Author's Response

Referee #1

This is a well-written manuscript that provides and interprets a comprehensive in situ dataset of phytoplankton production and species composition (including microzooplankton) from two different sites in the North Atlantic during pre-bloom conditions. These data complement and acknowledge the importance of the comparison with larger-scale satellite-derived data. The availability of the full dataset from Pangaea.de is particularly valuable (although I was not granted access despite being logged in to Pangaea?) to the wider scientific community and should allow the data to be used further e.g. comparison with other 'pre-bloom' datasets (cruises; time-series stations); modelling carbon fluxes, trophic cascades.

We agree with the reviewer that the dataset is valuable to the scientific community; the dataset will be open access once this manuscript is published.

The authors use and exploit a wide range of literature and explain the various theories behind the onset of the spring phytoplankton bloom well, particularly in the North Atlantic. However, I recommend the authors include and consider the net heat flux (NHF) as a trigger for the spring bloom (e.g. Smyth et al 2014 Ocean Net Heat Flux influences seasonal to interannual patterns of plankton abundance. PLoS ONE 9(6): e98709). Does the NHF explain the shifts in productivity and composition of the different size fractions in this study?

The reviewer is correct that Net Heat Flux may be involved in spring bloom initiations, and as such we have now considered it in the manuscript. However, net heat flux was negative for the majority of the times series (C. Lindemann pers. comm., Giering et al., *in review*) and does not explain the shifts in productivity or composition. (L479 – 482)

The authors enumerated ciliates and dinoflagellates and refer to the microzooplankton as potentially important grazers of the phytoplankton and I suggest more could be made on the importance of grazers (micro- and mesozooplankton) in controlling (or otherwise) the onset and composition of the spring bloom.

We agree with the reviewer that top down pressure through grazing may influence the onset and composition of the spring bloom. We have now discussed this in more detail, however we do not have the required measurements of grazing rates to determine the level of control by zooplankton. (L641 - 645)

Specific comments: Methods section 2.1: can the authors state how many times the two stations were sampled and negate the use of 'repeatedly'?

We have made explicit how many time the stations were sampled. (L157 - 158)

Methods: General suggestion that where possible state how many replicate samples were taken e.g. 13C, Chla, PIC etc

We have stated when replicate samples were collected. (L207)

Section 4.4, p115, L6: spelling mistake 'out' should be 'our'

This has been corrected. (L564)

Referee #2

Question : Can the differences observed between the ICB and NWB bloom biomass and composition be the result of a different timing of the bloom ? If T °C are different and the bloom progresses northwards, how do you compare both stages ?

While it is possible that the two sites were in different stages of bloom formation, satellite Chl *a* indicates that the two sites were in the early stages of bloom formation, with the rapid increase in Chl *a* occurring at approximately the same time later in the season. That the NWB was colder and further north could be factors, both of which are discussed in section 4.2: the small difference in irradiance and temperature is unlikely to have a significant effect. Although blooms generally progress northwards, the timing of bloom formation is far more complex (Henson et al., 2009) and as such it is possible to compare two sites as we have done here, as long as the physiochemical and biological features are considered.

Page 3 line 23 : Correct "nanno" sized diatoms ; what is the dominant genera then ? Minidiscus sp. ?

We have corrected this, and added in that Minidiscus spp. were the dominant genera. (L43 - 44)

Page 4 line17 : the authors insist on the importance of the timing and magnitude of the bloom to determine its biogeochemical impact, but in the paper a clear focus is set, rightfully so, on community structure, clearly this is important so I would add this variable to the list at the end of this sentence "and the variability in, bloom timing, magnitude and community structure"

We have added this in as suggested. (L65)

Page 5 line 18 : you browse through the 3 bloom development hypotheses, maybe you could state their name : CDH, CTH, you do it with the first two, but not the last one line 18 : DRH (disturbance-recovery hypothesis)

We have now defined the DRH hypothesis explicitly as requested. (L93 – 94)

Page 7 line 12 : "During the spring bloom: : :would occur early in the growth season (March-April)" this sentence is grammatically awkward, and March-April does not seem very 'early' in the season if you are trying to confront your observations with one of the three bloom development hypotheses, which predict much earlier bloom developments ? Also correct "occurr" with "occur".

We have reworded the sentence as suggested. We consider March-April early in the season as seasonal Chl *a* from satellites shows that phytoplankton blooms in this region do not peak until later in the season (Henson et al., 2009). We have corrected the typo. (L141 - 144)

Page 7 line 10 : I am not a native English speaker, but I am not sure that "succeeded" can be used with "being" in "some groups being succeeded due to competition"

We have reworded as suggested. (L137 - 138)

Page 10 line 9 "particulate biogenic silica samples were collected in the same manner as PIC" is a bit imprecise, did you also rinse the filters with trace ammonium solution (pH 10) ? Also I don't understand the reference chosen for this method (Brown et al. 2003), in this paper the authors only adress the 32Si uptake protocol, and use glass vials for extraction, which has no impact on 32Si concentrations, but will give completely wrong results for particulate silica due to leaching from the glass. A more adequate method reference would be Ragueneau Tréguer 1994, but please indicate more precisely how BSi extractions were carried out (type of tubes used for extraction), and whether a correction for lithogenic silica was at all made.

We apologise for the confusion concerning the protocol for particulate silicate samples and have reworded and expanded this section to provide more detail. The filters were rinsed with trace ammonium solution. Brown et al. (2003) measure biogenic silica as well 32Si, however we have now added the reference to Ragueneau and Tréguer (1994) as suggested. Extractions were carried out in polypropylene tubes and no corrections were made for lithogenic silica. (L218 – 223)

Page 12 line 24 : figure 5a is cited before any mention of Figure 4 is made, please swap figure order or rename figure numbers accordingly in the text. & Page 14 line 2 : first mention of Figure 4

We have swapped the figure order as suggested

Page 16 section 3.4.3. some homogeneity with the previous paragraph for coccolithophores would be best. Either identify all taxa down to the species level (you do it for Guinardia striata but not for the others where only a genera name is given). If not determined, indicate sp. or spp. if one or several species were observed.

Diatoms were only identified to genus level while coccolithophores were identified to species level. We have reworded the text to reflect this. (L383)

The next sentence and associated graph (Figure 5) are very confusing. The sampling strategy for diatoms and bSiO2 is not clear to me from this paragraph. I understand two vertical profiles were done at each visit for bSiO2, but only one for diatom cell counts. But you mention a "significant variability observed in bSiO2 between the station visits", don't you mean AT each visit that there was a significant variability between the first and second vertical profile ? Then when was the SEM vertical profile sampled? on the other cast than the lugol samples ?

We apologise for the confusion, we did indeed mean significant variability between each CTD profile as suggested. We have corrected the text accordingly. The SEM samples were collected on the other cast than the Lugol samples, we have now made this clear. (L387, 389 - 390)

Figure 5 is very hard to follow, and I have several issues with it : - it would be best to convert the "Day of the year" axis into the actual sampling dates, (later on page 17 line 1 you mention "a peak concentration was reached on 10 April", thus it would be clearer to have the same reference to date in both your text and figure. -then to align both graphs vertically, so that one histogram bar from Fig b, corresponds precisely to the bSiO2 concentration given in fig a. – There is no mention anywhere as to which depth these bSiO2 and diatom concentrations correspond to ? as they are in mmol m-3 and cells ml-1, they are not integrated and must reflect one depth ? If you sampled vertical profiles, why not show integrated concentrations in fig a and then the representative community below ? Was just one sample counted at each visit for diatoms ? -What's the justification for bSiO2 double casts sometimes very close in time (two consecutive days) and sometimes several days apart ? -in the legend (b) diatom "species" again should be replaced with "genera", or "sp./spp." should be added to each taxon in the figure. - "Psuedo-nitzschia" in the legend has a typo and should be "Pseudo" -the two middle grey colors are hard to distinguish one from another, please add some motive to your bars, or make the last one white so you only use 3 shades of grey instead of 4. –

We apologise that this figure was hard to follow. To improve consistency we have now referred to day of year in the text and have listed both dates and day of year in all tables, however we have not converted the figures to actual sampling dates as this does not allow for continuous axes. Aligning both graphs vertically would not allow for BSi from both sites to be presented and therefore we have left it as is. The data presented in this figure are from surface samples (5 - 15 m), which we have now made explicit in the methods, the figure caption and in table 3. Diatoms were only counted from surface samples so vertical profiles of diatoms are not available for integrating. Diatoms were only sampled from the pre-dawn cast while bSiO2 was sampled from both the pre-dawn cast and the second cast. We cannot provide a justification for the inconsistency in time between CTDs; this study was part of a large multidisciplinary cruise with many different deployments, as such we could not control the timing of all CTD casts. We have corrected the caption and the typo. We have changed the figure to colour to remove ambiguity. (L190, Fig. 4 caption, Table 3, L 285, 298, 395, 398, 399, 449, 568, 569)

Since you also measured PIC and counted coccolithophores, I don't understand why you did not put up a similar figure for this group, the direct comparison of PIC vs bSiO2 in the same graph, and of diatom and cocco counts in another would have been nice. –

A direct comparison of integrated PIC and $bSiO_2$ is made in Table 2 and cells counts of diatoms and coccolithophores is made in Table 3. We feel that these comparisons are best represented in these tables rather than in an additional figure.

I could not find anywhere an indication of which depth were sampled and counted for diatoms and cocco? you don't say so in section 2.3 of your methods, nor in your Figure 5, nor in your Table 3. Are the presented counts only surface samples? How do they compare with the vertical profiles? Were bSiO2 and PIC always maximum at surface levels?

