Iron Regulation of North Atlantic Eddy Phytoplankton Productivity

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Abstract Cyclonic ocean eddies drive upwelling of deep waters enhanced in nutrients, which can elevate phytoplankton productivity. At mid-latitudes in the North Atlantic, satellite images show enhanced chlorophyll-a associated with eddies. However, surface macronutrient concentrations are often not fully depleted in this region, implying enhanced macronutrient supply is not the primary control. We conducted high resolution sampling through two mid-latitude Atlantic eddies in late spring, located 800 and 350 km east of the Newfoundland Grand Banks. Waters outside of both eddies had unused residual macronutrients, low dissolved iron, and iron-stressed phytoplankton. Inside both eddies, plankton biomass was higher and macronutrient concentrations lower. However, full macronutrient drawdown and an absence of iron stress were only present in the eddy nearer the continental shelf. From these two examples, iron supply and proximity to shelf iron sources appear to be important factors regulating productivity and macronutrient utilization in mid-latitude North Atlantic cyclonic eddies.

Plain Language Summary Satellites show that circulating currents of water, eddies, in the mid-high latitude North Atlantic often have elevated amounts of phytoplankton. This has been ascribed to enhanced nutrient and light availability. However, the background field (that is, outside eddies) in this region have elevated light in late spring and summer, and macronutrient concentrations (nitrate, phosphate, silicate) are not particularly depleted. To investigate this in more detail, we sailed through two North Atlantic eddies in late spring making measurements of phytoplankton, nutrients, and trace elements. Our results indicated that the background field was depleted in the micronutrient iron relative to other nutrients and additional experimental tests confirmed that phytoplankton were iron-stressed. We therefore hypothesize that elevated iron supply to sunlit surface waters, via eddy-driven upwelling, is a key factor enhancing phytoplankton productivity in this region. This was supported by concentrations of manganese, a tracer of sedimentary iron, which were elevated within the eddy where Fe stress was fully relieved. Our results suggest enhanced iron supply to surface waters in eddies is an important factor regulating the distribution of phytoplankton in this region; this in turn would be an important regulator of higher trophic levels, including fish and seabird stocks.

1. Introduction

Deep ocean waters tend to be enriched in all nutrients required by phytoplankton relative to the surface mixed layer (with the widespread exception of manganese, Mn) (Bruland & Lohan, 2003; Van Hulten et al., 2017). As a result, upwelling in a nutrient limited system should enhance phytoplankton productivity relative to surrounding waters, providing food for higher trophic levels. However, full biological utilization of upwelled macronutrients, nitrogen (N) and phosphorus (P), and the associated consumption of upwelled dissolved inorganic carbon (DIC), also depend on other factors restricting phytoplankton productivity (Moore et al., 2013; Sigman & Boyle, 2000). These include top-down grazing pressure, and bottom-up growth limitation by thermal energy (i.e., water temperature), light, and the availability of micronutrients, such as iron (Fe, Cullen, 1991; Price et al., 1994).

Upwelling of deep-water in cyclonic mesoscale eddies can supply nutrients into the photic zone over spatial scales of tens to hundreds of kilometers (Falkowski et al., 1991; Gaube et al., 2014; McGillicuddy...
et al., 1998; Oschlies, 2002). Previous biogeochemical studies of cyclonic eddies have focused mostly on the N-limited subtropics, where elevated eddy productivity has been associated with upwelling and efficient utilization of macronutrients (e.g., Benitez-Nelson et al., 2007; Falkowski et al., 1991; Johnson et al., 2010; Li & Hansell, 2008; McGillicuddy et al., 2007, 1998; Sedwick et al., 2018). Cyclonic mesoscale eddies, with enhanced phytoplankton concentrations relative to background levels, are also common in the mid-latitude North Atlantic (Gaube et al., 2014; Richardson, 1993; Shoosmith et al., 2005). Residual macronutrients in ambient waters of the surface mixed layer in this region persist well beyond springtime increases in surface irradiance (Browning et al., 2020; Sanders et al., 2005). Eddy-driven upwelling of macronutrients therefore appears insufficient to explain this phenomenon (e.g. Leterme & Pingree, 2008; Lochte & Pfannkuche, 1987).

