Iron limitation of the postbloom phytoplankton communities in the Iceland Basin

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Measurements performed on a cruise within the central Iceland Basin in the high-latitude (>55°N) North Atlantic Ocean during late July to early September 2007 indicated that the concentration of dissolved iron (dFe) in surface waters was very low, with an average of 0.093 (±0.010–0.218, n = 43) nM, while nitrate concentrations ranged from 2 to 5 μM and in situ chlorophyll concentrations ranged from 0.2 to 0.4 mg m⁻³. In vitro iron addition experiments demonstrated increased photosynthetic efficiencies (Fv/Fm) and enhanced chlorophyll accumulation in treatments amended with iron when compared to controls. Enhanced net growth rates for a number of phytoplankton taxa including the coccolithophore Emiliania huxleyi were also observed following iron addition. These results provide strong evidence that iron limitation within the postspring bloom phytoplankton community contributes to the observed residual macronutrient pool during summer. Low atmospheric iron supply and suboptimal Fe:N ratios in winter overturned deep water are suggested to result in the formation of this seasonal high-nutrient, low-chlorophyll (HNLC) condition, representing an inefficiency of the biological (soft tissue) carbon pump in the region.


1. Introduction

Iron availability has now been demonstrated to perform a fundamental role in controlling photosynthesis and phytoplankton biomass accumulation in all the classical high-nutrient, low-chlorophyll (HNLC) systems [Boyd et al., 2007; de Baar et al., 2005]. In contrast, it is generally assumed that the high-latitude (~50°N) North Atlantic Ocean fundamentally differs from the other high-latitude regions of the global oceans (i.e., the HNLC Southern Ocean and subpolar North Pacific), as iron is considered not to be a limiting micronutrient [Martin et al., 1993].

A pronounced spring bloom is observed in the high-latitude North Atlantic. Deep winter overturning (>600 m) injects nitrate into surface waters, resulting in prebloom concentrations of >10 μM NO₃ [Ducklow and Harris, 1993; Sanders et al., 2005]. Increased incident surface irradiance in the spring subsequently results in a shoaling of the mixed layer to less than the critical depth [Siegel et al., 2002; Sverdrup, 1953]. This transient period during which the average light intensity of the mixed layer is increasing and nutrient concentrations are high provides a window of opportunity for the onset of a large phytoplankton bloom. Chlorophyll concentrations during the spring bloom peak at >2 mg m⁻³ in parts of the high-latitude North Atlantic and subsequently significant drawdown of surface macronutrients occurs along with high rates of export [Honjo and Manganini, 1993].

The sequence of events surrounding the spring bloom is well established [Sverdrup, 1953]. However, despite the transient spring period of high biomass and hence productivity and export, in many regions of the open North Atlantic, including the Iceland and Irminger Basins, residual nitrate (>2 μM NO₃) and phosphate (>0.15 μM PO₄³⁻) concentrations have been observed during the postbloom summer period [Sanders et al., 2005]. Persistent high-macronutrient conditions throughout the postbloom period represent an inefficiency of the biological (soft tissue) carbon pump [Sarmiento and Toggweiler, 1984]. Moreover the existence of such residual nutrients in the high-latitude Atlantic is potentially of global significance to the partitioning of carbon between the atmosphere and ocean [Marinov et al., 2008a, 2008b].

North Atlantic Deep Water (NADW) is formed in the subpolar gyre, in the Greenland Sea and in the Norwegian Sea of the high-latitude North Atlantic, and contributes approximately half of the global production of deep waters. Atmospheric pCO₂ is particularly sensitive to inefficiencies in the biological pump in regions of deep water formation [Knox and McElroy, 1984; Sarmiento and Toggweiler, 1984; Sarmiento and Orr, 1991; Siegenthaler and Wenk, 1984]. Indeed, modeling studies have indicated that com-
plete nutrient removal in the high-latitude North Atlantic would potentially be more significant in lowering atmospheric pCO₂ than either the HNLC sub-Arctic or equatorial Pacific, and is second only to the Southern Ocean in terms of influence [Marinov et al., 2008a; Sarmiento and Orr, 1991].

The mechanism(s) responsible for maintaining residual macronutrients in the high-latitude North Atlantic likely comprise some combination of the factors that have previously been identified in the more classical HNLC systems [Cullen, 1991]. The potential for high-grazing rates, particularly on small phytoplankton groups by rapidly growing heterotrophic protists [Banse, 1982], has frequently been identified as a factor capable of limiting the standing stock of major sections of the autotrophic community [Frost, 1991; Walsh, 1976]. Consequently grazer termination of the bloom has been hypothesized [Banse, 2002]. Additionally, the large diatoms, that potentially could escape high-grazing mortality because of good defenses [Hamm et al., 2003], may be silicate limited, preventing further drawdown of residual nitrate and phosphate [Dugdale and Wilkerson, 1998; Henson et al., 2006].

