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Silicate:nitrate ratios of upwelled waters control the phytoplankton community sustained by mesoscale eddies in sub-tropical North Atlantic and Pacific

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Abstract

Mesoscale eddies in sub-tropical gyres physically perturb the water column and can introduce macronutrients to the euphotic zone, stimulating a biological response by which phytoplankton communities can become dominated by large phytoplankton. Mesoscale eddies are therefore important in driving export in oligotrophic regions of the modern ocean. The character and magnitude of the biological response sustained by eddies are, however, variable. Here we present data from mesoscale eddies in the Sargasso Sea (Atlantic) and the waters off Hawai'i (Pacific), alongside mesoscale events that affected the Bermuda Atlantic Time Series (BATS) over the past decade. From this analysis, we suggest that the phytoplankton community structure sustained by mesoscale eddies is predetermined by the relative abundance of silicate over nitrate (Si^*) in the upwelled waters. We present data that demonstrate that mode-water eddies (MWE) in the Sargasso Sea upwell locally formed waters with high Si^* to the euphotic zone, and that cyclonic eddies in the Sargasso Sea introduce waters with low Si^*, a signature that originated in the iron-limited Southern Ocean. We propose that this phenomenon can explain the observed abundance of large-diatom species in MWE and small prokaryotic phytoplankton in cyclonic features. In contrast to the Atlantic, cyclonic eddies in waters off Hawai'i induce North Pacific Intermediate Water (NPIW) that has high Si^* and therefore also appears capable of establishing diatom populations. These observations suggest that the structure of phytoplankton communities sustained by eddies may not be directly related to the physical nature of the eddy but rather to the chemical composition of the upwelled waters. This paper links the biological production and export efficiency of mesoscale eddies to events in spatially and temporally disparate locations.

1 Introduction

Coupling between physical and biological processes in oceanic systems sets constraints on primary production in the upper ocean that control both the energy entering the ecosystem and the potential for the amount of carbon exported from the upper ocean via the biological carbon pump (Ducklow, 2001; Volk, 1985). Mesoscale eddies provide a mechanism of physical-biological coupling (McGillicuddy et al., 1999; Oschlies, 2002; Oschlies and Garcon, 1998) that may be particularly significant in the large oligotrophic gyres such as the North Atlantic Sub-Tropical Gyre (NASG), where estimates of export flux made locally are in excess of geochemical estimates (Jenkins et al., 1988). Three main types of mesoscale eddy have been studied: mode-water eddies (MWE) and cyclonic eddies that cause an upward displacement of the nutracline, and anti-cyclonic eddies that cause a downward displacement of the nutracline. MWE and cyclonic mesoscale eddies can lift macronutrients into the euphotic zone and stimulate a biological response in the phytoplankton community, leading to enhanced export (McGillicuddy et al., 1999).

The episodic introduction of macronutrients from mesoscale eddies is thought to both stimulate phytoplankton growth and induce a shift from smaller to larger phytoplankton, which may subsequently export carbon from the euphotic zone more efficiently (Bibby et al., 2008; Brown et al., 2008; Mouriño-Carballido, 2009; Vaillancourt et al., 2003). Such changes in community composition, enhanced production and export have been reported from a wide variety of mesoscale eddies; however, the character and magnitude of biological responses are variable, probably owing to the transient nature of eddies (Benitez-Nelson et al., 2007; Falkowski et al., 1991; Martin and Pondaven, 2003; McGillicuddy et al., 2007; Oschlies, 2002; Oschlies and Garcon, 1998). An interesting observation from recent studies is the difference in phytoplankton community composition that is maintained in both MWE and cyclonic eddies in the Sargasso Sea region of the NASG. MWE can sustain large-diatom communities dominated by species such as *Chaetoceros* spp., which are rare for the region, while cyclonic eddies are dominated by small prokaryotic phytoplankton that are more typical of the region (Bibby et al., 2008; Mouriño-Carballido, 2009; Ewart et al., 2008). In addition, measures of biogenic silicate production (0.9–1.1 mmol Si m^{-2} d^{-1}) and accumulation (15–20 mmol Si m^{-2}) in a MWE in the Sargasso Sea have been reported that are six times greater than those recorded for the nearby Bermuda Atlantic Time Series (BATS) site (Krause, 2010). Correspondingly, the estimated biogeogenic SiO_2 export rate of 1.27 mmol Si m^{-2} d^{-1} in this MWE was 20 times higher than the BATS average, suggesting that MWE can maintain substantial diatom growth and export (Krause, 2010). Two studies over 3-year (Sweeney et al., 2003) and 9-year (Mouriño-Carballido, 2009) periods observed a total of 8 MWE, 13 cyclonic eddies and 6 anti-cyclonic eddies that affected the BATS station. In these studies, only MWE features were shown to sustain significant diatom communities; for example, Mouriño-Carballido reported a statistically significant difference in the contribution of diatom pigments to the total chlorophyll-*a* concentration integrated over the top 160 m of the water column in MWE compared with cyclonic eddies that had affected the BATS site between 1993 and 2002 (Mouriño-Carballido, 2009). While the age of eddy features may have an important role in determining the phytoplankton community composition (Rii et al., 2008; Sweeney et al., 2003), the species differences between MWE and cyclonic eddies in the Sargasso Sea appear to be robust. A potential mechanism that has been proposed to account for the magnitude of biological response between MWE and cyclonic eddy communities in the Sargasso Sea involves the effects of wind stress. Wind stress causes enhanced upwelling at the centre of MWE and downwelling in cyclonic eddies. This can persist throughout the lifetime of the eddy and thus sustain larger biological signals in MWE than cyclonic eddies (McGillicuddy et al., 2007; Martin and Pondaven, 2003). However, in contrast to the situation in the Atlantic, cyclonic eddies studied in the North Pacific Sub-Tropical Gyre (NPSG) have been shown to sustain high numbers of large diatoms for long periods and may even be active mechanisms of silica export in this region (Benitez-Nelson et al., 2007).