Previous work in the North Atlantic has shown the potential for phytoplankton communities to be Fe limited (Browning et al., 2020; Martin et al., 1993; Nilsdottir et al., 2009; Ryan-Keogh et al., 2013), or co-limited by Fe and light (Blain et al., 2004; Moore et al., 2006). Accordingly, enhanced upwelled Fe supply may be key for elevating eddy phytoplankton concentrations above the background in this region in late spring-summer, when irradiance is elevated. To investigate this, we performed detailed biogeochemical measurements through the surface waters of two late-spring, mid-latitude cyclonic eddies in the North Atlantic. The first of these was a transient feature, associated with the subpolar frontal zone of the western Labrador Basin. In contrast, the other was one of several reoccurring eddies in the western basin, tied bathymetrically to the Newfoundland Grand Banks (Kearns & Paldor, 2000; Kearns & Rossby, 1998; Richardson, 1993; Rossby, 1996).

2. Materials and Methods

Fieldwork was conducted on the RRS Discovery in June 2017 (DY080; Browning et al., 2020). Prior to and during the cruise, the two studied eddies were identified using remotely sensed images of chlorophyll-a and sea surface temperature (SST) retrieved by the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua sensor and the Advanced Very High Resolution Radiometer, respectively, and provided by the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS). A combination of MODIS images downloaded from the NASA Ocean Color website (https://oceancolor.gsfc.nasa.gov) (L2 and L3 products) and Ocean Color Climate Change Initiative (OC-CCI) multisensor products (https://www.oceancolour.org/) were used for subsequent analysis. Eddy 1 was occupied on June 22nd and Eddy 2 on June 26–27th (Figure 1). Images shown in Figure 2 were from the following dates: 19th June 2017 (Eddy 1; Chlorophyll-A (L2) and SST (L2)), 11th June 2017 (Eddy 2; Chlorophyll-A (L2)), 10–17th June 2017 composite (Eddy 2; SST (L3)). These images were from the cloud-free periods nearest to the dates of eddy site occupation. Satellite-derived fields of sea surface height anomalies (SSHA) (merged 5-days L4 product downloaded from: https://opendap.jpl.nasa.gov/opendap) and surface ocean current vectors (Ocean Surface Current Analysis Real-time product; ESR, 2009) identified the eddy sites as zones of depressed SSHA with cyclonic motion.

Hull-mounted Acoustic Doppler current profiling (ADCP) systems were used to record ocean velocities (RDI OceanSurveyor 75 kHz and 150 kHz). During postprocessing, misalignment angle and amplitude factor were corrected by water track calibration (Fischer et al., 2003). After averaging velocities over the depth range 40–120 meters, eddy vorticity was estimated from maximum across-track velocities and assuming solid body rotation in between (Castelão & Johns, 2011; Chelton et al., 2011). Conductivity-temperature-depth (CTD) casts were conducted throughout Eddy 2 only (Figure S1). For Eddy 2, mixed layer depths were determined visually from vertical profiles of temperature and salinity (Figure S1). Drifting floats in the region were also used to calculate current velocities to compare with ADCP and satellite-derived estimates (drifting buoy ID 4401627, dates 3–5th June 2017 for Eddy 1 and ID 4401635, dates twelfth May–15th June 2017 for Eddy 2). Current speeds were calculated as distances traversed between drifter transmission time points. Argo and drifting float data were downloaded from: http://www.coriolis.eu.org.

