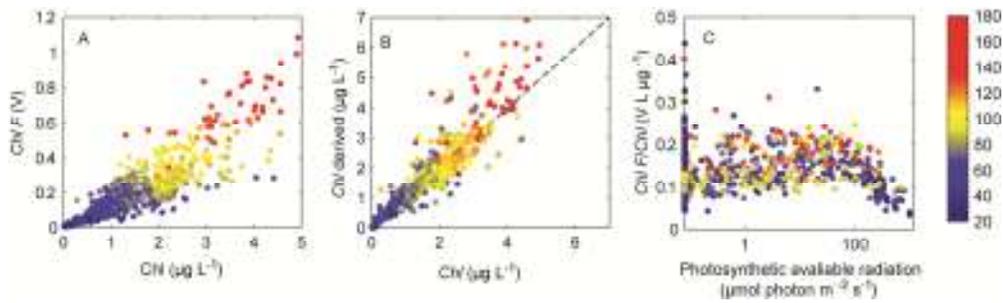
## 22 **Acknowledgements**

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29

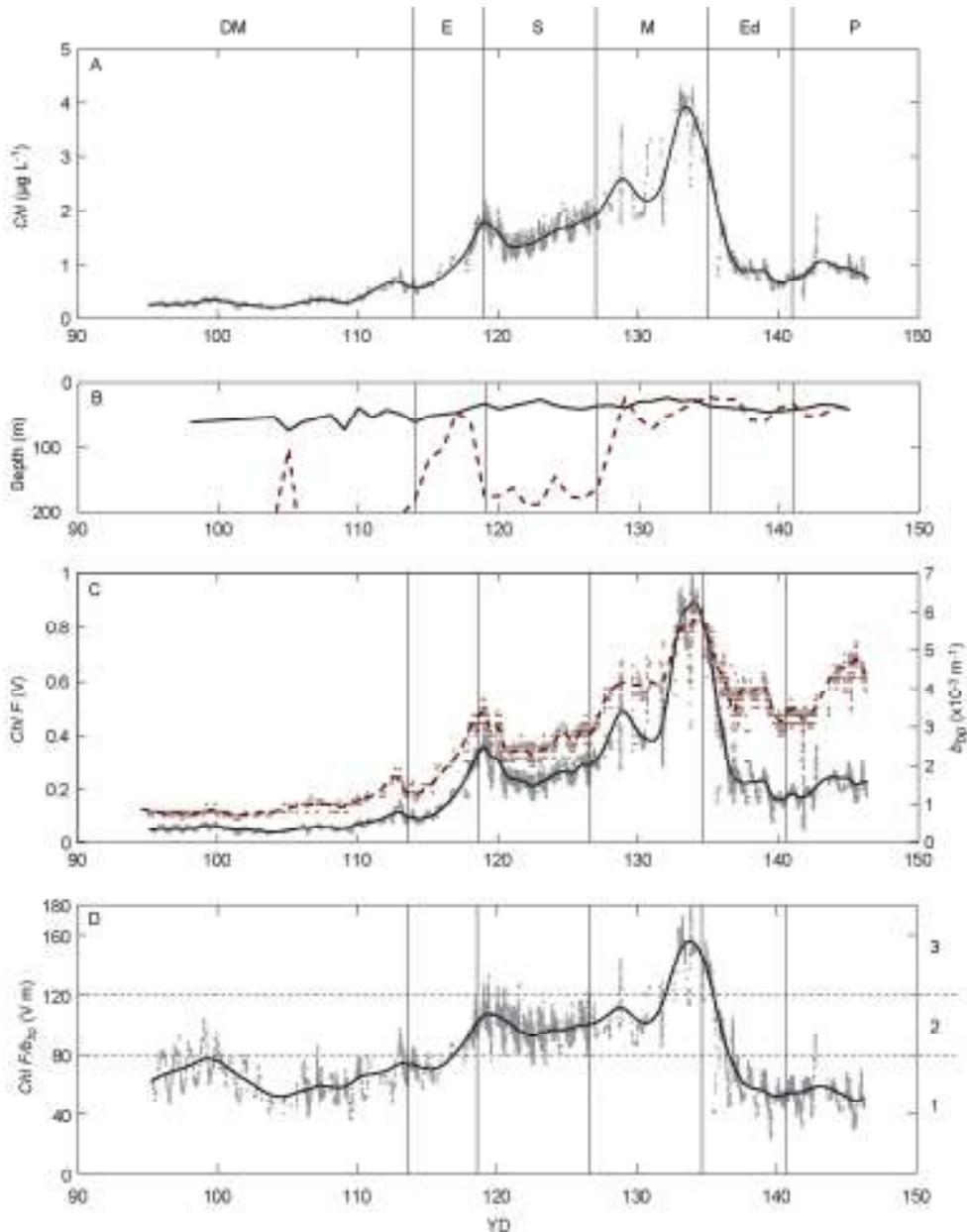


1  
2 Figure 1. Map of NAB 2008 study area with the Lagrangian float path (red line) and four  
3 Seaglider paths (gray lines). Autonomous platforms were deployed during the *R/S Bjarni*  
4 *Saemundsson* cruise in early April 2008; squares indicate ship stations. Additional ship samples  
5 were collected on a process cruise on the *R/V Knorr* in May 2008 (stars). Inset map indicates  
6 study location relative to Iceland.  
7



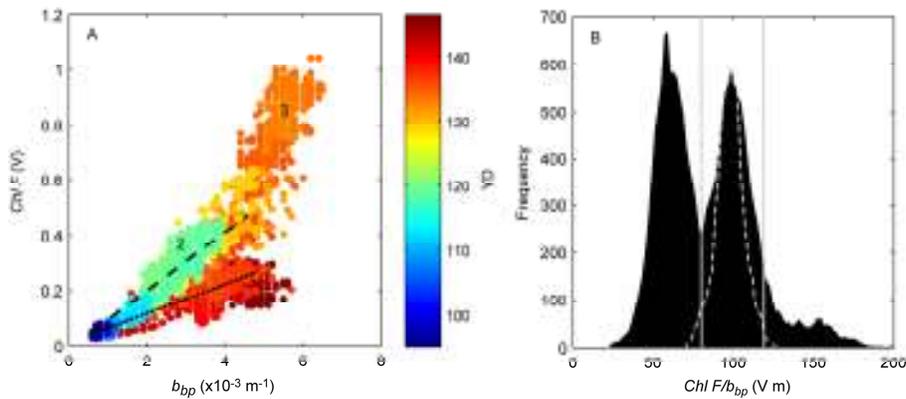
1  
 2 Figure 2. Chlorophyll data from *R/V Knorr* CTD profiles in May, color coded by the optical  
 3 community index,  $Chl F/b_{bp}$  (color bar on right; units are V m). (A)  $Chl F$  vs. extracted  
 4 chlorophyll concentration,  $Chl$ , was used to develop a non-linear best-fit function of temperature,  
 5 PAR, depth and YD for converting float  $Chl F$  to  $Chl$  (D'Asaro, 2011). (B) Best-fit derived  $Chl$   
 6 vs. extracted  $Chl$  shows deviation at higher concentrations (1:1 gray dashed line). (C)  $Chl F$   
 7 normalized to  $Chl$  exhibits photoquenching at high PAR (surface samples).