We apologise, this was an oversight on our part. Samples for diatoms and coccolithophores were collected from surface samples (5 - 15 m). We have now made this explicit in the methods, the figure and the table. bSiO2 and PIC were not always maximum at surface levels but phytoplankton counts are unavailable from the other depths for a comparison. (L190, Fig. 4 caption, Table 3))

Page 22 line 3: correct "occurr" with "occur"

We have corrected this. (L534)

Page 23 line 6: correct "and out in situ" with "and our in situ"

We have corrected this. (L564)

Page 24 line 3 to line 6 : I am not sure I follow this argument that the species best correlated to bSiO2 is the major exporter of bSiO2, plus you mix 'exporter' and 'producer' of bSiO2 in the same sentence, and these two definitions could be quite different: :

We have reworded this sentence to differentiate between producer and exporter, suggesting that the major producer of $bSiO_2$ has the potential to be the major exporter of $bSiO_2$. (L591 – 592)

Page 24 : can the determination of the genera Minidiscus sp. be confirmed with SEM images ? It would be interesting to know for sure. I agree this genera can be important and easily overlooked in lugol samples, since you have SEM samples, it would be nice to confirm identification. Also I find that the paper by Boyd and Newton 1995 for the NABE program should be cited somewhere : they did observe a Nanoneis sp. Bloom one year (one of the smallest diatom species known, and probably occupying a similar niche with Minidiscus sp.), and Chaetoceros sp. bloom the following year at the same site.

We have confirmed using SEM images that the major genus was Minidiscus. We have now incorporated the paper by Boyd and Newton 1995 into our discussion. (L600, 608)

Page 24 line 17, line 20; page 25 line 4 : correct "nanno" with "nano"

We have corrected this (L603)

- **Phytoplankton dynamics in contrasting early stage North**
- 2 Atlantic spring blooms: composition, succession, and
- 3 potential drivers
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- 19
- 20 Running head: Spring Bloom Phytoplankton Composition
- 21

22 Abstract

23 The spring bloom is a key annual event in the phenology of pelagic ecosystems, making a

24 major contribution to the oceanic biological carbon pump through the production and export

25 of organic carbon. However, there is little consensus as to the main drivers of spring bloom

26 formation, exacerbated by a lack of in situ observations of the phytoplankton community

27 composition and its evolution during this critical period.

- 28 We investigated the dynamics of the phytoplankton community structure at two contrasting
- 29 sites in the Iceland and Norwegian Basins during the early stage (25th March 25th April) of
- 30 the 2012 North Atlantic spring bloom. The plankton composition and characteristics of the
- 31 initial stages of the bloom were markedly different between the two basins. The Iceland

32 Basin (ICB) appeared well mixed to > 400 m, yet surface chlorophyll a (0.27-2.2 mg m⁻³) and

33 primary production (0.06-0.66 mmol C m⁻³ d⁻¹) were elevated in the upper 100 m. Although

34 the Norwegian Basin (NWB) had a persistently shallower mixed layer (< 100 m), chlorophyll

 $a (0.58-0.93 \text{ mg m}^{-3})$ and primary production (0.08-0.15 mmol C m⁻³ d⁻¹) remained lower

36 than in the ICB, with picoplankton (< $2 \mu m$) dominating chlorophyll *a* biomass. The ICB

37 phytoplankton composition appeared primarily driven by the physicochemical environment,

38 with periodic events of increased mixing restricting further increases in biomass. In contrast,

- 39 the NWB phytoplankton community was potentially limited by physicochemical and/or
- 40 biological factors such as grazing.

41 Diatoms dominated the ICB, with the genus *Chaetoceros* (1-166 cells mL⁻¹) being succeeded

42 by *Pseudo-nitzschia* (0.2-210 cells mL⁻¹). However, large diatoms (> 10 μ m) were virtually

43 absent (< 0.5 cells mL⁻¹) from the NWB, with only small nano-sized (< 5 μ m) diatoms (i.e.

44 *Minidiscus* spp.) present (101-600 cells mL⁻¹). We suggest micro-zooplankton grazing,

45 potentially coupled with the lack of a seed population of bloom forming diatoms, was

46 restricting diatom growth in the NWB, and that large diatoms may be absent in NWB spring

47 blooms. Despite both phytoplankton communities being in the early stages of bloom

48 formation, different physicochemical and biological factors controlled bloom formation at the

- 49 two sites. If these differences in phytoplankton composition persist, the subsequent spring
- 50 blooms are likely to be significantly different in terms of biogeochemistry and trophic
- 51 interactions throughout the growth season, with important implications for carbon cycling

52 and organic matter export.

53 **1.** Introduction

54 The spring bloom is a key annual event in the phenology of pelagic ecosystems, where a

55 rapid increase in phytoplankton biomass has a significant influence on upper ocean

56 biogeochemistry and food-availability for higher trophic levels (Townsend et al., 1994;

57 Behrenfeld and Boss, 2014). Spring blooms are particularly prevalent in coastal and high

58 latitude waters. The high levels of phytoplankton biomass and primary production that occur

59 during these blooms, and its subsequent export out of the surface ocean, result in a significant

60 contribution to the biological carbon pump (Townsend et al., 1994; Sanders et al., 2014). The

61 North Atlantic spring bloom is one of the largest blooms on Earth, making a major

62 contribution to the annual export of ~1.3 Gt C yr⁻¹ from the North Atlantic (Sanders et al.,

63 2014). The timing and magnitude of the spring bloom can have a significant biogeochemical

64 impact (Henson et al., 2009); hence it is important to understand both the controls on, and the

65 variability in, bloom timing, magnitude and community structure. Despite its importance,

66 there remains little consensus as to the environmental and ecological conditions required to

67 initiate high latitude spring blooms (Townsend et al., 1994; Behrenfeld, 2010; Taylor and

68 Ferrari, 2011b; Smyth et al., 2014).

69 Phytoplankton blooms occur when growth rates exceeds loss rates (i.e. a sustained period of 70 net growth); phytoplankton growth rate constraints include irradiance, nutrient supply, and 71 temperature, while losses can occur through predation, advection, mixing out of the euphotic 72 zone, sinking and viral attack (Miller, 2003). Therefore, the rapid increase in (net) growth 73 rates during the spring bloom must be due to either an alleviation of those factors 74 constraining growth, a reduction in factors determining losses, or (more likely) some 75 combination of both.

76 The critical depth hypothesis (Sverdrup, 1953), the seminal theory of spring bloom initiation,

proposes that there exists a critical depth such that when stratification shoals above this

depth, phytoplankton growth will exceed mortality and a bloom will occur. However, this

79 hypothesis has been more recently brought into question as bloom formation has been

80 observed to start earlier than expected (Mahadevan et al., 2012), and in the absence of

81 stratification (Townsend et al., 1992; Eilertsen, 1993). Several new theories have now been

82 developed to explain these occurrences (reviewed in Behrenfeld and Boss, 2014; Fischer et

83 al., 2014; Lindemann and St. John, 2014).

84 Eddies and oceanic fronts have both been identified as sources of stratification prior to the 85 wider onset of seasonal stratification (Taylor and Ferrari, 2011a; Mahadevan et al., 2012). 86 However, they do not explain blooms in the complete absence of stratification, which can 87 instead be explained by the critical turbulence hypothesis (Huisman et al., 1999; Taylor and 88 Ferrari, 2011b; Brody and Lozier, 2014; Smyth et al., 2014). These theories distinguish 89 between a convectively driven actively mixed layer and a density-defined mixed layer such 90 that if convective mixing reduces sufficiently, blooms can occur in the actively mixing layer 91 although the density-defined mixing layer remains deep. Therefore, blooms are able to form 92 in the apparent absence of stratification, as defined by the presence of a thermocline. An 93 alternative to the hypotheses concerning physical controls on bloom formation is the 94 disturbance-recovery hypothesis proposed by Behrenfeld (2010), which suggests that the 95 decoupling of phytoplankton and microzooplankton contact rates in deep winter mixed layers 96 results in phytoplankton net growth from winter onwards due to reduced mortality (via 97 grazing). It is also possible that there are multiple biological and physical controls, acting on 98 different spatial and temporal scales, that drive the heterogeneous bloom distributions 99 observed via remote sensing (e.g. Lindemann and St. John, 2014).

100 Significant interannual and decadal variability in the structure and timing of spring blooms in 101 the North Atlantic has been documented (Henson et al., 2009). Such variability in bloom 102 timing has been attributed to the variation in the winter mixed layer depth (WMLD); a deeper 103 WMLD results in a delayed bloom in the subarctic North Atlantic (Henson et al., 2009). A 104 strong latitudinal trend exists in the North Atlantic where the spring bloom propagates north 105 due to seasonal relief from light limitation at high latitudes (Siegel et al., 2002; Henson et al., 106 2009). Both the role of the WMLD in interannual variability in bloom timing and the 107 northwards progression of bloom start dates highlight how physical processes have a clear 108 and significant impact on bloom formation. The controls on the variability in bloom 109 magnitude are less certain, although it appears to be a combination of WMLD variability 110 influencing the start date as well as biological factors such as phytoplankton composition and 111 grazing (Henson et al., 2009).

112 Despite considerable discussion on the various factors that may or may not influence bloom

113 initiation, timing, magnitude and phenology, few studies have actually examined the in situ

114 phytoplankton community. Instead, because of the need for temporally resolved data,

satellite-derived products and models have been used in much of the previous work on spring

116 blooms. However, such methods cannot address the potential influence of the complex

117 plankton community structure on the development of a spring bloom.