Recently, Si*, the difference between available silicate [$Si(OH)_4$] and nitrate [NO_3^-], has been used as a tracer of the return path of deep waters upwelled in the Southern Ocean into the thermoclines of ocean systems (Sarmiento et al., 2004). The global distribution of Si* indicates that Sub-Antarctic Mode Water (SAMW) acts as a significant source of nutrients to the thermocline in the North Atlantic, whereas North Pacific Intermediate Waters (NPIW) play a more important role in thermocline nutrient supply in the Pacific (Sarmiento et al., 2004); recent modelling studies further support this suggestion (Palter et al., 2010). In addition to acting as a tracer, we propose that the distinct Si* signatures of these water masses, negative in SAMW and positive in NPIW, also play a role in dictating phytoplankton community responses to euphotic zone nutrient input. Si* can be considered an important indicator of nutrient availability related to the requirement of diatoms (Ragueneau et al., 2000; Brzezinski et al., 2003). When sufficient light and nutrients (including iron) are available, diatoms accumulate biomass with silicate and nitrate in a molar ratio of ~1:1 (Brzezinski et al., 2003, 2005). Consequently, in order for a diatom population to efficiently utilize any available nitrate, it might be expected that the ambient Si* would have to be > 0 (Ragueneau et al., 2000). Here, we investigated the possibility that the nature of the biological response instigated by upwelling mesoscale eddies, and the observed discrepancy in large-diatom abundance between MWE and cyclonic eddies in the Atlantic and between cyclonic eddies in the North Atlantic and Pacific sub-tropical gyres, are related to the chemical composition of the upwelled waters impacting the euphotic zone.

2 Methods

2.1 General field work

The EDDIES project consisted of four cruises on the *R.V. Oceanus* over two summer field seasons (OC404-1 11 June–3 July 2004; OC404-4 25 July–12 August 2004; OC415-1 20 June–15 July 2005; and OC415-3 7 August–25 August 2005) in the Bermuda region of the Sargasso Sea (sub-tropical North Atlantic). E-Flux I (4 November–22 November 2004) and E-Flux III (10 March–28 March 2005) were conducted in the lee of the Hawaiian Islands aboard the *R.V. Kaimikai-O-Kanaloa* and *R.V. Wecoma*, respectively. Prior to each cruise, candidate eddies in the appropriate location were detected and tracked using satellite data, including the geostationary operational environmental satellites (GOES-10 and AVHRR) to detect sea surface temperature (SST), MODIS imagery to monitor surface chlorophyll-*a*, and satellite altimetry data from the CCAR (http://www.7300.nrlssc.navy.mil/altimetry) (Dickey et al., 2008; Leben et al., 2002; Seki et al., 2001; Siegel et al., 1999) Each eddy was sampled by CTD hydrocasts at several sampling stations. These stations were strategically chosen to sample sections from the outside of each eddy and through the eddy centre of each feature. The locations of these stations were based on ongoing ADCP measurements and, in the EDDIES project, were supported by along-track XBT profiles (0–700 m) to quantify the main thermocline signal.