Such arguments were the leading candidate mechanisms in the classical HNLC systems [Dugdale and Wilkerson, 1998; Frost, 1991; Walsh, 1976], until the unequivocal demonstration of iron limitation for at least some components of the phytoplankton community [Boyd et al., 2007; Martin and Fitzwater, 1988; Martin et al., 1994]. Subsequently it was recognized that these factors may all interact and contribute to the maintenance of residual macronutrients in HNLC systems [Cullen, 1991; Dugdale and Wilkerson, 1998; Morel et al., 1991; Price et al., 1994].

Although iron availability has been assumed to exert little control on phytoplankton growth and biogeochemical cycling in the North East Atlantic [Martin et al., 1993], the high-latitude North Atlantic receives very low dust and hence atmospheric iron inputs, which are comparable with the HNLC North Pacific [Jickells et al., 2005]. Additionally, early work highlighted very low dissolved iron (dFe) concentrations in the region during late spring/early summer (June) and provided evidence for increased CO₂ fixation and particulate organic carbon production following iron additions within bottle experiments [Martin et al., 1993]. More recent measurements have shown low dFe (0.02–0.16 nM) south of Iceland [Measures et al., 2008] and experimental manipulations [Blain et al., 2004; Moore et al., 2006] and in situ physiological measurements [Moore et al., 2006] further to the south (~40°N) have indicated the potential for iron limitation in the North Atlantic Ocean.

The aim of the current study was to establish if iron availability influences phytoplankton growth during post-bloom conditions in the Iceland Basin and hence whether low iron supply plays a role in the persistence of any postbloom residual macronutrient pool. A number of complementary techniques were employed, including measurements of dFe concentrations and in vitro bioassay experiments. Interpretation of such bottle experiments is complicated by the potential for artifacts following removal of the natural population from the in situ environment [Cullen, 1991]. Consequently biophysical measurements of both in situ and experimental phytoplankton populations were performed as a potential means of overcoming these weaknesses [Geider and La Roche, 1994].

2. Methods

2.1. General

Data were obtained during a two leg cruise from 25 July to 9 September 2007. During the first leg of the cruise, three bioassay experiments (A–C) and six stations (800–1000 m) were sampled in the middle of the sub polar gyre in the Iceland Basin. On the second leg of the cruise, a further experiment (D) was carried out closer to the Iceland Shelf (Figure 1a), and stations were occupied between Iceland and the UK. Hydrographic data were collected using Seabird 9/11+ CTD systems, incorporating a 2π irradiance sensor. CTD data were used to calculate mixed layer depths (MLD), the diffuse attenuation coefficient (kd) and hence maximum, minimum and mean (Eavg) irradiances within the mixed layer, hereafter quoted as a function of the surface value (Eo).

2.2. Sample Collection

Discrete water samples and vertical profiles of temperature and salinity were collected using two separate CTD rosette systems. A trace metal clean titanium CTD rosette with 10 L trace metal clean Teflon coated OTE bottles, fitted with silicone O rings and plastic coated springs, was used for the collection of samples analyzed for dissolved iron (dFe), dissolved aluminum (dAl) and incubation experiments. Additionally, water for the incubation experiments and surface dFe determinations was also collected using a trace metal clean tow fish [Bowie et al., 2001] while the ship was steaming at 10 knots. The seawater was pumped into a dedicated clean chemistry container using a Polytetrafluoroethylene (PTFE) diaphragm pump (Almeco –15). Discrete samples for other measurements such as macronutrients were frequently taken from either a stainless steel CTD rosette with standard Niskin bottles or from the titanium CTD rosette, depending on the order of the casts. Samples for the analysis of surface chlorophyll and macronutrients were also collected from the ship’s sea underway seawater supply, which has an intake at a depth of ~5 m.