The traditional text book view of a phytoplankton spring bloom is that the pre-bloom pico-118 119 phytoplankton (cells $< 2 \mu m$) dominated community is directly succeeded by a diatom 120 dominated community (Margalef, 1978; Barber and Hiscock, 2006); as conditions become 121 more favourable for growth, a diatom bloom develops, 'suppressing' growth of other 122 phytoplankton groups. Through either increased predation, nutrient stress or a changing 123 physical environment (Margalef, 1978), diatoms decline and are then replaced by other 124 phytoplankton such as dinoflagellates and coccolithophores (Lochte et al., 1993; Leblanc et 125 al., 2009). In this way, a series of phytoplankton functional type successions occur as the spring bloom develops. That diatoms often dominate intense spring blooms is well accepted 126 127 (Lochte et al., 1993; Rees et al., 1999), however the dynamics of the interplay between 128 diatoms and the rest of the community have been questioned (Barber and Hiscock, 2006). 129 The rapid proliferation of diatoms in a spring bloom does not necessarily suppress other 130 phytoplankton (Lochte et al., 1993; Barber and Hiscock, 2006), and the "rising tide" 131 hypothesis states that instead of succession, the favourable conditions for diatoms also favour 132 other phytoplankton groups and therefore all phytoplankton will respond positively and grow 133 (Barber and Hiscock, 2006). The apparent suppression of the phytoplankton community by 134 diatoms is due to the relatively high intrinsic growth rates of diatoms resulting in 135 concentrations dwarfing the rest of the community. The "rising tide" hypothesis is a 136 contrasting theory to succession, however it may be that the phytoplankton community 137 response will not be universal, with some taxa-specific succession due to competition or 138 increased grazing (Brown et al., 2008). Furthermore, succession may appear to occur if 139 phytoplankton loss rates are taxonomically specific, such that while many phytoplankton 140 groups concurrently grow, successive loss of specific groups occurs. 141 The overall goal of our study was to determine the phytoplankton community structure, and its evolution during the spring bloom in the North Atlantic, linking the community structure 142

143 to the physical environment and examining whether succession to a diatom dominated

144 environment would occur early in the growth season (March-April). Sampling for this study

- 145 was carried out as part of the multidisciplinary EuroBASIN "Deep Convection Cruise". The
- 146 timing and location of this cruise (19th March 2nd May 2012) was chosen to try and observe
- 147 the transition from deep winter convection to spring stratification, and examine the physical
- 148 controls on the dynamics of phytoplankton, carbon export and trophic interactions. A recent

149 study has previously suggested that winter convection in the North Atlantic and Norwegian

150 Sea sustains an overwintering phytoplankton population, thus providing an inoculum for the

- 151 spring bloom (Backhaus et al., 2003), although this transition has not been explicitly
- 152 examined before.

153 **2.** Methods

154 2.1 Sampling

155 The Deep Convection cruise repeatedly sampled two pelagic locations in the North Atlantic (Fig. 1), sited in the Iceland (ICB, 61.50 °N, 11.00 °W) and Norwegian (NWB, 62.83 °N, 156 157 2.50 °W) Basins, onboard the R/V *Meteor*. The ICB was visited four times, and the NWB 158 visited three times during the course of the cruise. Samples were collected from multiple 159 casts of a conductivity-temperature-depth (CTD) - Niskin rosette, equipped with a 160 fluorometer, at each station. Water samples for rates of primary production (PP), community 161 structure and ancillary parameters (chlorophyll a [Chl a], calcite [PIC], particulate silicate 162 [bSiO₂] and macronutrient concentrations) were collected from predawn (02:30-05:00 GMT) 163 casts from six light depths (55 %, 20 %, 14 %, 7 %, 5 % and 1 % of incidental PAR). The 164 depth of 1 % incident irradiance was assumed to equate to the depth of the euphotic zone 165 (e.g. Poulton et al., 2010). Optical depths were determined from a daytime CTD cast on 166 preceding days at each site. Additional samples for coccolithophore community structure and 167 ancillary parameters were collected from a second CTD cast, while samples for detailed size 168 fractionated Chl a were collected from a third cast.

169 **2.2 Primary production**

Carbon fixation rates were determined using the ¹³C stable isotope method (Legendre and 170 Gosseline, 1996). Water samples (1.2 L) collected from the six irradiance depths were 171 inoculated with 45-46 µmol L^{-1 13}C labelled sodium bicarbonate, representing 1.7-1.8 % of 172 173 the ambient dissolved inorganic carbon pool. Samples were incubated in an on-deck 174 incubator, chilled with sea surface water, and light depths were replicated using optical filters 175 (Misty-blue and Grey, LEETM). Incubations were terminated after 24 hours by filtration onto 176 pre-ashed (> 400 °C, > 4 hours) Whatman GF/F filters. Acid-labile carbon (PIC) was 177 removed by adding 1-2 drops of 1 % HCl to the filter followed by extensive rinsing with freshly filtered (Fisherbrand MF300, ~0.7 µm pore size) unlabelled seawater. Filters were 178 179 oven dried (40°C, 8-12 hours) and stored in Millipore PetriSlidesTM. A parallel 55 % bottle

- 180 for size fractionated primary production (< $10 \mu m$) was incubated alongside the other
- 181 samples, with the incubation terminated by pre-filtration through 10-µm polycarbonate
- 182 (NucleporeTM) filters and the filtrate was filtered and processed as above.

183 The isotopic analysis was performed on an Automated Nitrogen and Carbon Analysis prep

184 system with a 20-20 Stable Isotope Analyser (PDZ Europa Scientific Instruments). The ¹³C-

- 185 carbon fixation rate was calculated using the equations described in Legendre and Gosseline 186 (1996). The > 10- μ m PP fraction was calculated as the difference between total PP and < 10-
- 187 μm PP.

188 **2.3 Community structure**

189 Water samples for diatom and micro zooplankton counts, collected from predawn cast

190 surface samples (5-15 m), were preserved with acidic Lugol's solution (2 % final solution) in

191 100-mL amber glass bottles. Cells were counted in 50 mL Hydro-Bios chambers using a

192 Brunel SP-95-I inverted microscope (X200; Brunel Microscopes Ltd). Samples for flow

193 cytometry were fixed with glutaraldehyde (0.5 % final solution) and stored at -80°C before

- being analysed using a FACS Calibur (Beckton Dickinson) flow cytometer (Zubkov et al.,
- 195 2007).

196 Water samples (0.5-1 L) for coccolithophore cell numbers and species identification were

197 collected from surface samples (5-15 m) onto cellulose nitrate filters (0.8-µm pore size,

198 Whatman), oven dried and stored in Millipore PetriSlidesTM. Permanent slides of filter halves

199 were prepared and analysed using polarizing light microscopy following Poulton et al.

- 200 (2010). Coccolithophores were analysed to species level following Frada et al. (2010). For
- 201 confirmation of species identification, a subset of filter halves were analysed by scanning

202 electron microscope (SEM) following Daniels et al. (2012). Coccolithophore species were

203 identified according to Young et al. (2003).

204 2.4 Chlorophyll a

205 Water samples (250 mL) for total Chl *a* analysis were filtered onto Fisherbrand MF300

filters. Parallel samples were filtered onto polycarbonate filters (10- μ m) for > 10 μ m Chl *a*.

207 Samples for detailed size fractionated Chl *a*, collected in duplicate from a single depth in the

208 upper water column (12-35 m), were filtered in parallel onto polycarbonate filters of various

- 209 pore size (2, 10, 20-µm) and MF300 filters (effective pore size 0.7 µm). Filters were
- 210 extracted in 8 mL of 90 % acetone (Sigma) for 20-24 hours (dark, 4°C). Measurements of

- 211 Chl *a* fluorescence were analysed on a Turner Designs Trilogy Fluorometer, calibrated using
- a solid standard and a chlorophyll *a* extract.

213 **2.5** Ancillary parameters

214 Particulate inorganic carbon (PIC) measurements were made on water samples (500 mL) 215 filtered onto polycarbonate filters (0.8 µm pore-size, Whatman), rinsed with trace ammonium solution (pH ~10) and oven-dried (6-8 hours, 30-40 °C). The analysis was carried out 216 217 following Daniels et al. (2012) except that extractions were carried out in 5.0 mL of 0.4 mol 218 L^{-1} nitric acid, erroneously reported as 0.5 mL in Daniels et al. (2012). Particulate silicate (bSiO₂) samples were collected onto polycarbonate filters (0.8 µm pore-size, Whatman), 219 rinsed with trace ammonium solution (pH \sim 10) and oven-dried (6-8 hours, 30-40 °C). 220 Digestion of $bSiO_2$ was carried out in polypropylene tubes using 0.2 mol L⁻¹ sodium 221 hydroxide, before being neutralised with 0.2 mol L⁻¹ hydrochloric acid (Ragueneau and 222 223 Tréguer, 1994; Brown et al., 2003). The solutions were analysed using a SEAL QuAAtro 224 autoanalyser and no corrections were made for lithogenic silica. Macronutrients (nitrate,

- 225 phosphate, silicic acid) concentrations were determined following Sanders et al. (2007) on a
- 226 Skalar autoanalyser.

227 Samples for total dissolved inorganic carbon (C_T) were drawn into 500 ml borosilicate

bottles. No filtering of samples occurred prior to analysis. Samples were stored in the dark

and analysed within 12 hours of sampling, thus no poisoning was required. C_T was

230 determined using coulometric titration (Johnson et al., 1987) with a precision of $\leq 2 \ \mu mol \ kg^{-1}$

- ¹. Measurements were calibrated against certified reference material (CRM, Dickson, 2010).
 Seawater pH_T was measured using the automated marine pH sensor (AMpS) system as
- 233 described in Bellerby et al. (2002) modified for discrete mode. This system is an automated

spectrophotometric pH sensor that makes dual measurements of thymol blue. The pH_T data

used in this study were computed using the total hydrogen ion concentration scale and has a

236 precision of 0.0002 pH_T and an estimated accuracy of better than 0.0025 pH_T units against

- 237 CRM standards. The measured C_T and pH_T, with associated temperatures and salinity, were
- input to CO2SYS (Lewis and Wallace, 1998) to calculate saturation state of CaCO₃ using the
- dissociation constants for carbonic acid of Dickson and Millero (1987), boric acid from
- 240 Dickson (1990b), sulphuric acid following Dickson (1990a) and the CO₂ solubility
- coefficients from Weiss (1974).