Surface (~2 m depth) seawater was pumped (Teflon bellows pump; Dellmeco) into a laboratory overpressurized with HEPA-filtered air, using a towed water sampling device equipped with acid-washed tubing. Chemical and biological sampling followed identical procedures to those described in Browning et al. (2020).

Briefly, macronutrient and trace element samples were collected filtered (0.45 + 0.2 μm Sartorius Sartobran
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300 filter cartridges) into acid-washed vials. Macronutrient samples were stored at −20°C and analyzed ashore using an autoanalyzer system (QuAAtro; SEAL Analytical). Trace element samples were acidified on-ship and then analyzed ashore after >6 months using ICP-MS (Element XR). Concentrations of dissolved Fe were determined following preconcentration on a SeaFAST device with quantification by isotope dilution (Rapp et al., 2017), whilst dissolved manganese (Mn) concentrations were determined following preconcentration using a Preplab device (PS Analytical) with quantification by standard addition. Chlorophyll-a concentrations were determined following acetone extraction on a Turner Designs Trilogy laboratory fluorometer (Welschmeyer, 1994). Flow cytometry samples were preserved with 1% final concentration paraformaldehyde (Alfa Aesar/Thermo Fisher) at −80°C and analyzed ashore using a FACSCalibur flow cytometer (Becton Dickenson, Oxford, United Kingdom; Browning et al., 2014). A FASTOcean FRRf (Chelsea Technologies Group) was used to determine values of minimum fluorescence ($F_o$) and maximum fluorescence ($F_m$), which were blank corrected before calculation of the apparent PSII photochemical efficiency, $F_v/F_m = (F_m - F_o)/F_m$. Samples were dark acclimated in a water bath continuously replenished with ships flow-through water supply for 30–60 min prior to FRRf measurement.

Figure 1. Eddy sites. (a), (b) Site locations within the context of satellite-derived chlorophyll-a (a) and temperature (b). Boxed regions identify the study locations, wherein the elevated chlorophyll-a signature of the two eddies can readily be distinguished from the background field. Both are monthly composites for June 2017 (the month of cruise sampling). Bathymetric contours are shown for 0.5 and 1 km depths (black lines). (c) Eddy locations in relation to regional bathymetry and simplified surface ocean currents (simplified after Talley, Pickard, Emery, and Swift (2011), Figure 9.1); bathymetry from Smith and Sandwell, 1994 (version 8.2)). GBN = Grand Banks of Newfoundland; NAC=North Atlantic Current; SNAC = southern branch of the NAC; LC = Labrador Current.
Particulate organic carbon (POC) concentrations were determined using an elemental analyzer (Euro Elemental Analyser), following sulfurous acid fuming. Biogenic silicate (BSi) concentrations were determined following digestion in 4 mL 0.2 M NaOH (Sigma-Aldrich) and analysis for silicic acid (see previous). Samples for phytoplankton pigment analysis were stored frozen at −80°C but thawed in transport to the laboratory. Samples were nevertheless analyzed following the method of Van Heukelem and Thomas (2001). As described in Browning et al. (2020), recovery of chlorophyll-a from the HPLC analysis was approximately 20% in comparison to fluorometrically determined concentrations performed on ship. However, within the HPLC pigment data set itself, chlorophyll-a correlated near-linearly with summed diagnostic pigments (DP) (Chl-A = 1.1 × DP − 0.01; R² = 0.78; p = 2 × 10⁻¹⁶; n = 195), suggesting a relatively internally consistent data set (Trees et al., 2000). Pigment data were however only interpreted qualitatively, via approximation of phytoplankton size groups (Uitz et al., 2006).