2.3. Iron-Light Enrichment Experiments

Incubation experiments were performed using a similar method to that employed previously in the HNLC Southern Ocean [Moore et al., 2007]. Briefly, water for incubation experiments was collected using either the trace metal titanium CTD rosette system (experiments A and B) or the trace metal clean tow fish (experiments C and D) and transferred unscreened into acid washed 4.8 L polycarbonate bottles (Nalgene). Incubation bottles and three initial samples were filled randomly, then either left as controls or amended with acidified FeCl₃ to a final concentration of 2 nM above the ambient dFe concentration. All bottle tops were sealed with film (Parafilm) and bottles were double bagged with clear plastic bags to minimize contamination risks on deck. On deck incubations were performed over 5–6 days at two different irradiance levels, high light (HL) and low light (LL). The incubators for the HL and LL light treatments were shaded using a combination of neutral density and blue lagoon filters to levels corresponding to...
35% and 4% of $E_0$, respectively. The temperature in the incubators was controlled by running surface seawater. Typical experimental treatments consisted of high-light and low-light controls (HLC and LLC) and high-light and low-light iron (HLFe and LLFe) amended. For experiment A, only the HL light regime was used. For experiment C the HL and LL bottles were swapped over after 24 h in order to investigate the potential for a direct rapid effect of incubation irradiance on phytoplankton physiology (see below).

For each treatment triplicate bottles were incubated and typically subsampled two times during the experiments for chlorophyll, macronutrients and biophysical active fluorescence measurements. The first time point was at 24 h for experiments C and D and at 48 h for A and B. Subsampling was carried out under a class 100 laminar flow hood. At the initial and end time point, samples were also collected for phytoplankton identification and enumeration by microscopy and dFe to check for contamination (experiments A–D). For experiment A an additional time point after one day was taken for phytoplankton identification. No contamination was detected by postincubation dFe measurements in any of the bottles within our experiments. A high degree of consistency in response was found within all parameters measured in triplicate bottles. (See Table 2.)

### 2.4. Dissolved Iron

Samples for dissolved iron (dFe) analysis were gently pressure filtered using 0.2 $\mu$m pore size cartridge filters (Sartobran-P300, Sartorius) using nitrogen gas at 1.1 bar pressure. Samples were analyzed using an automated flow injection chemiluminescence method, following the modified Obata method [de Jong et al., 1998; Obata et al., 1993, 1997] with 8-hydroxyquinoline (8-HQ) immobilized on Toyopearl gel [Landing et al., 1986] as preconcentration/matrix removal resin. All solutions were prepared with 18.2 $M\Omega$ cm$^{-1}$ deionized water (Milli-Q, Millipore). A 179.1 $\mu$M Fe standard (stock 1) was prepared on a weekly basis from a 1000 ppm AAS standard (Fisher). A 1791 nM stock solution (stock 2) was prepared daily from stock 1 before commence of analysis.

All samples were acidified to a pH 2 with ultra pure HCl (Fisher Optima) and stored for a minimum of 24 h. A 0.01% solution of $H_2O_2$ (Romil Upa) (1 $\mu$L $H_2O_2$ per mL sample) was added one hour prior to analysis to ensure all FeII present in the sample was oxidized to FeIII. The samples were buffered to a pH $4 \pm 0.5$ using 0.12 M NH$_4$Ac buffer before preconcentration on the 8-HQ column. The preconcentrated iron was eluted with 0.3 M HCl (Romil Spa), and subsequently buffered up to pH $9.3 \pm 0.2$ with NH$_4$OH and mixed with $H_2O_2$ and luminol to produce the chemiluminescence reaction which was detected using a photomultiplier tube (Hamatsu).

Each sample was run in triplicate. The blank, was calculated from the difference in dFe concentrations between seawater samples with normal and double amounts of HCl and buffer added. The analytical blank varied between 0.017 and 0.042 nM with a mean value of 0.028 ± 0.009 (n = 13) nM dFe. Samples were corrected for the blank. The detection limit, calculated as 3 times the standard deviation of the lowest standard addition, was on average 0.027 ± 0.017 (n = 11) nM dFe. SAFe [Johnson et al., 2005] and IRONAGES samples [Bowie et al., 2006] were used as reference material with an average of 0.085 ± 0.013 nM (±1 standard deviation (SD), n = 5) for SAFe and 0.56 ± 0.05 nM (±1 SD, n = 6) for IRONAGES; these results agree well with the reported values.

### 2.5. Chlorophyll, Taxonomic Analysis, and Nutrients

Samples for chlorophyll analysis, 100–200 mL, were filtered using GF/F and 5 $\mu$m polycarbonate filters (Whatman) to obtain size-fractionated samples and then extracted into 90% acetone for 24 h in the dark before analysis with a fluorometer (TD70; Turner Designs) [Welschmeyer, 1994]. Phytoplankton samples (250 mL) were preserved in 2% alkaline lugols iodine and subsamples were counted ashore using light microscopy [Poulton et al., 2007].
[18] Macronutrients (nitrate + nitrite, hereafter nitrate, phosphate and orthosilicic acid) were analyzed on board during the first leg of the cruise using standard colorimetric techniques on an autoanalyzer (Skalar San Plus) [Sanders and Jickells, 2000].