2.2 Analytical measurements

Discrete water samples and in situ vertical profiles of temperature and salinity were collected using CTD systems, which consisted of a rosette of Niskin bottles attached to a frame containing a Seabird 9/11+CTD. Discrete samples were taken using this system to measure parameters such as phytoplankton pigmentation and inorganic nutrient analysis. In addition to sampling standard depths throughout the euphotic zone, the phytoplankton community at the deep chlorophyll maximum (DCM) was specifically targeted with reference to the real-time output from the fluorometer on the CTD rosette. In the EDDIES project, nutrient measurements were collected using a highly sensitive nanomolar technique with long-path-length spectrophotometry (Li and Hansell, 2008), and in the E-Flux project by a continuous segmented flow system consisting of components of both a Technicon Autoanalyser II™ and an Alpkem RFA 300™ (Rii et al., 2008). Phytoplankton pigment data were determined by HPLC analysis of the total phytoplankton community, as described previously (McGillicuddy et al., 2007; Rii et al., 2008). Discrete measurements from this sampling are now publicly available (through http://science.whoi.edu/users/olga/eddies/EDDIES_Project.html and http://www.soest.hawaii.edu/oceanography/eddy/). In this analysis, total chlorophyll-*a* concentration was used to estimate the relative phytoplankton abundance, while total fuxoanthin concentration was used to estimate the relative diatom abundance (Rii et al., 2008), with the ratio of fucoxanthin:chlorophyll-*a* providing an index of the proportional contribution of diatoms to total community biomass. One-way analysis of variance (one-way ANOVA) was used to compare differences in variables between different eddy types.

2.3 Retrospective analysis of BATS data

Eddy features affecting the BATS site in the period 1993–2002 have been previously identified (Mouriño-Carballido, 2009) using the analysis of eddy field animations generated from the objective analysis of satellite altimetry for the domain spanning latitude 23–28° N and longitude 75–45° W. Only eddy features that exhibited a strong signal, that affected the BATS site for relatively long periods of time, and were influenced by the centre of the eddy features were used in this previous analysis (Mouriño-Carballido, 2009). BATS sampling dates thus determined to be influenced by the centre of eddy features in the period 1993–2002 were therefore used to study the distributions of nitrate and silicate in the present analysis. Details of the BATS sampling scheme, analytical methods, data quality control and inter-calibration procedures appear in the BATS Methods Manual (Knap et al., 1993). Data are available from the BATS website at http://bats.bios.edu/.

3 Results

Here we present results of nutrient profiles and phytoplankton pigment composition of mesoscale eddy features specifically targeted in research cruises to the Sargasso

Sea region of the NASG (EDDIES project 2004–2005, McGillicuddy et al., 2007) and from mesoscale eddies that form in the lee of the Hawaiian islands (NPSG) (E-Flux project 2004, Benitez-Nelson et al., 2007). These in situ measurements have been complemented by analysis of mesoscale eddy features that affected the BATS location in the Sargasso Sea (Mouriño-Carballido, 2009). We used $\mathrm{Si}^*=[\mathrm{Si(OH)}_4]-[\mathrm{NO}_3^-]$ (Sarmiento et al., 2004) both as a tracer of water masses and as an indicator of the relative availability (or deficiency) of both nutrients for the phytoplankton community.