8

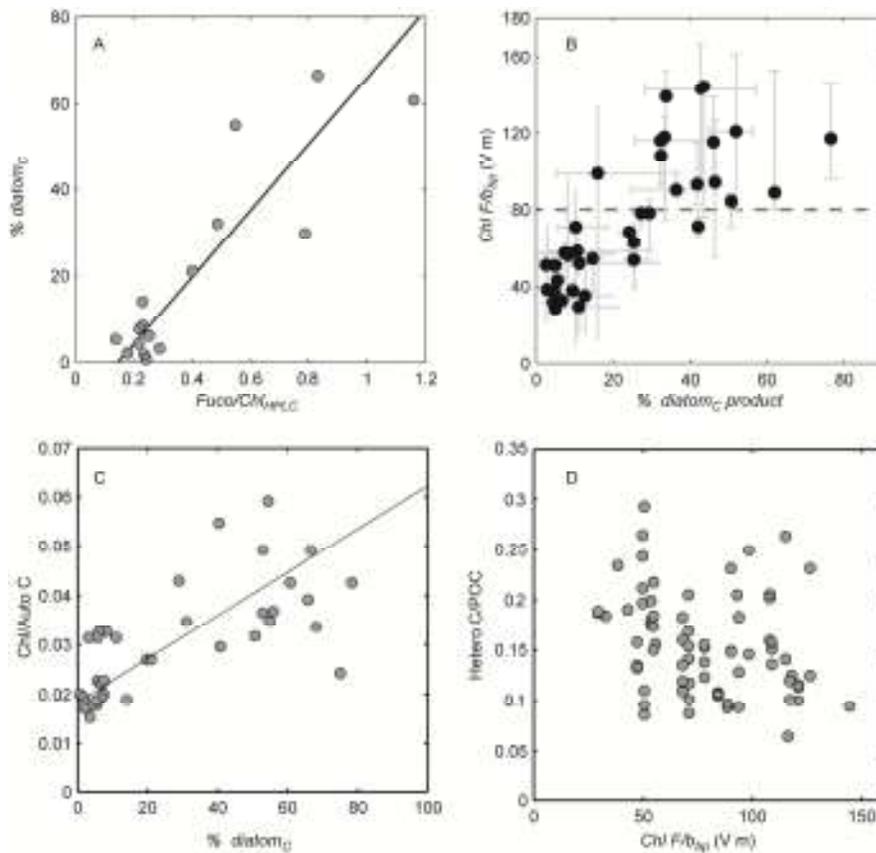


1  
 2 Figure 3. Float data collected for 10 – 50 m for YD 95 –146 (4 April to 25 May 2008). Vertical  
 3 lines and letters indicate periods in bloom evolution (see section 3.1); DM – *Deep Mixing*, E –  
 4 *Early Bloom*, S – *Storm*, M – *Main Bloom*, Ed – *Eddy*, P – *Post Bloom*. Dots represent initial

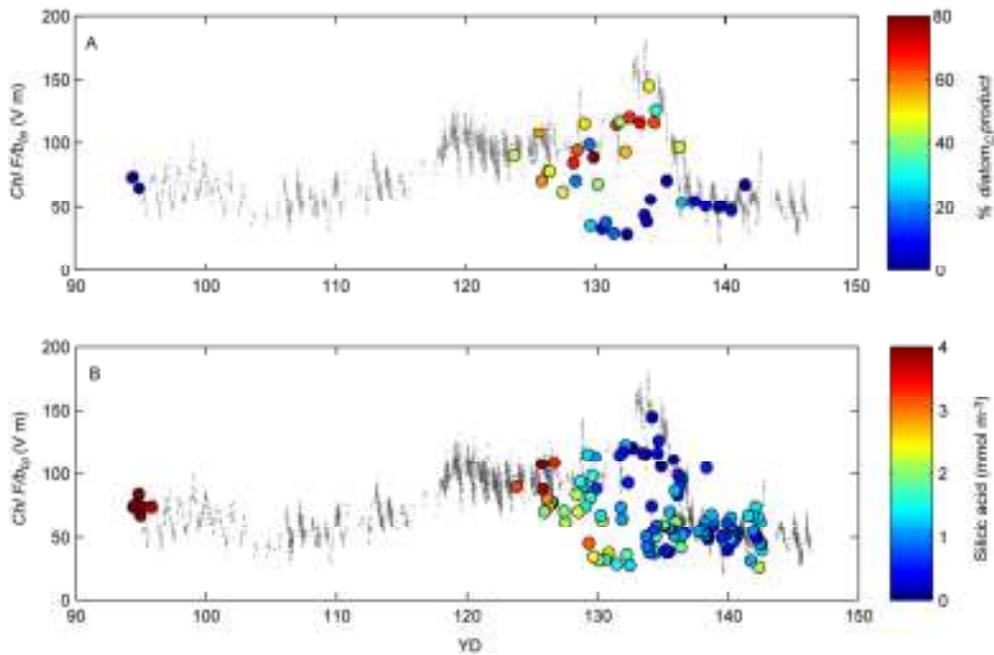
1 median filtered data (7 point running median); superimposed line is smoothing spline fit (Matlab  
2 code *spaps.m*, smoothing parameter 0.1). (A) *Chl* derived from *Chl F*. (B) Mixed layer depth  
3 (dashed line) and depth of 0.415 mol photons  $\text{m}^{-2} \text{d}^{-1}$  isolume (solid line). (C) *Chl F* (solid line)  
4 and  $b_{bp}$  (heavy solid line). (D) Optical community index,  $Chl F/b_{bp}$ . Horizontal dashed lines  
5 indicate transitions between Groups 1 – 2 and 2 – 3. Also see Fig. 6.  
6