[19] Samples were drawn directly from Niskin bottles into polystyrene vials and stored at 4°C until analysis, which commenced within 12 h of sampling. Consistency of the data was ensured by the analysis of commercial nutrient standards (Ocean Scientific International, United Kingdom), at regular intervals on the cruise and by the comparison of deep water nutrient concentrations between stations. In addition, nutrients were analyzed in samples collected from the ship’s underway supply. Detection limits were 0.1 μM for N and Si and 0.02 μM for P. Blanks were 0.05 μM for N and Si and 0.01 μM for P.

[20] On the second leg of the cruise nutrient analysis was carried out with a flow injection autoanalyzer (Lachat Quick Chem 800) using the manufacturers recommended methods. Samples were measured in triplicate to identify instrument precision. Standards were prepared in deionized water and the samples were run in a carrier stream of deionized water. The matrix effect which results from the difference in ionic strength between seawater and deionized water was corrected for by running a number of low-nutrient sea water strength standards (Ocean Scientific International, United Kingdom), prepared for by running a number of low-nutrient sea water standards between seawater and deionized water was corrected for by running a number of low-nutrient sea water strengths of 1/100 and 1/1000.

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[26] Incubation experiments were all initiated in waters with 2.8–5 μM residual nitrate concentrations (Table 1). Initial chlorophyll concentrations ranged from 0.2 to 0.4 mg m⁻³ for the three experiments (A–C) undertaken in the central Iceland Basin, to ~0.6 mg m⁻³ for the northerly
experiment (D) initiated closer to the Iceland shelf. Consistent with transect data (Figure 1b), higher initial values of \( F_v/F_m \) were observed in the northerly experiment (D) (Table 1). Initial concentrations of dFe were <0.1 nM for 2 of the southerly experiments (A and C), with a higher initial concentrations for experiment B initiated within the mode water eddy.

[27] The composition of the phytoplankton community varied between experiments. The initial abundances of the coccolithophore *Emiliania huxleyi* ranged from 130 to 270 cells mL\(^{-1}\) for all experiments. The centric diatom species *Proboscia alata* and *Lauderia annulata* dominated diatom biomass for the northerly experiment (D) toward the Iceland shelf. In contrast, *Cylindrotheca closterium* dominated diatom biomass within the southerly experiments (A–C). Mixed layer depths were shallow, ranging from ∼20–40 m. Combined with relatively low-irradiance attenuation (Table 1), the shallow MLD resulted in mean irradiances of ∼20–40% of the surface value within the mixed layer (Table 1). Consequently LL treatments approximated irradiances at the base of the mixed layer while HL treatments approximated mean mixed layer irradiances.

[28] Despite some variability in initial conditions, a rapid physiological response to iron addition was observed (after <24 or 48 h) in all experiments (Figure 2). Values of \( F_v/F_m \) in iron amended treatments were in all cases significantly higher than controls (ANOVA, Tukey-Kramer means comparison test, \( p < 0.05 \)). However, physiological responses to different light levels and throughout the time course of the experiments were complex (Figures 3–5). In particular, \( F_v/F_m \) in HL treatments typically decreased with time relative to corresponding LL treatments, irrespective of iron addition (Figure 4), potentially representing accumulation of long-lived photoinhibitory damage to PSII [Kolber et al., 1994; Moore et al., 2007]. Irrespective of the precise mechanism, the swap between HL and LL treatments after 24 h within experiment C confirmed the rapid physiological nature of this response (not shown).

[29] Furthermore, for southerly experiments (A–C), initial (predawn) in situ values of \( F_v/F_m \) (Table 1) were lower than subsequent values measured within controls (Table 1 and Figure 2). This rapid divergence of controls and in situ values can be speculated to result from a number of mechanisms. For example, increased photoinhibition may potentially occur in situ within the shallow mixed layers, particularly in the low attenuation southerly region (i.e., experiments A–C), where peak (surface) irradiances and UV exposure [Vassilev et al., 1994] likely exceeded those within high-light incubations. Alternatively, the lack of the effect within the potentially more Fe replete northerly population (D) may suggest a low level of Fe contamination, which was only detectable from the biological response within southerly experiments (A–C). However, the differing response between experiments A–C and D may also be linked to the contrasting community structure.