Experimental tests for phytoplankton Fe stress were performed at sea by incubating 125 mL of unfiltered seawater (acid-washed LDPE bottles), collected under trace-metal-clean conditions, with or without added Fe (final concentration of added Fe = 2 nmol L⁻¹). Samples were collected around dawn and dusk (mid-morning for Experiment 3). Both control and +Fe treatments were conducted in triplicate. Bottles were sealed with Parafilm, bagged, and placed in an on-deck incubator for 24 (Eddy 1) or 48 (Eddy 2) hours. The incubator was screened with blue filters (Lee Filters ‘Blue Lagoon’) and subjected to continuous seawater exchange from the ships underway flow-through supply. Samples were dark acclimated for 60 min prior to Fv/Fm measurement for each replicate (see above). Differences in incubation timescales between Eddies

Figure 2. Satellite observations of eddies. Lines represent cruise transects through the eddies with filled dots indicating sampling locations and open circles representing sites where photophysiological responses to Fe addition were tested. The direction of travel was northwards for Eddy 1 and southwards for Eddy 2. For Eddy 2, CTD casts were made at the latter sites (see Fig. S1). Chlorophyll-a and SST images (MODIS Aqua) are from clear-sky days that do not correspond to the exact date of cruise transects (due to poor satellite coverage during transect dates; see Methods for dates/compositing periods). The thin red lines in ‘b’ and ‘c’ represent surface drifting buoy passages used to calculate surface current velocities. Arrows in ‘c’ and ‘f’ are satellite-derived surface current velocities (background field) and mean 40–120 m ADCP-derived current velocities (cruse track).
Enhanced phytoplankton concentrations within the eddies (i.e. positive chlorophyll-a or POC anomalies relative to the background field) could have either resulted from more favorable conditions for phytoplankton accumulation (i.e., after eddy formation), and/or entrainment of waters already hosting elevated phytoplankton (McGillicuddy, 2002). A method to distinguish phytoplankton trapping at eddy formation without subsequent enhancement, from trapping with subsequent enhancement, is to track temporal changes in chlorophyll-a within the eddy using satellite-derived concentrations (Gaube et al., 2014). A decline would

1 and 2 were unlikely to have a major impact on \( F_v/F_m \) responses to Fe supply, which typically respond rapidly following recovery from Fe stress (<24 h) with smaller subsequent changes (Gervais et al., 2002; Moore et al., 2007; Ryan-Keogh et al., 2013).

### 3. Results and Discussion

Two eddies were traversed to investigate their surface ocean biogeochemistry (Table 1). Eddy sizes were on the order of 80 km (major axis diameter) by 25 km (minor axis diameter) for the elliptically shaped Eddy 1, and 140 km diameter for the more circular Eddy 2 (Figure 2). Satellite observations indicated both eddies had cyclonic rotation and depressed sea surface heights. Mean ADCP-derived current speeds at 40–120 m depth showed maximum swirl velocities at the eddy boundaries of 0.55 m s\(^{-1}\) (Eddy 1) and 0.85 m s\(^{-1}\) (Eddy 2). Surface current speeds calculated from movement of autonomous drifting floats trapped within the eddies were similar, at 0.45 ± 0.18 m s\(^{-1}\) (Eddy 1) and 0.68 ± 0.23 m s\(^{-1}\) (Eddy 2), and generally matched satellite observations (Figure 2, Figures S2 and S3). Vorticities of Eddy 1 and 2 were estimated as 0.5\(\Phi \) and 0.2\(\Phi \), respectively. Angular velocity of Eddy 2 was therefore around 40% of Eddy 1. Eddy 2 was crossed centrally whereas Eddy 1 was crossed to the east of the rotation center, as indicated by the ADCP-derived current speeds, which remained above 0.3 ms\(^{-1}\) in the latter (Figure 3a). The off-centered crossing of Eddy 1 is not evident in Figure 2a, presumably because ocean color observations were made 3 days before the ship crossing, with the eddy migrating westward in the intervening time. Both eddy cores were colder and fresher than surrounding waters, indicating that they were isolated poleward of the North Atlantic Current (or ‘Subpolar Front’; Rossby, 1996, Figure 3 and Figure S1). They also had higher plankton biomass (chlorophyll-a and/or POC) and lower concentrations of nitrate than surrounding waters (Table 1; Figure 3 and Figure S1).