- 242 Satellite data on Chl *a*, photosynthetically available radiation (PAR) and sea surface
- temperature (SST) were obtained from the Aqua Moderate Resolution Image
- 244 Spectroradiometer (MODIS) as 4 km resolution, 8 day composites. Data were extracted as
- 245 averaged 3 x 3 pixel grids, centred on the sampling locations. Day length was calculated
- 246 according to Kirk (1994). The R/V *Meteor* was not fitted with a PAR sensor, thus satellite
- 247 measurements were the only available source of PAR data.

248 **2.6 Data availability**

- 249 Data included in the paper are available from the data repository PANGAEA via Daniels and
- 250 Poulton (2013) for the measurements of primary production, chlorophyll *a*, particulate
- 251 inorganic carbon and particulate silicate, cell counts of coccolithophores, diatoms and
- 252 microzooplankton; Esposito and Martin (2013) for measurements of nutrients; Paulsen et al.
- 253 (2014) for measurements of picoplankton and nanoplankton; and Bellerby (2014) for
- 254 measurements of the carbonate chemistry.

255 **3.** Results

256 **3.1 General oceanography**

The two sites were characterised by very different water column profiles throughout the study period. In the NWB, a pycnocline persisted over the upper 400 m with a variable mixed layer (20 - 100 m, Fig. 2D). In contrast, the ICB appeared well mixed over the upper 400 m when considered over the equivalent density range (Fig. 2A). However, weak unstable stratification was observed in the upper 100 m when examined over a much narrower range in density (Fig. 2A inset).

- 263 Sea surface temperature (SST) showed little variation at both sites (Table 1), while the ICB
- 264 (8.6 8.9 °C) was consistently warmer than the NWB (6.5 7.2 °C). Satellite estimates of
- 265 SST were colder than in situ measurements and exhibited greater variability (Fig. 3A).
- 266 However, the general pattern of the ICB being warmer than the NWB was observed from
- both in situ measurements and satellite derived ones. Sea -surface salinity (SSS), pH_T and Ω_{Ca}
- were relatively stable throughout the study with total ranges of 35.1 35.3, 8.0 8.1 and 3.0 -
- 269 3.2, respectively (Table 1).
- 270 Initial surface water concentrations of nitrate (NO₃) and phosphate (PO₄) were ~12 mmol N
- 271 m⁻³ and ~0.7-0.8 mmol P m⁻³ at both sites (Table 1). Silicic acid (dSi) was high throughout
- the study period (mostly > 4 mmol Si m^{-3}), with slightly higher concentrations in the NWB

(5.3 - 5.7 mmol Si m⁻³) than the ICB (< 5 mmol Si m⁻³). Drawdown of 1 mmol m⁻³ of NO₃
and dSi occurred in the ICB between the 19th and 27th April, but then returned to previous
levels by the 29th April. Nutrient drawdown did not occur in the NWB during the cruise
period.

277 Both sites showed a similar trend of increasing daily PAR during the study (Fig. 3B); a

twofold increase in the NWB (from 12.3 to 28.4 mol quanta $m^{-2} d^{-1}$) and a slightly smaller

increase in the ICB (from 13.5 to 24.3 mol quanta $m^{-2} d^{-1}$). Daily irradiance continued to

280 increase after the cruise finished, peaking around 40 - 45 days later at values in excess of 40

281 mol quanta m⁻² d⁻¹ (Fig. 3B). The general trend of increasing PAR was also reflected in the

day length (Fig. 3B). At both sites, the euphotic depth shoaled as the study progressed, from

283 115 m to 50 m in the ICB and from 80 m to 56 m in the NWB (Table 2). However, the

euphotic depth again deepened by 36 m between the 3rd and 4th visits to the ICB.

For the duration of the cruise until the 27th April (Day 118), surface and euphotic zone

integrated particulate silicate ($bSiO_2$) increased in the ICB, peaking at 0.66 mmol Si m⁻³ and

287 37.1 mmol Si m^{-2} , respectively (Fig. 4A, Table 2), with a significant decline in bSiO₂ after

this date. Lower values of bSiO₂, with little temporal variation, were found in the NWB,

although a small increase in surface bSiO₂ was observed between the 14th and 22nd April

290 (from 0.05 to 0.08 mmol Si m⁻³, Fig. 4A). Standing stocks of PIC were less variable than

bSiO₂. Highest surface values were observed during the last visit to the NWB (0.20 mmol C

 $292 m^{-3}$), while integrated calcite peaked at 11 mmol C m⁻² on the 27th April in the ICB (Table 2).

293 3.2 Chlorophyll a

294 Profiles of CTD fluorescence in the NWB had a relatively consistent structure with high

fluorescence in the stratified upper water column (Figs. 2E & 2F). Intra-site variation can be

seen in the relative fluorescence values in surface waters, but a consistent increase over time

was not observed. Fluorescence profiles in the ICB were more variable (Figs. 2B & 2C),

- ranging from profiles with high surface fluorescence (10th April, Day 101) to profiles with
- elevated fluorescence throughout the upper 300 m.
- 300 Acetone extracted measurements of chlorophyll a (Chl a) ranged from 0.1 to 2.3 mg m⁻³ with
- 301 highest values generally in surface waters (5 15 m). Surface Chl *a* was variable in the ICB,
- 302 with the lowest surface values $(0.27 0.31 \text{ mg m}^{-3})$ measured during the first visit (Table 2).
- 303 Peak Chl *a* values in the ICB occurred on the 10^{th} April (2.2 mg m⁻³), after which Chl *a*
- 304 declined reaching a low of 0.62 mg m⁻³ by the end of the study (but remaining above initial

- 305 Chl *a* values). Initial surface Chl *a* values were higher in the NWB (0.58 mg m^{-3}) than the
- 306 ICB, and generally increased throughout the cruise. However, the magnitude of this increase
- 307 was significantly smaller than in the ICB, peaking at only 0.93 mg m⁻³. Euphotic zone
- 308 integrated Chl *a* showed a similar pattern to surface Chl *a* across both stations, with highest
- 309 values on the 10^{th} April (ICB, 146.4 mg m⁻²).
- 310 Satellite estimates of Chl *a* also showed an increase in Chl *a* at both sites during the cruise
- 311 (Figs. 3C & 3D), although these values ($< 0.4 \text{ mg m}^{-3}$) were much lower than measured in
- 312 situ Chl *a* (Table 2). The large increase in Chl *a* associated with North Atlantic spring blooms
- 313 occurred between 20 and 30 days after the cruise (Figs. 3C & 3D). Both sites were
- 314 characterised by two peaks in Chl *a* throughout the year, one in late spring (mid-June) and
- another in late summer (mid-August). The largest satellite-derived Chl *a* values occurred in
- the ICB in late spring (1.7 mg m⁻³, Fig. 3C), while in the NWB, peak Chl *a* occurred during
- 317 the late summer bloom (1.6 mg m^{-3} , Fig. 3D).
- 318 Size fractionated Chl *a* revealed very different communities at the two sites (Table 2 and Fig.
- 5). Initially in the ICB, approximately a quarter of the Chl *a* biomass was derived from the >
- 320 10 µm fraction (24 28 %; Table 2, Fig. 5A). On subsequent visits this increased
- 321 significantly to 56 94 % (Table 2, Fig. 5A). A general trend of an increasing contribution
- 322 from the > 10 μ m fraction was also observed in those samples collected for more detailed
- 323 size fractionation (Fig. 5C). The detailed size fractionation showed that excluding the first
- 324 ICB visit where samples were not collected, the > $10 \,\mu m$ fraction was completely dominated
- 325 by the > 20 μ m fraction in the ICB (Fig. 5C). Conversely, the > 10 μ m fraction formed only a
- 326 minor component (< 21 %) of the Chl *a* biomass in the NWB, although the > 10 μ m
- 327 contribution did increase throughout the cruise (Table 2, Fig. 5B). Detailed size fractionation
- 328 in the NWB showed that the biggest increase in contribution came from the 2-10 μ m fraction,
- increasing from 14 % to 32 % (Fig. 5D), which was due to an increase in the absolute value
- 330 of 2 10 μ m Chl *a* (from 0.09 to 0.31 mg m⁻³).
- **331 3.3 Primary production**
- 332 Primary production (PP) in surface waters (5 15m) ranged from 0.41 to 4.89 mmol C m⁻³ d⁻¹
- in this study (Table 2), with PP generally decreasing with depth. Surface PP correlated well
- with euphotic zone integrated PP (r = 0.98, p < 0.001, n = 7). The largest change in PP
- 335 occurred in the ICB, between the 26th March and the 10th April, when peak PP rates were
- 336 observed in both the surface waters (4.89 mmol C m⁻³ d⁻¹) and integrated over the euphotic

zone (221.9 mmol C m⁻² d⁻¹, Table 2). Following this peak, PP in the ICB declined, although 337 it generally remained higher than pre-peak PP rates. The > 10 μ m PP fraction contributed 338 339 between 35 - 61 % of the total PP in the ICB. In contrast, the range and maximum rate of PP in the NWB was much lower than the ICB (0.67 - 1.11 mmol C m⁻³ d⁻¹, Table 2) with the > 340 $10 \,\mu\text{m}$ PP making up a much smaller fraction (< $20 \,\%$). However, a clear increase in the > $10 \,\mu\text{m}$ 341 µm PP fraction was observed between the 14th April (5 %) and the 25th April (20 %). The 342 general trend in total and size-fractionated PP at both sites reflected that observed in the Chl a 343 344 measurements.