[30] Overall, despite the potential complexities resulting from variable irradiance regimes, physiological responses (Figures 2, 4b, and 5b) were comparable to similar experiments performed within the HNLC eastern equatorial Pacific [Greene et al., 1994] and Southern Ocean [Moore et al., 2007]. Rapid responses of \( F_v/F_m \) to iron amendment also occur in iron starved cultures [Greene et al., 1992] and have consistently been observed in purposeful in situ iron enrichment experiments in HNLC regions [Boyd et al., 2001; Gervais et al., 2002].

[31] Although some form of “bottle effect” was clearly evidenced by the rapid divergence of in situ and control values (Figures 4b and 5b), biophysical parameters such as \( F_v/F_m \) should be independent of differences in grazing between the in situ population and those constrained within bottles [Cullen, 1991]. Consequently our bioassay experiments provided unequivocal evidence of physiological iron stress within at least a proportion of the natural community [Greene et al., 1994; Kolber et al., 1994].

### 3.3. Incubation Experiments: Biomass, Nutrient Drawdown, and Species Response

[32] For southerly (central Iceland Basin) experiments (A–C), chlorophyll increased above initial concentrations in the control bottles and, for a given light level, chlorophyll was significantly higher in the iron amended bottles than controls. Final chlorophyll concentrations in iron-amended

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**Table 1. Initial Conditions for the Bioassay Experiments**

<table>
<thead>
<tr>
<th></th>
<th>Experiment A</th>
<th>Experiment B</th>
<th>Experiment C</th>
<th>Experiment D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude (°N)</td>
<td>59–42.66</td>
<td>59–12.57</td>
<td>58–52.13</td>
<td>62–55.20</td>
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<tr>
<td>Longitude (°W)</td>
<td>18–45.09</td>
<td>19–53.59</td>
<td>20–22.03</td>
<td>19–32.90</td>
</tr>
<tr>
<td>Sample depth (m)</td>
<td>10</td>
<td>10</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>MLD (m)</td>
<td>28</td>
<td>20</td>
<td>20</td>
<td>35</td>
</tr>
<tr>
<td>( K_o ) (m(^{-1}))</td>
<td>0.08</td>
<td>0.09</td>
<td>0.13</td>
<td>0.11</td>
</tr>
<tr>
<td>( E_{avg} ) (%( E_0 ))</td>
<td>41.18</td>
<td>46.24</td>
<td>21.91</td>
<td>12.25</td>
</tr>
<tr>
<td>SST (°C)</td>
<td>13.47</td>
<td>13.24</td>
<td>12.25</td>
<td>11.13</td>
</tr>
<tr>
<td>dFe (nM)</td>
<td>0.17 (±0.12)</td>
<td>0.37 (±0.03)</td>
<td>0.15 (±0.06)</td>
<td>0.15 (±0.06)</td>
</tr>
<tr>
<td>Nitrate (μM)</td>
<td>3.27 (±0.02)</td>
<td>5.00 (±0.02)</td>
<td>2.88 (±0.03)</td>
<td>2.83 (±0.33)</td>
</tr>
<tr>
<td>Silicic acid (μM)</td>
<td>0.33 (±0.01)</td>
<td>0.70 (±0.01)</td>
<td>0.35 (±0.01)</td>
<td>0.03 (±0.02)</td>
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<tr>
<td>Chl (mg m(^{-3}))</td>
<td>0.24 (±0.01)</td>
<td>0.39 (±0.02)</td>
<td>0.37 (±0.01)</td>
<td>0.58 (±0.14)</td>
</tr>
<tr>
<td>Chl &gt;5μm (mg m(^{-3}))</td>
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<td>0.06 (±0.00)</td>
<td>0.053 (±0.01)</td>
<td>ND</td>
</tr>
<tr>
<td>Chl &lt;5μm (mg m(^{-3}))</td>
<td>0.20 (±0.00)</td>
<td>0.33 (±0.03)</td>
<td>0.320 (±0.01)</td>
<td>ND</td>
</tr>
<tr>
<td>( F_v/F_m )</td>
<td>0.36 (±0.00)</td>
<td>0.33 (±0.00)</td>
<td>0.28 (±0.00)</td>
<td>0.40 (±0.02)</td>
</tr>
</tbody>
</table>

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\( ^a \)Shown are mean values (±1 SE) for triplicate initial samples. MLD, mixed layer depth; \( K_o \), diffuse attenuation coefficient for photosynthetically available radiation PAR; \( E_{avg} \), mean irradiance expresses as percent of the surface irradiance \( E_0 \); SST, sea surface temperature; Chl, chlorophyll; ND, not determined.
bottles were 1.5–2 fold larger than those of the control bottles after 5–6 days for all the southerly experiments (A–C). Net growth rates ($\mu_{\text{net}}$) calculated from total chlorophyll accumulation were thus around 1.5–2 fold higher under iron amendment (Table 1). The $<5 \mu m$ fraction constituted $>80\%$ of the total chlorophyll under initial conditions for central Iceland Basin experiments (Table 1). For all size fractions $\mu_{\text{net}}$ was higher in iron amended treatments than the controls (Table 2). In contrast, for the northerly experiment (D), no significant increase in chlorophyll was observed in any treatment except LLFe (Table 2).