Enhanced phytoplankton concentrations within the eddies (i.e. positive chlorophyll-a or POC anomalies relative to the background field) could have either resulted from more favorable conditions for phytoplankton accumulation (i.e., after eddy formation), and/or entrainment of waters already hosting elevated phytoplankton (McGillicuddy, 2016). A method to distinguish phytoplankton trapping at eddy formation without subsequent enhancement, from trapping with subsequent enhancement, is to track temporal changes in chlorophyll-a within the eddy using satellite-derived concentrations (Gaube et al., 2014). A decline would

### Table 1

| Property | Out | In | Eddy 1 | Eddy 2 |
|----------|-----|----|--------|--------|
| Temperature (ºC) | 12.3 ± 0.21 (n = 291) | 11.5 ± 0.0 (n = 59)* | 15.8 ± 1.6 (n = 586) | 12.5 ± 1.0 (n = 955)* |
| Salinity (PSU) | 35.0 ± 0.1 (n = 291) | 34.6 ± 0.0 (n = 59)* | 35.8 ± 0.3 (n = 586) | 34.4 ± 0.3 (n = 955)* |
| Nitrate (µmol L\(^{-1}\)) | 4.17 ± 0.22 (n = 12) | 2.26 ± 0.88 (n = 3) | 2.07 ± 1.59 (n = 12) | <0.02 ± 0.00 (n = 7)* |
| Phosphate (µmol L\(^{-1}\)) | 0.30 ± 0.02 (n = 12) | 0.25 ± 0.03 (n = 3) | 0.17 ± 0.11 (n = 12) | 0.14 ± 0.03 (n = 7) |
| Silicic acid (µmol L\(^{-1}\)) | 1.75 ± 0.28 (n = 12) | 0.42 ± 0.39 (n = 3)* | 0.35 ± 0.22 (n = 12) | 0.31 ± 0.11 (n = 7) |
| DFe (nmol L\(^{-1}\)) | 0.17 ± 0.08 (n = 12) | 0.13 ± 0.04 (n = 2)* | 0.22 ± 0.09 (n = 12) | 0.28 ± 0.12 (n = 7) |
| DMn (nmol L\(^{-1}\)) | 0.93 ± 0.13 (n = 12) | 0.86 ± 0.15 (n = 3) | 1.15 ± 0.21 (n = 12) | 1.63 ± 0.12 (n = 7)* |
| Chlorophyll-a (µmol L\(^{-1}\)) | 1.20 ± 0.31 (n = 12) | 3.37 ± 1.21 (n = 3) | 1.12 ± 0.88 (n = 12) | 1.25 ± 0.45 (n = 7) |
| POC (µmol L\(^{-1}\)) | 16.1 ± 2.9 (n = 12) | 40.1 ± 16.1 (n = 3) | 10.8 ± 3.80 (n = 12) | 19.6 ± 3.6 (n = 7)* |
| BSI (µmol L\(^{-1}\)) | 0.47 ± 0.29 (n = 12) | 1.3 ± 0.3 (n = 3)* | 0.70 ± 0.50 (n = 12) | 0.45 ± 0.19 (n = 7) |