345 **3.4 Community structure**

346 **3.4.1** Community structure – picoplankton and nanoplankton

347 Flow cytometry identified Synechococcus, autotrophic picoeukaryotes and autotrophic 348 nanoplankton ($< 10 \,\mu$ m) in relatively high abundance in all samples (Table 3). In general, 349 Synechococcus and picoeukaryotes were more abundant in the NWB than the ICB. In the NWB, a contrasting pattern between *Synechococcus*, nanoplankton and picoeukaryotes was 350 351 observed; while Synechococcus and the nanoplankton increased significantly from 2,617 to 5,483 cells mL⁻¹ and 484 to 1,384 cells mL⁻¹ respectively, a large decrease in picoeukaryotes 352 was also observed, from 18,016 to 8,456 cells mL⁻¹. A less coherent pattern was observed in 353 the ICB, where peak concentrations of both *Synechococcus* $(2,112 \text{ cells mL}^{-1})$ and 354 picoeukaryotes (6,982 cells mL⁻¹) occurred on the 19th April, with a general decline after this 355 356 date.

357 **3.4.2 Community structure – coccolithophores**

358 The coccolithophore species identified by polarised light microscopy were: *Emiliania*

359 huxleyi, Coccolithus pelagicus, Calcidiscus leptoporus, Coronosphaera mediterranea and

360 Syracosphaera pulchra. More detailed SEM observations found a number of other species at

361 low cell densities not clearly identified by the light microscope: Algirosphaera robusta,

362 Acanthoica quattrospina, Calciopappus caudatus, Gephyrocapsa muellerae, Syracosphaera

- 363 corolla, S. marginaporata, S. molischii, S. nodosa, S. ossa and unidentified Syracosphaera
- 364 spp. Many of these coccolithophore species have cell diameters between 10 and 20 μ m, with
- 365 the notable exceptions of *E. huxleyi*, *G. muellerae* and the smaller *Syracosphaera* spp.
- 366 (Young et al., 2003). Two morphotypes of *E. huxleyi* were observed in all samples (A and B)
- 367 with morphotype A consistently dominant (71 100 % of total *E. huxleyi* numbers). The

- 368 coccolithophore composition at both sites were similar, with *E. huxleyi* generally the most
- abundant species (4.4 28.1 cells mL⁻¹, Table 3) at both sites, while *Coccolithus pelagicus*
- 370 was present in all samples at relatively low cell densities $(0.15 2.79 \text{ cells mL}^{-1})$. The NWB
- 371 was also characterised by the presence of A. robusta (2.7 12.7 cells mL⁻¹), while S.
- 372 *marginaporata* $(0 21.3 \text{ cells mL}^{-1})$ was only present in the ICB.
- 373 A general increase in coccolithophore abundance was observed in the ICB, with a large
- 374 increase between the 10th and 18th April (7.7 42.8 cells mL⁻¹). *Emiliania huxleyi* abundance
- decreased between the 27th and 29th April (26.7 13.2 cells mL⁻¹), but *C. pelagicus* remained
- 376 relatively constant (0.81 0.84 cells mL⁻¹). In the NWB, coccolithophores generally followed
- 377 the trend of increasing Chl *a* with increases in abundance over time (Table 3). Within the
- 378 coccolithophore communities, the largest relative increase in species abundance was by *C*.
- 379 *pelagicus* with a sevenfold increase (0.38 to 2.66 cells mL⁻¹) between the 14^{th} and 22^{nd} of
- 380 April in the NWB.

381 3.4.3 Community structure – diatoms and microzooplankton

- 382 The diatom taxa identified by light microscopy were: *Chaetoceros*, *Cylindrotheca*,
- 383 Dactyliosolen, Guinardia, Leptocylindrus, Navicula, Pseudo-nitzschia, Rhizosolenia,
- 384 *Thalassionema*, and *Thalassiosira*. Whilst samples for diatom counts were collected only
- 385 once per visit to each station, particulate silicate (bSiO₂) samples were collected from two
- 386 CTD casts per visit. As the major source of bSiO₂, the significant variability observed in
- 387 bSiO₂ between the two CTD casts at each visit (Fig. 4A) suggested a temporal variability in
- the diatom cell abundance not captured in the Lugol's counts. Therefore, diatom abundance
- 389 counts were supplemented using SEM image based diatom counts from samples collected
- 390 from those CTDs where Lugol's samples were not collected (Fig. 4B). However, due to the
- 391 relatively smaller volumes examined by SEM (~ 4.2 mL versus 50 mL), there is a greater
- inherent error in the counts and as such Lugol's counts were used wherever possible.
- 393 The diatom community was highly variable in the ICB (Fig. 4). Initially present only in very
- 394 low abundances (1.3 cells mL⁻¹, Table 3), a peak concentration of 249 cells mL⁻¹ was reached
- 395 15 days later on the 10th April (Day 101). The population then decreased over the rest of the
- 396 study, down to 88 cells mL⁻¹, but remained above initial levels. A shift in composition was
- 397 observed after the population peaked, from a *Chaetoceros* dominated community (67 71 %)
- 398 on the 7th to 10th April (Days 98 to 101) to one dominated by *Pseudo-nitzschia* (65 73 %,
- Fig. 4B) on the 27th to 29th April (Days 118 to 120). Diatoms were virtually absent from light

400 microscope measurements of the NWB, reaching a maximum of only 0.5 cells mL⁻¹ (Table
401 3).

402 The main microzooplankton groups present were planktonic ciliates and small ($\sim 5 - 10 \,\mu m$)

403 naked dinoflagellates (e.g. *Gyrodinium* and *Gymnodinium*). Microzooplankton concentrations

404 were ~ 4 times higher in the NWB (10.8 - 17.6 cells mL⁻¹, Table 3) than in the ICB (2.5 - 4.7

405 cells ml⁻¹, Table 3). Dinoflagellates initially dominated in the NWB (8.5 cells mL⁻¹), but were

406 succeeded by ciliates $(11.9 - 12.9 \text{ cells mL}^{-1})$. Both dinoflagellates and ciliates were present

407 in similar concentrations in the ICB, except for the final visit, when dinoflagellates 408 dominated (4.2 cells mL⁻¹).

409 **4. Discussion**

410 **4.1** Time series or mixing?

411 The dynamic nature of the ocean causes inherent difficulties in interpreting data collected 412 from fixed-point, Eulerian time-series, such as those in this study. The distribution of 413 phytoplankton in the ocean exhibits significant heterogeneity, which can be driven by 414 mesoscale physical processes (Martin, 2005). Therefore, Eulerian time-series are vulnerable 415 to advection such that instead of repeatedly sampling the same phytoplankton community, 416 each sample is potentially from a different population, possibly with a different composition. 417 Before examining the development of the phytoplankton community, it is therefore necessary 418 to consider the physicochemical environment. Eddies and other mesoscale features would 419 potentially cause significant variations in measured SST, SSS, nutrients and carbonate 420 chemistry. With the possible exception of the nutrient concentrations, which will also be 421 affected by the biology present, the measured physicochemical parameters were stable 422 throughout the study period (Table 1). Therefore, although we cannot rule out the influence 423 of mesoscale features and advection during the study, the relative consistency of the sampled 424 physicochemical environment suggests that the community structure is representative of the 425 location, rather than from multiple eddies, and thus we can examine how the community 426 developed during the cruise and compare between two geographically separated sites.

427 **4.2 Drivers of the phytoplankton bloom**

Density profiles in the Iceland Basin (ICB) were seemingly indicative of a well-mixed water
column (Fig. 2A), yet elevated fluorescence in the upper 100 m of the water column suggests
that phytoplankton cells were not being evenly mixed throughout the water column (Fig. 2B).

431 A detailed examination of the upper 100 m found small changes in the density profiles (Fig.

432 2A inset), corresponding to the elevated fluorescence, however the change in density with

433 respective to depth was smaller ($\Delta \sigma_t < 0.025$ over 1 m) than most metrics used to identify

434 mixed layers (e.g. Kara et al., 2000). Elevated fluorescence with only minimal stratification is

435 consistent with the critical turbulence hypothesis (Huisman et al., 1999); here it is likely that

- 436 active mixing had ceased, allowing phytoplankton net growth, while the response of the
- 437 physical environment was slower than the biological response, and stratification was only just438 beginning to develop.
- 439 Although ICB upper water column fluorescence was elevated throughout the study, there was
- 440 significant variation in the magnitude and structure of the fluorescence profiles (Figs. 3B &
- 441 3C), as well as a peak and decline in surface chlorophyll *a* (Chl *a*) and primary production
- 442 (PP). The general theory of bloom formation is that once conditions are favourable for bloom
- 443 formation, the pre-bloom winter ecosystem will transition into a blooming ecosystem,
- 444 identifiable by increasing Chl *a* biomass and PP. However, we did not observe this smooth

transition. Instead we observed periods of stability, characterised by increased stratification,

- 446 Chl *a* and PP, followed by periods of instability where increased mixing weakened the
- 447 developing stratification. Increased mixing detrains phytoplankton out of the surface waters,
- 448 reducing both Chl *a* biomass and PP, and exporting them to depth (Giering et al., *in review*).
- 449 One such mixing event occurred between the 27th and 29th April (Days 118 and 120), where 450 minor stratification ($\Delta \sigma t = 0.019$) disappeared ($\Delta \sigma t < 0.001$) over the upper 25 m, surface Chl
- 451 *a* halved from 1.18 mg m⁻³ to 0.62 mg m⁻³, and the fluorescence profile became well-mixed 452 (Fig. 2C). Furthermore, surface nutrients were replenished (Table 1), all of which are
- 453 indicative of a mixing event.
- 454 The transition period from winter to spring was also observed in satellite data from the ICB. 455 Bloom metrics (Siegel et al., 2002; Henson et al., 2009) of satellite Chl a estimate that the 456 main spring bloom did not begin until ~ 20 days after our study period (dashed line in Fig. 3C). However, there was a significant increase (r = 0.99, p < 0.015, n = 4) in Chl a during 457 458 the study period (Fig. 3C inset), consistent with our in situ observations, that suggests that 459 while the environment was not yet stable enough for sustained and rapid phytoplankton 460 growth, intermittent net phytoplankton growth did occur. Therefore, we suggest that the early 461 stages of a spring bloom are characterised by periods of instability and net growth, and that 462 rather than a single smooth transition into a bloom, for a period of weeks prior to the main 463 spring bloom event, phytoplankton form temporary mini-blooms during transient periods of
 - 15

stability. The export flux from these pre-bloom communities is a potentially significant foodsource to the mesopelagic (Giering et al., *in review*).