[33] Responses of individual phytoplankton taxa to experimental manipulations varied. The coccolithophore Emiliania huxleyi showed a positive response in all experiments. In particular $\mu_{\text{net}}$ for E. huxleyi increased from $\sim$0 to 0.27 d$^{-1}$ for experiment A (Figure 3). Cylindrotheca closterium also increased in abundance within HLC for all experiments, with an average HLC $\mu_{\text{net}} = 0.35 \pm 0.05$ d$^{-1}$ compared to an average LLC values of 0.03 $\pm$ 0.06 d$^{-1}$. Furthermore, there was an additional increase in abundance of this species in response to iron amendment compared to the controls (Figure 3c).

[35] Chlorophyll accumulation was higher under Fe amended conditions for the larger ($>5 \mu m$) size fraction within all the experiments where measurements were made (A–C) (P < 0.05, ANOVA, Tukey). However, the $<5 \mu m$ fraction also responded to Fe amendment, with significant differences observed for experiments B–C (P < 0.05, ANOVA, Tukey). HL and LL treatments also differed within experiment B, with chlorophyll accumulation in the HLFe treatments being higher than LLFe for both size classes, while HLC and LLC were only significantly different in the larger size class (P < 0.05, ANOVA, Tukey). In contrast, differences between light treatments were not significant within experiment C.

[37] Using the data of [Ho et al., 2003; Sunda and Huntsman, 1995; Twining et al., 2004b], we estimate that...
cellular Fe:N ratios of <0.02 mmol/mol are growth rate
limiting even for oceanic taxa including *E. huxleyi*. Post-
bloom surface dFe:NO$_3$ ratios were frequently lower than
this value in the central Iceland Basin. In particular, starting
dFe:NO$_3$ ratios were <0.02 for 2 of our three southerly
experiments (Table 1). Consequently, (continued) develop-
ment of iron limitation could be predicted as biomass
increased within the bottles. However, interpretation of
chlorophyll accumulation or nutrient drawdown within such
experiments must be treated with caution because of poten-
tial unrealistic ecosystem dynamics [Cullen, 1991; Geider
and La Roche, 1994]. Potential reductions in loss terms,
including grazing, sinking and advection will all increase
net growth in bottles. Indeed, within HL controls approx-
imating mean in situ light conditions, significant drawdown
of residual macronutrients, along with accumulation of
chlorophyll and some phytoplankton groups, was observed
in all our experiments (Figures 3 and 4 and Table 2).

[38] Consequently we cannot discount intense grazing as
a contributing factor to postbloom HNLC conditions

\[ \text{Figure 3. Results of bioassay experiment A. (a) Chlorophyll concentration against time and (b) nitrate}
\] concentration against time. Shown are mean values (±1 SE, n = 3). (c) Plot of the abundance of the
diatom *C. closterium* and (d) the coccolithophore *E. huxleyi* against time. Shown are counts of one sample
per condition.
[Banse, 2002; Cullen, 1991; Frost, 1991; Morel et al., 1991; Price et al., 1994]. However, along with consistently enhanced biomass accumulation and macronutrient drawdown in iron amended treatments in southerly experiments, the low ambient dFe concentrations and rapid response of biomass/grazing-independent physiological variables combined to strongly suggest that iron availability influences phytoplankton growth during postbloom conditions in the central Iceland Basin.

Despite a clear physiological response (Figure 2d), weaker biomass increases and complete nutrient drawdown in HL treatments for the northerly experiment (D) supports the suggestion of a more iron replete community in this region closer to shallow bathymetry (Figure 1a). For this experiment, increased bulk chlorophyll accumulation in LLFe treatments only may indicate an increased ability to acclimate to lower than in situ light levels under conditions of higher iron availability [Raven, 1990; Sunda and Huntsman, 1997].