*Indicates statistically significant different from outside of eddies (t-test \(p < 0.05\)). \(\Delta F_v/F_m\) indicates statistically significant different mean \(F_v/F_m\) between control and +Fe treatments (t-test \(p < 0.05\)).
Figure 3. Physical and biogeochemical characterization of Eddies 1 and 2. (a), (b) Transects through eddies; blue shading intensity corresponds inversely to salinity, used to approximately delineate the eddy cores. Current speeds in the upper panels are mean values for the upper 40–120 m depth range, derived from shipboard ADCP measurements. (c) Photophysiological ($F_v/F_m$) response of phytoplankton to Fe supply at the five sites indicated in ‘a’ and ‘b’; bar heights represent mean responses, dots represent the replicate treatment responses ($n = 3$), and gray horizontal lines represent initial values. Increases in $F_v/F_m$ between Fe treated samples and untreated controls/initial values indicates recovery from Fe stress. In ‘a’, one Fe concentration value for Eddy 1 has been omitted (0.88 nmol L$^{-1}$, which exceeds the y-axis scale). SST = Sea surface temperature; PNE = photosynthetic nanoeukaryotes; PPE = photosynthetic picoeukaryotes. The units of calculated N:Fe are μmol:nmol.
be expected for trapping only, resulting from exchange with surrounding waters with lower chlorophyll-a (Olson, 1986; Gaube et al., 2014). Frequent cloud cover meant that satellite-derived chlorophyll-a trends in the two eddies were incomplete (Figures S2 and S3), but the sparse data available give no indication of declines over a four-month period prior to our occupation of either eddy. Consequently, whilst our observations were insufficient to quantitatively partition measured eddy chlorophyll-a between trapping and enhancement mechanisms, they suggest that trapping was not the sole causal mechanism (Gaube et al., 2014; Lehahn et al., 2007).

How then were elevated chlorophyll-a and POC concentrations in the eddies sustained above levels in surrounding waters? Macronutrient distributions were inconsistent with a primary role for enhanced macronutrient supply: N, P and Si were not fully depleted in surface waters outside the eddies, suggesting they were not restricting growth, and the associated standing stock, of phytoplankton. Other potential differences between the interiors of the eddies and surrounding waters may have included temperature, light availability, and grazing.

The importance of temperature (i.e. that of warmer waters leading to increased phytoplankton growth rates; Eppley, 1972) can probably be disregarded to first order, as temperatures were lower in the higher biomass cores of both eddies. However, we cannot fully rule out the impact of temperature on phytoplankton biomass via more complex ecosystem dynamics (e.g. Pomeroy & Deibel, 1986). The timing of our sampling was around or after that of the 2017 peak bloom magnitude at the eddy latitudes (assigned as maximum surface chlorophyll-a concentration in Browning et al., 2020), suggesting light availability was not the primary limiting factor (Behrenfeld & Boss, 2018; Henson et al., 2009; Mignot et al., 2018; Siegel et al., 2002). Indeed, incident surface irradiance reaches maximum annual values (∼40 mol photons m⁻² d⁻¹; Behrenfeld et al., 2013) and mixed layer depths are generally shallow at this time (MLD < 30 m; derived from n = 26 CTD casts from the DY080 North Atlantic cruise at 43–53°N; Browning et al., 2020; also see de Boyer Montégut et al., 2004). Furthermore, enhanced phytoplankton biomass inside eddies would increase light attenuation—reducing rather than enhancing irradiance in the mixed layer. Combining these factors into calculations of phytoplankton light limitation alongside the availability of nutrients (N and Fe) also suggested that the impact of differences in light on phytoplankton growth rate inside and outside of eddies would be relatively small at this time of year under the ambient nutrient concentrations (Figure S4, Text S1). The impact of grazing cannot be discounted immediately: reduced grazing within eddy cores would lead to enhanced phytoplankton accumulation and macronutrient drawdown, matching our observations.