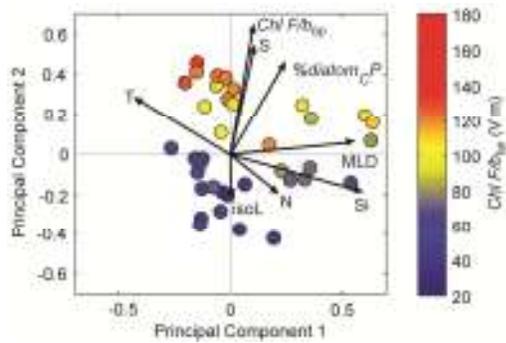
1  
 2 Figure 4. Optical community index and its components from entire float deployment; data from  
 3 10 – 50 m. (A)  $Chl F$  vs.  $b_{bp}$  shows three groups: Group 1 (dotted line); Group 2 (dashed line);  
 4 Group 3, no regression calculated. Some data points in Group 3 are obscured by Group 2. Color  
 5 coding is YD. (B) Frequency distribution of the optical community index (additional 2 point  
 6 median filter). Centroids corresponding to the regression lines in panel A. Gray dashed line  
 7 corresponds to the frequency distribution of the optical community index during period YD 120  
 8 – 127.  
 9



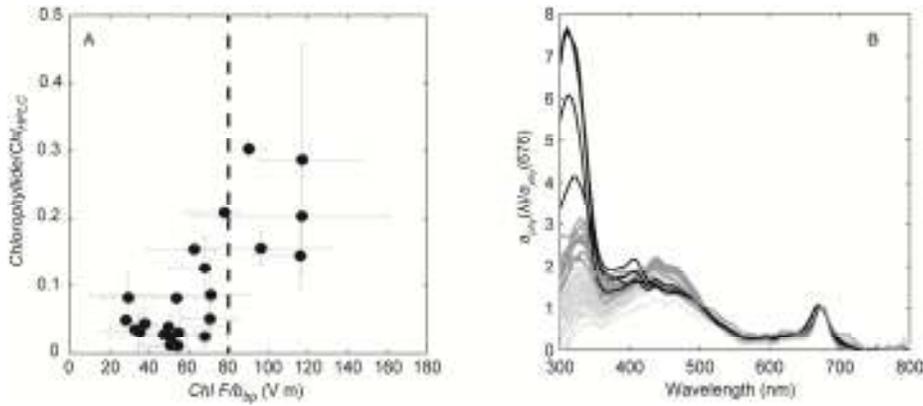
1  
 2 Figure 5. Community composition. Gray circles in Panels A, C and D are for individual water  
 3 samples; black circles in Panel B are averages for each profile. (A) *Fuco/Chl<sub>HPLC</sub>* (g/g) is  
 4 correlated with % *diatom<sub>C</sub>*. (B) Optical community index is related to phytoplankton community  
 5 composition, represented as % *diatom<sub>C</sub> product*. Bars are the range of individual values within  
 6 each profile; horizontal line indicates the division between Groups 1 and 2 based on Fig. 4B. (C)  
 7 *Chl*-to-autotrophic carbon increases with the fraction of diatoms. (D) Ratio of heterotrophic  
 8 carbon biomass to total POC is not correlated with optical community index.  
 9



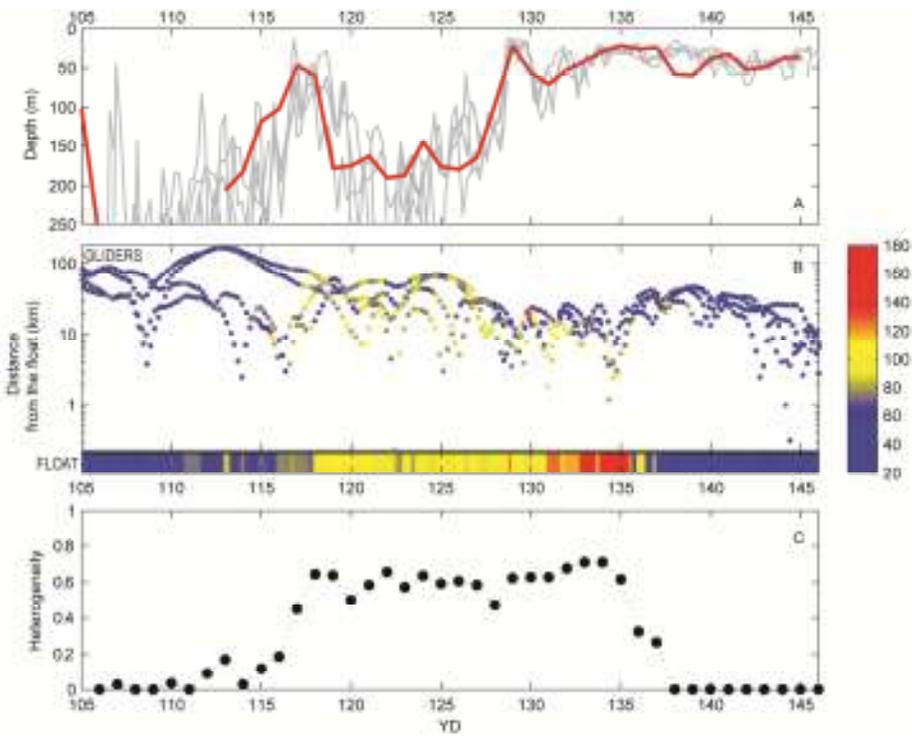
1  
 2 Figure 6. Optical community index,  $Chl F/b_{bp}$ , from ship CTD profiles (circles) superimposed on  
 3 float data (gray); 10 – 50 m median is plotted for each ship profile. (A) The optical community  
 4 index color coded by % *diatom<sub>C</sub> product* (n=42). The index was high when the relative diatom  
 5 abundance was high. (B) Same but color coded by Si concentration. Highest values of  $Chl F/b_{bp}$   
 6 were concurrent with lowest values of Si (n = 123).  
 7