3.4. Potential for an Iron-Limited HNLC Postbloom Condition

[40] Considerable mesoscale variability below the mixed layer was observed in depth profiles of dFe in the central Iceland Basin (dFe profiles and associated data for this region are presented in Table 3). We thus consider average vertical profiles of dFe and nitrate constructed from the data collected in the central Iceland Basin (Figure 6). DFe concentrations in the surface averaged around 0.1 nM and similar low values were observed throughout and immedi-

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**Figure 4.** Results of bioassay experiment B. (a) Chlorophyll concentration, (b) Fv/Fm, (c) nitrate concentration, and (d) silicate concentration against time. Shown are mean values (±1 SE, n = 3).
ately below the mixed layer. Concentrations of dFe increased with depth to around 0.4 nM within mode waters between ~400–600 m and >0.6 nM for depths >1000 m. These concentrations are consistent with previous observations in the area [Johnson et al., 1997; Martin et al., 1993; Measures et al., 2008]. Detailed hydrographic data indicated that deepest winter mixing penetrated to around 800 m in our study region. In addition to providing the macronutrients to fuel the spring bloom, deep winter mixing will also input dissolved iron into surface waters. The dFe:NO$_3^-$ ratio was <0.05 mmol/mol at depth down to 800 m (Figure 6d) and hence the ratio of Fe to N input during winter overturning will similarly be <0.05 mmol/mol. Cellular Fe:N ratios for iron replete phytoplankton range from ~0.05–0.9 (average ~0.5) mmol/mol [Ho et al., 2003; Sunda and Huntsman, 1995; Twining et al., 2004a, 2004b]. Consequently, winter overturning inputs of NO$_3^-$ to the surface waters of the central Iceland Basin will not be accompanied by sufficient dissolved iron to satisfy complete macronutrient removal by iron replete phytoplankton growth, a situation which also occurs in classical HNLC regions [Boyd et al., 2000; Hutchins and Bruland, 1998; Martin and Fitzwater, 1988].

[41] Assuming that mode waters (~400–600 m) are representative of end of winter conditions, prebloom surface dFe concentrations would have been ~0.4 nM. Alternatively, integrating our mean dFe profile from the maximum depth of winter mixing to the surface yields an estimated...
winter dFe concentration of ~0.3 nM. These values are again consistent with previous estimates [Measures et al., 2008]. Similarly, end of winter surface nitrate concentrations would have been around 12 mM (Figure 6). Taking the most conservative values for cellular Fe:N ratios under iron replete growth [Ho et al., 2003; Sunda and Huntsman, 1995] and average mixed layer depths of 30–40 m over the growth period, potential annual new production of 360–480 mmol N m\(^{-2}\) a\(^{-1}\) would require a minimum 18–24 μmol Fe m\(^{-2}\) a\(^{-1}\), with actual requirements likely to be considerably higher.

[41] Winter mixing would only input 12–16 μmol Fe m\(^{-2}\) a\(^{-1}\) (Figure 6). Measured surface water dissolved aluminum concentrations in the region were low (1–3 nM; E. P. Achterberg, unpublished data, 2007), consistent with previous observations [Measures et al., 2008] and suggestive of low atmospheric iron inputs. We estimate following [Measures et al., 2008] that atmospheric inputs of iron would likely have been around 5 μmol Fe m\(^{-2}\) a\(^{-1}\) and hence an overall deficit of iron relative to NO\(_3\) is likely to remain, even accounting for this term and ignoring any nitrate which may be deposited from the atmosphere.

[42] Our data therefore confirm that the supply of iron from winter overturning in the central Iceland Basin is expected to be inadequate to support complete summer macronutrient drawdown. However, overall iron supply may only be marginally below that required for complete nitrate utilization to occur. Such a scenario explains the observed intensity of the spring bloom and the modest residual nitrate levels. Moreover, iron uptake and export during the bloom likely contributes to the reduced bioavailable iron levels which subsequently appear to limit the growth rates of at least some phytoplankton groups by early summer [Martin et al., 1993], consequently contributing to the development of a relatively weak HNLC condition. We

Table 2. High-Light Control, High-Light Fe, Low-Light Control, and Low-Light Fe for the Bioassay Experiments