Changes in dissolved Fe concentrations through the eddies were less clear than for macronutrients (Figure 3; Table 1). Both inside and outside Eddy 1, Fe concentrations were depleted (0.16 ± 0.07 nmol L⁻¹, mean ± s.d., n = 14) and were more variable throughout Eddy 2 (outside eddy 0.22 ± 0.09 nmol L⁻¹, n = 12; inside eddy 0.28 ± 0.12 nmol L⁻¹, n = 7). Ratios of nitrate to dissolved Fe (N:Fe) demonstrated that Fe was more deficient than N relative to assumed average phytoplankton requirements throughout Eddy 1 and at the boundary of Eddy 2, but within Eddy 2, N was the more deficient (primarily resulting from trends in nitrate; Table 1; Moore, 2016; Browning et al., 2017). Photophysiological assessment of Fe stress (Fv/Fm) at discrete locations along eddy transects was compromised by large diurnal variations in irradiance through Eddy 2, but low values throughout Eddy 1, in combination with more restricted irradiance changes, suggested that waters within Eddy 1 were Fe stressed (Behrenfeld & Milligan, 2013). Less ambiguously, changes in Fv/Fm in incubated seawater samples spiked with additional Fe implied nutrient limitation patterns consistent with the trends inferred from the N:Fe ratios: Fe addition led to significant Fv/Fm enhancements around Eddy 1 and at the boundaries of Eddy 2, suggesting phytoplankton were Fe-stressed in those areas. Conversely, Fe addition at the center of Eddy 2 did not change Fv/Fm, implying phytoplankton were not Fe-stressed there (Table 1; Figure 1c; Browning et al., 2014, 2017, 2020; Moore et al., 2006; Ryan-Keogh et al., 2013).

Indications of marked, but different, variations in phytoplankton community structure were found in surface waters across the two eddies (see Methods for details regarding potential degradation of pigment samples). Across Eddy 1, both flow cytometry cell counts and phytoplankton pigments pointed toward a higher proportion of larger cells within the eddy relative to surrounding waters. Enhanced biogenic silica concentrations were also observed within Eddy 1, suggesting higher diatom abundance relative to surrounding waters. Conversely, community structure measurements across Eddy 2 suggested a greater proportion of...
smaller phytoplankton within the eddy, presumably because nitrate was depleted to below the detection limit (e.g., Chisholm, 1992; Ward et al., 2013).

Although co-regulatory processes cannot be ruled out, our measurements support a mechanism whereby enhanced plankton biomass and nitrate drawdown within cyclonic eddies was at least partially driven by elevated Fe availability in the euphotic zone relative to surrounding waters. Incomplete drawdown of nitrate in Eddy 1 implies that the N:Fe ratio in waters supplied by within-eddy upwelling was higher than in Eddy 2, where Fe was sufficiently available to fully exhaust supplied nitrate. Differences in N:Fe could also result from enhanced retention and recycling of Fe over N (Boyd et al., 2012, 2015; Ellwood et al., 2014, 2020; Rafter et al., 2017), therefore meaning that times of sampling relative to eddy lifetimes could be important in regulating the differences in observed N drawdown (i.e., Eddy 1 being sampled earlier in its lifetime than Eddy 2). Furthermore, a lower dilution rate by surrounding higher N:Fe waters in Eddy 2, favored by its larger size, would also help maintain lower within-eddy N:Fe ratios (Abraham et al., 2000; Lévy et al., 2012). Whilst such mechanisms could all enhance Fe availability relative to N in Eddy 2, co-varying elemental signatures also suggested a role for different sedimentary Fe supply to each eddy.

Continental shelves are expected to constitute a dominant, but spatially heterogeneous, Fe supply term to intermediate depth waters in this region (Achterberg et al., 2018; Birchhill et al., 2019; Conway & John, 2014; Rijkenberg et al., 2014; Tonnard et al., 2020). Eddy 1 was located more than 800 km away from the shelf break whereas Eddy 2 was 350 km away, adjacent to, and potentially having entrained Fe from, the Flemish Cap and Grand Banks of Newfoundland (Figure 1c; Rijkenberg et al., 2014; Tonnard et al., 2020). This hypothesis is supported by distributions of dissolved Mn (Figures 3a and 3b). Open ocean Mn is typically depleted below the euphotic zone, meaning deep-water upwelling would not necessarily be associated with elevated Mn (Van Hulten et al., 2017). However, terrestrial sources of Mn cause localized enhancements (Burdige, 1993; Evans & Parslow, 1985; Lam & Bishop, 2008; Van Hulten et al., 2017). In contrast to Eddy 1, Eddy 2 had significantly higher Mn concentrations inside the eddy than outside (t-test p < 0.0001), consistent with a continental Mn, and by inference, Fe, source (Table 1; Figure 3). We therefore hypothesize that an important fraction of the supplied surface Fe and Mn in Eddy 2 originated from nearby shelf and slope sources, transported into the euphotic zone via eddy upwelling.