466 In contrast to the instability of the ICB, the Norwegian Basin (NWB) was relatively stable 467 with a strong and persistent pycnocline (Fig. 2D), as well as elevated fluorescence in the 468 upper mixed layer (Fig. 2E). However, a variable mixed layer that did not consistently 469 shallow in the NWB (Fig. 2D) suggests variability in the strength of the physical forcing, that 470 may explain why although Chl a and PP increased throughout the cruise, they remained 471 below that observed in the ICB during the study period (Table 2). Furthermore, the net 472 community growth rate (Chl *a* derived, μ_{Chl}), was relatively low (0.02 d⁻¹), suggesting that as 473 was the case for the ICB, the main spring bloom was yet to start. This was also confirmed 474 from the satellite Chl a, which showed a very similar pattern to the ICB: although Chl a 475 increased during our study period (Fig. 3D inset), the main bloom did not start until ~ 20 days 476 later (Fig. 3D). Therefore despite very different physical environments, the two sites both 477 represented early stages in the development of spring blooms. 478 Unlike the ICB, the factors limiting bloom formation in the NWB cannot easily be attributed

- to the physicochemical environment. A switch from negative to positive net heat flux has
- 480 been linked to spring bloom formation (Taylor and Ferrari, 2011b; Smyth et al., 2014), but
- 481 here the net heat flux was negative for the majority of the study at both sites (C. Lindemann,

482 pers. comm., Giering et al., *in review*). Irradiance is a key driver of phytoplankton growth and 483 bloom formation; the main spring bloom did not occur until daily PAR reached its seasonal maximum of 45 mol photons m⁻² d⁻¹ (Figs. 3B, 3C & 3D). The general increase in daily PAR 484 485 over our study period was coupled with an increase in Chl a and PP in the NWB, suggesting 486 that despite a stratified environment, irradiance was an important driving factor. Although the 487 magnitude of the daily flux of PAR at both sites was similar, Chl a and PP were higher in the 488 less stable ICB than the NWB, suggesting that irradiance was not the only driver of the NWB 489 phytoplankton community. Irradiance levels can also have a secondary influence on the 490 requirements for phytoplankton growth. While macronutrients were replete at both sites, we 491 did not measure micronutrients such as iron (Fe). The cellular Fe demand increases in low

- 492 light conditions (Moore et al., 2006), and as such Fe may be limiting at this early stage of
- 493 bloom formation in the Norwegian Basin. However, without measurements of Fe (or
- 494 phytoplankton photophysiology), we cannot directly test this hypothesis. Although
- 495 temperature limits phytoplankton gross growth rates (Eppley, 1972), the relatively small

- difference in temperature between the NWB and the ICB (~1.5 2.5 °C) is unlikely to have a
 significant impact on gross growth rates (Eppley, 1972).
- 498 Besides physicochemical drivers of bloom formation, the plankton community itself can play 499 a large role in the development and formation of a bloom. Physiological parameters such as 500 net growth rates (μ_{Chl}) and 'assimilation efficiency' (i.e. PP normalised to biomass, in this 501 case Chl a) can provide an insight into the state of the phytoplankton community. The NWB 502 community had a noticeably lower assimilation efficiency (13.5 - 15.8 g C [g Chl a]⁻¹ d⁻¹) than that in the ICB (15.7 - 27.0 g C [g Chl a]⁻¹ d⁻¹), thus the relative increase in biomass in 503 504 the NWB was slower, as reflected in the growth rates where the maximum estimated (net) 505 growth rate in the NWB ($\mu_{Chl} = 0.05 \text{ d}^{-1}$) was much lower than in the ICB ($\mu_{Chl} = 0.22 \text{ d}^{-1}$). 506 Assimilation efficiency varies with both environmental conditions and species composition, 507 and therefore the composition of the phytoplankton community is likely to be another key
- 508 driver behind the contrasting phytoplankton dynamics observed in the ICB and NWB.

509 **4.3** Overall community composition

- 510 The contrasting structures of Chl a and PP size fractions observed at the two sites (Fig. 5, 511 Table 2), were reflected in the contrasting composition of the phytoplankton communities 512 (Table 3). In the ICB, a change in dominance in both Chl a and PP, from $< 10 \,\mu\text{m}$ to the > 10µm fraction, occurred as the diatom abundance increased between the 26th March and the 7th 513 514 April. An increase in the abundance of the $< 10 \,\mu m$ community was also observed during this 515 period, composed mainly of < 2 µm *Synechococcus* and pico-eukaryotes (Table 3, Fig. 5C). 516 However, with most of the diatom population having cells > $20 \,\mu m$ (Fig. 5C), their relatively 517 large size allowed the diatoms to dominate both the Chl a and PP while remaining 518 numerically inferior. The decline in total Chl a and PP later in our study was reflected by a 519 decreasing abundance of most of the phytoplankton community (Table 3). However, the 520 relative decrease of pico-phytoplankton (Synechococcus and picoeukaryotes) was greater 521 than that of the diatoms, such that the > 10 μ m fraction increased its dominance for both Chl a (94 %) and PP (61 %). Therefore, although surface Chl a and PP declined after the 'mini-522 bloom event' which peaked around the 10th April, the community structure did not return to a 523 524 pre-bloom composition, but instead remained dominated by diatoms.
- 525 Interestingly, the phytoplankton response to the increased diatom abundance was not
 526 uniform, with the nanoplankton abundance decreasing and *Synechococcus* increasing only
- 527 after the peak in diatom abundance. Thus, we observed that the phytoplankton community
 - 17

- response during the spring bloom was not universal across functional types as has beenpreviously observed elsewhere (Brown et al., 2008).
- 530 In contrast to the ICB, a large shift in the NWB community was not observed. Pico-
- 531 eukaryotes dominated both in terms of abundance (Table 3) and Chl *a*, through the $< 2 \,\mu m$
- 532 fraction (Fig. 5D). This is consistent with previous observations of early stage spring blooms
- 533 (Joint et al., 1993). Although the $< 2 \mu m$ Chl *a* fraction showed little variation throughout the
- study (0.45 0.58 mg m⁻³), variation in the $< 2 \mu m$ phytoplankton composition did occur,
- 535 with an apparent succession from pico-eukaryotes to *Synechococcus* and nanoplankton. This
- 536 may represent a community shift early in development of the spring bloom or may
- 537 demonstrate the inherent variability within pre-bloom communities.
- 538 The increase in total Chl a in the NWB was driven primarily by the 2 to 10 μ m fraction,
- 539 which was likely composed of the nanoplankton, which itself had a threefold increase in
- 540 population size (from 484 to 1384 cells mL⁻¹, Table 3). The phytoplankton responsible for the
- observed increase in the >10 μ m Chl *a* and PP fraction cannot be confidently determined;
- 542 large diatoms were absent and thus could not contribute. The microzooplankton population
- 543 consisted of ciliates and dinoflagellates (*Gyrodinium* and *Gymnodinium*), both of which have
- been reported to be mixotrophic (Putt, 1990; Stoecker, 1999), and thus could potentially have
- 545 contributed to the Chl *a* measurements. Furthermore, it is possible that part of the
- 546 nanoplankton community, as measured by flow cytometry, was $> 10 \,\mu$ m and thus the
- 547 increasing concentration of nanoplankton could also contribute to the increase in the > $10 \,\mu m$ 548 fraction.

549 **4.4** Relative independence of the coccolithophore community

550 The traditional view on the seasonality of coccolithophores is that they succeed the diatom 551 spring bloom, forming coccolithophore blooms in late summer. However, here we observed a 552 typical North Atlantic community of coccolithophores (Savidge et al., 1995; Dale et al., 553 1999; Poulton et al., 2010), growing alongside the ICB diatom bloom, rather than just 554 succeeding the diatoms. This is consistent with the "rising tide" hypothesis of Barber and 555 Hiscock (2006), as well as observations from both in situ (Leblanc et al., 2009) and satellite 556 measurements (Hopkins et al., in review) suggesting that coccolithophores are present in 557 North Atlantic spring blooms. Despite the contrasting environment and overall community 558 structure of the NWB, the coccolithophore dynamics were similar, appearing independent of 559 the overall community dynamics. Species-specific growth rates of coccolithophores

- 560 (calculated from changes in cell concentration) found that *E. huxleyi* had the same net growth
- rate at both sites ($\mu = 0.06 \text{ d}^{-1}$), while the net growth rate of *C. pelagicus* was comparable to
- 562 *E. huxleyi* in the ICB, but was slightly higher in the NWB ($\mu = 0.13 \text{ d}^{-1}$). Culture experiments
- 563 of *E. huxleyi* and *C. pelagicus* have found comparable gross growth rates at temperatures
- below 10 °C (Daniels et al., 2014), and our in situ observations support this conclusion. That
- 565 *C. pelagicus* has higher net growth rates could also be indicative of higher grazing on the
- 566 relatively smaller *E. huxleyi* (Daniels et al., 2014).