1  
 2 Figure 7. PCA biplot for *R/V Knorr* CTD stations ( $n = 38$ ), color coded by median  $Chl F/b_{bp}$  for  
 3 10-50 m, where blue corresponds to Group 1, yellow to Group 2 and red to Group 3. Together  
 4 PCs 1 and 2 explain 68.7% of the variance. The length of a single parameter vector (black line  
 5 with arrow) describes its contribution to the PC, while the direction of the vector, starting from  
 6 the axes intersection, depicts the "biplot" gradient of the specific parameters: T – temperature, S  
 7 – salinity, IsoL – 0.415 isolume depth, MLD – mixed layer depth, N – nitrate, Si – silicic acid,  
 8  $Chl F/b_{bp}$  – optical community index, and %  $diatom_C P$  (here representing %  $diatom_C$  product for  
 9 brevity).  
 10



1  
 2 Figure 8. (A) Chlorophyllide concentration normalized to  $Chl_{HPLC}$  (g/g) was greater at higher  
 3 values of the optical community index. Bars are the range of individual samples within each  
 4 profile (23 profiles, 60 HPLC samples). (B) Phytoplankton absorption coefficient,  $a_{phy}$ ,  
 5 normalized to absorption at 676 nm; all available data are shown for completeness (n=63). Large  
 6 peaks near 300 nm occurred when the optical community index exceeded 80  $V \cdot m$  (dark grey and  
 7 black lines); black lines note spectra with shifts in the absorption peak from 325 – 330 nm to 310  
 8 – 315 nm.



1  
 2 Figure 9. Spatial heterogeneity in phytoplankton community composition, determined from four  
 3 gliders and the float. (A) Mixed layer depths, from gliders (gray line) and float (red line). (B)  
 4 Distances between gliders and Lagrangian float. Data are color coded as  $Chl F/b_{bp}$ ; dots  
 5 represent glider data and color bar at bottom represents float data. (C) Heterogeneity index for  
 6 community composition, defined in Section 2.4.

1 Table 1. List of measured variables and methodologies, as measured on different platforms. .

Parameter measured	Symbol /Acronym	Instrument or method for specific platform		
		Ship	Lagrangian Float	Seagliders
Temperature, Conductivity (Salinity)	T, S	SBE 911 <i>plus</i>	SBE 41	unpumped, custom SBE CT sensor
Chlorophyll fluorescence	<i>Chl F</i>	WET Labs FLNTU	WET Labs FLNTU	WET Labs BB2F
Volume scattering function, calculated optical backscattering	$\beta(700 \text{ nm})$ , $b_{bp}$	WET Labs FLNTU	WET Labs FLNTU	WET Labs BB2F
Photosynthetically active radiation	PAR	Biospherical QSP2300	LI-COR 192-SA	
Nutrients: nitrate and silicic acid	N, Si	Kallin et al. (2011), Lachat (1996, 1999)	ISUS (not reported)	
Chlorophyll from extracts	<i>Chl</i>	Knap et al. (1996)		
Chlorophyll, HPLC analysis	$Chl_{HPLC}$	Van Heukelem and Thomas (2001), Hooker et al. (2009)		
Phytoplankton absorption coefficient	$a_{phy}(\lambda)$	Mitchell and Kiefer (1988), Kishino et al., (1985)		
Phytoplankton cell carbon		Sieracki and Poulton (2011) and references therein		
Particulate organic carbon	POC	Cetinić et al. (2012)		

2

3

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