Our observation of enhanced plankton biomass, nitrate drawdown, and a Mn signature of enhanced Fe supply in Eddy 2 could be important for understanding the regional chlorophyll-a distribution in the mid-latitude North Atlantic. The Newfoundland Basin is characterized by intensive mesoscale eddy activity, especially in the west (Richardson, 1993). Eddy 2 is one of several that recur semi-predictably east of the Grand Banks due to interactions between the North Atlantic Current (NAC) and shelf slope (Kearns & Paldor, 2000). If our hypothesis that these eddies are fertilized by shelf-derived Fe is correct, the higher chlorophyll-a concentrations in the west of the mid-latitude North Atlantic than in the east (Figure 1a; Longhurst, 2007) could be partly caused by this mechanism. In turn, this could explain zonal gradients in zooplankton and higher trophic levels (Druon et al., 2019). Moreover, similar mechanisms could occur in bathymetrically tied eddies in other western boundary currents, such as the Kuroshio-Oyashio system (Itoh & Yasuda, 2010; Nishioka et al., 2011).

4. Conclusions

Ambient waters of the mid-latitude North Atlantic have residual macronutrients and elevated light in late spring, therefore to enhance phytoplankton concentrations in cyclonic eddies, phytoplankton losses must be diminished and/or eddies must have greater micronutrient availability. Our results support the latter hypothesis. Furthermore, greater N drawdown in eddy cores relative to their boundaries implied that, in addition to greater overall Fe supply, water entrained/upwelled into the euphotic zone had a lower N:Fe ratio than surrounding surface waters, assuming invariant N:Fe utilization and recycling ratios (although see Ellwood et al., 2020). Complete N drawdown in Eddy 2 implied an even lower N:Fe supply ratio. We suggest this was at least partly due to the closer proximity of Eddy 2 to shelf Fe sources. Both eddies enhanced post-bloom primary productivity, supporting higher trophic levels in proportion to overall nutrient supply rates; however, with more Fe potentially available from external sources, Eddy 2 had a greater macronutrient use efficiency, which would locally decrease the fugacity of CO₂ at the sea surface (Cooper et al., 1996).
Alongside other recent work (Conway et al., 2018; Ellwood et al., 2020; Evans & Parslow, 1985; Uchida et al., 2020), our results emphasize that Fe should not be neglected in detailed biogeochemical observations of mesoscale and submesoscale ocean phenomena (Gruber et al., 2011; Lévy et al., 2018; Mahadevan et al., 2014; Stramma et al., 2013). This is not only applicable in systems with residual macronutrients (e.g., Crawford et al., 2007; Evans & Parslow, 1985; Uchida et al., 2020; Xi et al., 2011), but also in macronutrient-depleted settings where Fe can be co-limiting to primary productivity alongside N (Browning et al., 2017; Mills et al., 2004; Saito et al., 2014).

**Data Availability Statement**

Biogeochemical data collected through the eddies are summarized in Table 1 and are provided in full in Data set S1, which has also been uploaded to PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.927312). The remote sensing data used in this study can be retrieved from the NASA Ocean Color website (https://oceancolor.gsfc.nasa.gov), the Ocean Color Climate Change Initiative (https://www.oceancolour.org/), and the Open-source Project for a Network Data Access Protocol (https://opendap.jpl.nasa.gov/opendap). We thank two reviewers for comments that improved the manuscript.

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