567 **4.5 Contrasting patterns of diatoms**

568 The diatom bloom in the ICB, which began between the 26th March (Day 86) and the 7th 569 April (Day 98), was initially dominated by *Chaetoceros* (71 - 67 % of total cell numbers, Fig. 570 4B). As the community developed however, Pseudo-nitzschia succeeded as the dominant diatom genera (65 - 73 % of total). Both Chaetoceros and Pseudo-nitzschia are common 571 572 spring bloom diatoms (Sieracki et al., 1993; Rees et al., 1999; Brown et al., 2003), with 573 Chaetoceros often dominant in the earlier stages of North Atlantic spring blooms (Sieracki et 574 al., 1993; Rees et al., 1999). Resting spores of Chaetoceros have also been observed to 575 dominate the export flux out of the Iceland Basin during the North Atlantic spring bloom in 576 May 2008 (Rynearson et al., 2013), suggesting dominance of the spring bloom prior to this 577 period, consistent with the early community observed in our study.

- 578 *Pseudo-nitzschia* (previously identified as *Nitzschia* in other studies), tends to dominate later
- 579 in the spring bloom (Sieracki et al., 1993; Moore et al., 2005), also consistent with this study.
- 580 This suggests that as a genera, *Chaetoceros* are either able to adapt more quickly than
- 581 *Pseudo-nitzschia*, or that they have a wider niche of growing conditions through a large
- 582 diversity of species. However, once established, *Pseudo-nitzschia* are able to outcompete
- 583 *Chaetoceros*, resulting in a community shift. That the succession of the diatom community
- observed in the ICB is consistent with that expected in the main diatom spring bloom,
- suggests that a mini-diatom bloom occurred prior to the formation of the main spring bloom.
- 586 The observed variability in the relationship between diatoms (the main source of bSiO₂) and
- 587 bSiO₂ was likely due to the species-specific variability in the cellular bSiO₂ content of
- 588 diatoms (Baines et al., 2010). The abundance of *Pseudo-nitzschia*, rather than *Chaetoceros*,
- best explained the trend in bSiO₂ (r = 0.92, p < 0.001, n = 8), suggesting that *Pseudo*-
- 590 *nitzschia* was the major producer of bSiO₂. Previously *Chaetoceros* has been observed as the

591 major exporter of bSiO₂ in the Iceland Basin (Rynearson et al., 2013). Here, as the major

592 producer of bSiO₂, *Pseudo-nitzschia* has the potential to also be the major exporter of bSiO₂.

- In contrast to the ICB, diatoms appeared to be virtually absent (< 0.5 cells mL⁻¹) in the NWB. 593 594 While the dSi:NO₃ ratio was below the 1:1 requirement for diatoms, consistent with previous 595 studies of North Atlantic blooms (Leblanc et al., 2009), dSi did not become depleted (always above 5 mmol Si m⁻³, Table 1) and thus was not limiting. Furthermore, significant and 596 597 increasing concentrations of particulate silicate (bSiO₂) were measured throughout the cruise 598 (Fig. 4A). As the main source of bSiO₂, diatoms would therefore be expected to be present. 599 Although absent in the Lugol's counts, examination of SEM images found significant 600 numbers (101 - 600 cells mL⁻¹) of small ($< 5 \mu$ m) diatoms (predominantly *Minidiscus* spp.) 601 that were too small to be identified by light microscopy. However, they may still constitute 602 an important component of the nanoplankton, as measured by flow cytometry. As a result of 603 their small cell size, nano-sized diatoms, such as *Minidiscus*, are easily missed when 604 identifying and enumerating the phytoplankton community, and as such their potential 605 biogeochemical importance may be greatly underestimated (Hinz et al., 2012). Other nano-606 sized diatom species have been observed as major components of the phytoplankton 607 community on the Patagonian Shelf (Poulton et al., 2013), in the Scotia Sea (Hinz et al.,
- 608 2012), the northeast Atlantic (Boyd and Newton, 1995; Savidge et al., 1995) and in the
- 609 Norwegian Sea (Dale et al., 1999).
- 610 The *Minidiscus* spp. observed in this study exhibited a significant increase in population size
- during the study, from initial concentrations of 100 to 200 cells mL^{-1} , then up to 600 cells
- 612 mL⁻¹ by the end of the study, and correlating well with both bSiO₂ (r = 0.93, p < 0.01, n = 6),
- 613 and Chl *a* (r = 0.93, p < 0.01, n = 6). Furthermore, the increasing concentration of
- 614 *Minidiscus* corresponded to the increase in the 2 to 10 µm Chl *a* size fraction (Fig. 5D). The
- 615 maximum net growth rate of *Minidiscus*, estimated from changes in cell abundances ($\mu =$
- 616 0.13 d⁻¹), was significantly higher than that calculated for the total community using Chl a
- $(\mu_{Chl} = 0.05 \text{ d}^{-1})$. While different methods were used to determine these growth rates, it does
- 618 suggest that conditions were favourable for the small nano-sized diatoms to grow more
- 619 rapidly than the bulk community.
- 620 The question therefore remains as to why the larger (> $10 \mu m$) diatoms were virtually absent
- 621 in an environment that is physically stable and nutrient replete, while small diatoms were able
- 622 to thrive? The fate and ecology of overwintering oceanic diatoms is poorly understood. Many
- 623 diatom species, both neritic and pelagic, are capable of forming resting stages that sink post

624 bloom (Smetacek, 1985; Rynearson et al., 2013), yet diatoms must be present in spring when 625 the diatom bloom begins. Therefore, either a diatom population is sustained in the upper 626 water column over winter (Backhaus et al., 2003), or the spring diatom community is sourced 627 from elsewhere (horizontally or vertically). In relatively shallow coastal environments, 628 benthic resting stages overwinter until spring when they are remixed up into the water 629 column, providing the seed population for the spring bloom (McQuoid and Godhe, 2004). It 630 is unlikely that oceanic diatom blooms are seeded from the sediment, as the depths are far too 631 great for remixing. However, viable diatom cells have been observed suspended at depth (> 632 1000 m) in the ocean (Smetacek, 1985), and it is possible that these suspended deep 633 populations are remixed to seed the spring bloom. An alternative hypothesis is based on the 634 observation that diatom blooms generally occur first in coastal waters before progressing to 635 the open ocean (Smetacek, 1985), suggesting that coastal diatom populations are horizontally 636 advected into pelagic waters, thus seeding the spring bloom in the open ocean from shelf 637 waters. The location of the source coastal populations, and their transit time to the open ocean 638 location, would then affect the timing of the diatom blooms 639 With such low concentrations of > 10 μ m diatoms (< 0.5 cells mL⁻¹) in the NWB, it is

640 possible that the overwintering diatom population was too small to seed the spring bloom.

641 Grazing pressure by microzooplankton and mesozooplankton may influence the composition

and timing of the onset of the spring bloom (Behrenfeld and Boss, 2014). The potential

643 grazing pressure from the significant microzooplankton population (10.8 - 17.6 cells mL⁻¹) in

644 the NWB may have exerted such a control on the observed diatom population that it could

not develop into a diatom bloom. Instead an alternative seed population of diatoms may be
 required to overcome the grazing pressure and initiate the diatom bloom in the NWB.

647 Whether the absence of large diatoms is a regular occurrence in the NWB, or whether inter-

648 annual shifts between small and large diatoms occur, as observed in the northeast Atlantic

649 (Boyd and Newton, 1995), will have significant implications for export and the functioning

of the biological carbon pump. The absence of larger diatoms in pelagic spring blooms in the

Norwegian Sea has also been observed by Dale et al. (1999), and it may be that large diatoms

- are completely absent from the pelagic south east Norwegian Sea. The lack of large diatoms
- 653 in the NWB could explain the seasonal profile of satellite Chl *a* (Fig. 3D); with no large
- diatoms present, the spring bloom is less intense, peaking at only ~60 % of the Chl *a*

655 concentration found in the ICB.

656 Clearly, further work is required to examine why large diatoms are absent from the initial
657 stages of the spring bloom in the NWB, and whether they ever become abundant in this
658 region.

659 **5.** Conclusions

660 During March-May 2012, satellite and in situ data from study sites in the Iceland Basin (ICB) and the Norwegian Basin (NWB) suggested that despite very different physical 661 662 environments, the two sites both represented early stages in the development of the North 663 Atlantic spring bloom. Spring bloom initiation in the ICB was limited by the physical 664 environment, with periods of increased mixing inhibiting bloom formation. The 665 physicochemical environment alone was not limiting bloom formation in the NWB as, in 666 spite of a stable stratified water column and ample nutrients, Chl *a* biomass and primary production were relatively low. Phytoplankton efficiency (Chl *a* -normalised primary 667 668 production) was also lower in the NWB, suggesting that the phytoplankton community 669 composition and/or physiology was also a limiting factor in bloom formation.

670 The phytoplankton community in the NWB was dominated by the $< 2 \mu m$ Chl *a* fraction,

671 with high concentrations of pico-eukaryotes (\sim 18,000 cells mL⁻¹) succeeded by

672 Synechococcus and nanoplankton. In contrast, although the initial dominance of the $< 10 \,\mu m$

673 Chl *a* fraction (pico-eukaryotes and nanoplankton) was succeeded by diatoms dominating in

674 the > 10 μ m Chl *a* fraction, the ICB phytoplankton community generally followed the "rising

tide" hypothesis, with most of the community positively responding to the onset of the

676 diatom bloom. Interestingly, coccolithophore dynamics were similar at both sites,

677 independent of the overall community, with similar concentrations of the main species

678 Emiliania huxleyi and Coccolithus pelagicus.

679 In terms of the diatom community, *Chaetoceros* initially dominated the ICB diatom bloom,

680 but was replaced by *Pseudo-nitzschia* as the bloom progressed, suggesting *Chaetoceros* as a

681 key species in diatom bloom formation, while *Pseudo-nitzschia* was the major source of

682 particulate silicate (bSiO₂). The lack of large (> $10 \mu m$) bloom forming diatoms in the NWB,

683 while small (< 5 μ m) diatoms were present in high numbers (101 - 600 cells mL⁻¹), suggests

that micro-zooplankton grazing, coupled with a potential lack of a seed population, was

restricting diatom growth in the NWB, or that large diatoms are absent in NWB spring

686 blooms.