<table>
<thead>
<tr>
<th>Experiment</th>
<th>ΔNO(_3) (μM)</th>
<th>(\mu^\text{Chl} ) (d(^{-1}))</th>
<th>(\mu^\text{Chl} &gt; 5\mu\text{m} ) (d(^{-1}))</th>
<th>(\mu^\text{Chl} &lt; 5\mu\text{m} ) (d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>A HLC</td>
<td>1.71 (±0.44)</td>
<td>0.22 (±0.06)</td>
<td>0.28 (±0.02)</td>
<td>0.23 (±0.08)</td>
</tr>
<tr>
<td>A HLFe</td>
<td>2.98 (±0.13)</td>
<td>0.32 (±0.00)</td>
<td>0.37 (±0.01)</td>
<td>0.36 (±0.01)</td>
</tr>
<tr>
<td>A LLC</td>
<td>0.32 (±0.04)</td>
<td>0.21 (±0.06)</td>
<td>0.16 (±0.01)</td>
<td>0.06 (±0.01)</td>
</tr>
<tr>
<td>A LLFe</td>
<td>0.74 (±0.08)</td>
<td>0.31 (±0.00)</td>
<td>0.22 (±0.00)</td>
<td>0.15 (±0.01)</td>
</tr>
<tr>
<td>B HLC</td>
<td>1.22 (±0.09)</td>
<td>0.13 (±0.05)</td>
<td>0.24 (±0.02)</td>
<td>0.10 (±0.02)</td>
</tr>
<tr>
<td>B HLFe</td>
<td>2.08 (±0.50)</td>
<td>0.23 (±0.25)</td>
<td>0.35 (±0.06)</td>
<td>0.19 (±0.04)</td>
</tr>
<tr>
<td>B LLC</td>
<td>0.11 (±0.06)</td>
<td>0.08 (±0.02)</td>
<td>0.15 (±0.01)</td>
<td>0.07 (±0.01)</td>
</tr>
<tr>
<td>B LLFe</td>
<td>0.74 (±0.08)</td>
<td>0.21 (±0.02)</td>
<td>0.29 (±0.01)</td>
<td>0.19 (±0.01)</td>
</tr>
<tr>
<td>C HLC</td>
<td>2.79 (±0.01)</td>
<td>0.05 (±0.01)</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>C HLFe</td>
<td>2.79 (±0.03)</td>
<td>0.03 (±0.01)</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>C LLC</td>
<td>0.92 (±0.09)</td>
<td>0.04 (±0.02)</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>C LLFe</td>
<td>1.05 (±0.04)</td>
<td>0.14 (±0.01)</td>
<td>ND</td>
<td>ND</td>
</tr>
</tbody>
</table>

\(\Delta\text{NO}_3\), total growth rate, and size fractionated growth rates at the end of each bioassay experiments A–D (t = 5–6 days). Shown are mean values (±1 SE) of triplicate end point bottles. ND, not determined.

![Figure 6](gb3001) Average vertical profiles of (a) temperature, (b) dFe, (c) NO\(_3\), and (d) the dFe:NO\(_3\) ratio compared to cellular Fe:N ratios within iron replete cultures [Ho et al., 2003; Sunda and Huntsman, 1995] which are comparable to in situ natural communities [Twining et al., 2004b]. Plotted values are mean values (±1 SE) from three to six profiles (depending on the depth) collected between 59.1 and 60°N and 18.7 and 20.6°W.
thus suggest that the high-latitude North Atlantic only differs from the more severe HNLC high-latitude systems of the sub-Arctic Pacific and the Southern Ocean in the sense that higher iron and lower macronutrient inputs markedly increase bloom intensity and reduce the magnitude of the postbloom residual macronutrient pool, which is at least partially maintained by iron limitation.

3.5. Wider Implications

The existence of a residual macronutrient pool within certain regions of the high-latitude North Atlantic represents an inefficiency in the biological soft tissue pump [Sarmiento and Toggweiler, 1984]. Persistence of such residual macronutrients within deep water formation regions raises preformed nutrient concentrations within North Atlantic Deep Water (NADW) and hence reduces the biological component of oceanic carbon storage [Marinov et al., 2008a, 2008b]. Consequently, depending on the spatial and temporal extent of the residual macronutrient pool, it is possible that the existence of postbloom HNLC conditions in the high-latitude North Atlantic contributes significantly to ocean-atmosphere CO$_2$ partitioning [Marinov et al., 2008a, 2008b]. Modeling studies have suggested that complete macronutrient depletion in this region could potentially reduce atmospheric pCO$_2$ by $\approx$10 ppm [Marinov et al., 2008b; Sarmiento and Orr, 1991].
However, we note that postbloom HNLC conditions may only contribute a fraction of this total, because of light limitation during late autumn.

4. Conclusions

[45] The results of the current study suggest that iron limitation of the postbloom phytoplankton community in the Iceland Basin is a factor contributing to the observed residual macronutrient pool. Mesoscale iron addition experiments have unequivocally shown that iron supply limits production in >1/3 of the global ocean where surface macronutrient concentrations are perennially high [Boyd et al., 2007]. Our study suggests that the high-latitude North Atlantic should be considered as an additional region where biogeochemical cycling may be sensitive to changes in iron inputs, for example, because of altered dust deposition patterns [Jickells et al., 2005].

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References


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