687 These results suggest that despite both phytoplankton communities being in the early stage of 688 bloom formation and exhibiting positive net growth rates, different physicochemical and 689 biological factors control bloom formation with the resulting blooms likely to be significantly 690 different in terms of biogeochemistry and trophic interactions throughout the growth season. 691 Clearly, more in situ studies are needed in the transitional period between winter and the peak 692 productivity of the spring bloom to examine compositional differences, growth and mortality 693 factors, and how regional variability impacts on upper ocean biogeochemistry and deep-sea 694 fluxes of organic material. Coupled studies of satellite derived products, including bloom 695 phenology and phytoplankton physiology, and in situ processes are needed to examine the 696 full spectrum of factors forming the spring bloom.

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Table 1: Physicochemical features of the Iceland Basin and Norwegian Basin stations: SST, sea surface temperature; SSS, sea surface salinity;

2 CT, dissolved inorganic carbon; ΩC, calcite saturation state; NO3, nitrate; PO4, phosphate; dSi, silicic acid.

						Carbonate Chemistry			Surface	Surface Macronutrients			
Location	Sta	Date	Day of Year	SST (°C)	222	$C_{\rm T}$ (umol m ⁻³)	nHr	0 ₀	NO ₂		dSi		
Iceland Basin	1	25 Mar	$\frac{10}{1000} \text{ Mar} \qquad 85 \qquad 8.7$		35.3	2149	8.0	31	12.3	0.79	4 7		
Teetand Dushi	1	25 Mar 86 8.7		87	35.3	2148	8.0	3.1	12.5	0.81	47		
	1		80	0.7	55.5	2148	0.0	5.1	12.0	0.01	4.7		
	2	7 Apr	98	8.7	35.3	2140	8.0	3.1	12.4	0.81	4.5		
	2	10 Apr	101	8.7	35.3	2139	8.1	3.2	11.5	0.75	4.3		
	3	18 Apr	109	8.8	35.3	2144	8.1	3.2	11.6	0.79	4.3		
	3	19 Apr	110	8.7	35.3	2150	8.1	3.2	11.9	0.76	4.1		
	4	27 Apr	118	8.9	35.3	2135	8.1	3.2	10.7	0.70	3.1		
	4	29 Apr	120	8.6	35.3	2148	-	-	12.0	0.80	4.2		
Norwegian	1	30 Mar	90	7.0	35.2	2142	8.1	3.0	12.1	0.67	5.3		
Basin	1	31 Mar	91	7.1	35.2	2161	8.1	3.0	12.5	0.81	5.4		
	2	12 Apr	103	7.2	35.2	2153	8.1	3.0	13.4	0.84	5.6		
	2	14 Apr	105	6.9	35.2	2152	8.1	3.0	13.5	0.82	5.6		
	3	22 Apr	113	6.5	35.1	2150	8.1	3.0	12.2	0.79	5.7		
	3	25 Apr	116	6.8	35.2	2143	8.1	3.0	12.5	0.82	5.7		

- **Table 2:** Biological features of the Iceland Basin and Norwegian Basin stations: Chl *a*, chlorophyll *a*; PP, primary production; bSiO₂, particulate
- 6 silicate; PIC, particulate inorganic carbon.

						Surface size fractions			Euphotic zone integrals					
Location	Sta.	Date	Day of Year	Surface Chl $a (mg m^{-3})$	Surface PP (mmol C m ⁻³ d ⁻¹)	>10 µm Chl <i>a</i> (%)	>10 µm PP (%)	Euphotic zone depth (m)	Chl a (mg m ⁻²)	bSiO ₂ (mmol Si m ⁻²)	PIC (mmol C m ⁻²)	PP (mmol C m ⁻² d ⁻¹)		
Iceland	1	25 Mar	<mark>85</mark>	0.27		28		115	22.3	8.3	7.7			
Basin	1	26 Mar	<mark>86</mark>	0.31	0.41	24	35	115	26.5	2.5	4.5	22.2		
	2	7 Apr	<mark>98</mark>	1.13		80		72	61.4	8.7	8.7			
	2	10 Apr	101	2.18	4.89	84	61	72	146.4	19.6	6.9	221.9		
	3	18 Apr	<mark>109</mark>	1.01		56		50	49.2	13.4	6.5			
	3	19 Apr	110	1.15	2.11	67	40	50	55.6	15.4	5.8	58.0		
	4	27 Apr	<mark>118</mark>	1.18		-		86	75.7	37.1	11.0			
	4	29 Apr	120	0.62	1.19	94	61	86	55.3	27.6	8.1	61.5		
Norwegian Basin	1	30 Mar	<mark>90</mark>	0.58		6		80	34.6	5.5	7.7			
	1	31 Mar	<mark>91</mark>	0.59	0.67	7	5	80	39.2	7.0	7.1	27.3		
	2	12 Apr	103	0.54		9		65	32.3	4.4	5.9			
	2	14 Apr	105	0.69	0.90	13	5	65	37.2	4.4	6.4	38.2		
	3	22 Apr	113	0.93		10		56	46.7	5.0	9.7			
	3	25 Apr	116	0.84	1.11	21	20	56	40.5	6.4	10.5	39.8		

Table 3: Surface phytoplankton abundance at the Iceland Basin and Norwegian Basin stations, measured by flow cytometry (*Synechococcus*,

10 pico-eukaryotes and nanoplankton), inverted microscopy (diatoms and microzooplankton) and polarizing light microscopy (coccolithophores).

					Phytoplankton abundance (cells mL ⁻¹)									
										Coccolithophores				
Location	Sta.	Date	Day of Year	Depth (m)	Synechococcus	Pico- eukaryotes	Nanoplankton (<10 µm)	Diatoms (>10 µm)	Micro- zooplankton	E. huxleyi	C. pelagicus	A. robusta	Others	
Iceland Basin	1	25 Mar	<mark>85</mark>	<mark>5</mark>	-	-	-	-	-	7.5	0.15		1.2	
	1	26 Mar	<mark>86</mark>	<mark>15</mark>	675	2347	1116	1.3	2.5	4.4	0.22		0.5	
	2	7 Apr	<mark>98</mark>	<mark>5</mark>	400	3375	215	-	-	5.2	0.19		4.1	
	2	10 Apr	<mark>101</mark>	<mark>10</mark>	480	6715	813	249.2	4.0	6.8	0.15		0.7	
	3	18 Apr	<mark>109</mark>	<mark>5</mark>	-	-	-	-	-	16.9	0.22		25.6	
	3	19 Apr	<mark>110</mark>	7	2112	6962	712	151.3	2.8	21.9	0.69		22.3	
	4	27 Apr	<mark>118</mark>	<mark>8</mark>	1299	1486	298	-	-	26.7	0.81		7.9	
	4	29 Apr	120	11	782	1215	313	87.8	4.7	13.2	0.84		7.5	
Norwegian	1	30 Mar	<mark>90</mark>	<mark>8</mark>	-	-	-	-	-	6.1	0.09	4.8	2.9	
Basin	1	31 Mar	<mark>91</mark>	<mark>10</mark>	2617	18016	484	0.2	10.8	7.2	0.28	3.8	1.0	
	2	12 Apr	103	<mark>8</mark>	-	-	-	-	-	11.8	0.41	2.7	0.3	
	2	14 Apr	105	10	3372	10433	858	0.1	17.6	16.0	0.38	3.7	5.1	
	3	22 Apr	113	7	-	-	-	-	-	27.9	2.66	12.7	11.7	
	3	25 Apr	<mark>116</mark>	7	5483	8456	1384	0.5	14.0	28.1	2.79	7.8	8.6	

13 Figure Captions

- 14 Fig. 1: Sampling locations in the Iceland Basin (ICB) and the Norwegian Basin (NWB),
- superimposed on a composite of MODIS sea surface temperature for 25 March 29 April
 2012.
- 17 **Fig. 2:** Upper water column profiles for the ICB (A, B, C) and the NWB (D, E, F), of A,D)
- 18 density, B,E) CTD fluorescence and C,F) CTD fluorescence normalised to peak CTD
- 19 fluorescence for each profile.
- 20 Fig. 3: Seasonal variation in A) satellite sea surface temperature (SST), B) satellite daily
- 21 incidental PAR and day length and C,D) satellite chlorophyll *a* (Chl *a*) for C) the Iceland
- 22 Basin (ICB) and D) the Norwegian Basin (NWB) for 2012. The grey region indicates the
- 23 period of the cruise. The vertical dotted lines in plots C and D indicate bloom initiation,
- 24 calculated following Henson et al. (2009). The insets in C & D show the variation in satellite
- 25 chlorophyll during the period of the cruise.
- 26 **Fig. 4:** Surface (5-15 m) measurements of A) Particulate silicate (bSiO₂) and B) diatom
- 27 species abundance in the Iceland Basin. Black symbols indicate where diatoms were counted
- 28 from Lugol's samples, while open symbols indicate SEM counts.
- 29 **Fig. 5:** Size fractionated chlorophyll *a* (Chl *a*) for A, C) the Iceland Basin, and B, D) the
- 30 Norwegian Basin. Plots A and B show the $< 10 \,\mu$ m and $> 10 \,\mu$ m fractions, C and D show the
- 31 < 2 μ m, 2-10 μ m, 10-20 μ m, and > 20 μ m fractions.
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