During the EDDIES and E-Flux programs a total of six cyclonic and two MWE were specifically targeted, and certain features were sampled on multiple occasions over time scales up to 2 months to assess the temporal development of the features. Three representative features of these programs were: (1) cyclonic eddy Opal (E-Flux program March 2005, Lat 19.52283° N Long −157.082° W, NPSG); (2) cyclonic eddy C5 (EDDIES program June 2005, Lat 30.9823° N Long −66.1807° W, NASG); and (3) MWE A4 (EDDIES program June–August 2005, Lat 30.1815° N Long −68.1593° W, NASG). The locations of the eddies were determined remotely by satellite altimetry (Dickey et al., 2008; Siegel et al., 2008) and more precisely through in situ measurements collected at sea (Benitez-Nelson et al., 2007; McGillicuddy et al., 2007). Figure 1 shows contour maps of vertical depth profiles of temperature (Fig. 1a–c), total chlorophyll-*a* concentration on a log scale (Fig. 1d–f), total dissolved nitrate concentration (Fig. 1g–i) and Si^* (Fig. 1j–l) from approximately 150-km transects through the physical centres of the three representative mesoscale features. The physical perturbation associated with the "centre" of each eddy system can be seen from the temperature profiles; this is slightly off-centre in the transect of cyclonic eddy C5. The distribution of chlorophyll throughout each feature was dominated by a DCM (Fig. 1d–f). The DCM in the centres of cyclone Opal and MWE A4 is a dominant feature, whereas in cyclonic eddy C5 chlorophyll is less enhanced with respect to the DCM community at the edge of the eddy. DCM form in well-stratified water columns throughout oligotophic ocean systems and are normally located at the top of the nutracline (Fig. 1g–i). The relative abundance of the macronutrient silicate $[\mathrm{Si(OH)}_4]$ over nitrate $[\mathrm{NO}_3^-]$, both measured in µM, can be seen from the contour plot of Si^* (Fig. 1j–l). Both cyclonic eddy Opal and MWE A4 have water with positive Si^* at depths in the eddy centre that are close to the base of the DCM and so may influence the phytoplankton community. Cyclonic eddy C5, however, has water with negative Si^* at the eddy centre close to the DCM. All three features have previously been shown to support chlorophyll biomasses in excess of what is normally measured at the Hawaiian Ocean Time Series (HOTS) and BATS at similar times of year; indeed, the highest chlorophyll concentration measured in the NASG MWE A4 was three orders of magnitude higher than anything previously measured at BATS (McGillicuddy et al., 2007). Microscopic analysis revealed that cyclonic eddy Opal supported diatom communities dominated by the large chain-forming diatoms *Chaetoceros* and *Rhizosolenia* spp. (Brown et al., 2008), whereas diatom communities supported by MWE A4 were dominated by *Chaetoceros* spp. only (Bibby et al., 2008). Previous studies have shown that cyclonic eddy C5 did not support diatom communities and was dominated by the cyanobacteria *Synechococcus* at levels higher than those seen in the background BATS community (Ewart et al., 2008).

In Fig. 2 we show the average phytoplankton community composition associated with the DCM at the eddy centre of a total of eight eddies studied as part of the EDDIES and E-Flux programmes. Due to nutrient exhaustion above and light limitation below, the DCM-associated communities (Cullen, 1982) are those most affected by the perturbed nutrient profiles associated with mesoscale eddy features; hence, any changes in community composition resulting from eddy activity are most likely to be observed here. For each eddy type (Cyclonic NPSG, Cyclonic NASG and MWE NASG) three parameters are shown: the ratio of fucoxanthin:chlorophyll-*a* an index of the proportional contribution of diatoms to total community biomass (Fig. 2a); Si^* at the DCM, a measure of the relative availability of silicate over nitrate at the DCM (Fig. 2b); and Si^* at 300 m, a measure of the relative availability of silicate over nitrate at a depth well below the euphotic zone but indicative of the ratio of nitrate and silicate supply to the euphotic zone (Fig. 2c). Each mesoscale feature was sampled on multiple occasions and the averages of each eddy type are reported (Cyclonic NPSG $n = 2$, Cyclonic NASG $n = 4$, and MWE NASG $n = 2$). Absolute concentrations of the diatom marker pigment fucoxanthin and ratios of fucoxanthin:chlorophyll-*a* indicated that the eddy types support different phytoplankton communities, with NPSG cyclones and NASG MWE, but not NASG cyclones, supporting populations of diatoms (Fig. 2a). Moreover, Si^* was lower in NASG cyclonic features at both the DCM and 300 m, which is in clear contrast to the higher values found in the other two systems. One-way ANOVA revealed significant differences in Si^* at both the DCM and at 300 m (DCM, $p = 0.0027$, $F = 7.76$; 300 m, $p < 0.0000001$, $F = 33.66$) and the ratio of fucoxantin:chlorophyll ($p < 0.0131$, $F = 5.11$) between eddy types. Subsequent Tukey-Kramer means comparison tests confirmed that both Si^* (at both the DCM and 300 m) and fucoxantin:chlorophyll were significantly ($\alpha = 0.05$) lower in cyclonic eddies within the NASG than both NASG mode-water and NPSG cyclonic features, the latter two systems being indistinguishable at the 95% confidence level. Anti-cyclonic eddies, although not considered in this paper, generally support low biomass phytoplankton communities dominated by *Prochlorococcus* ecotypes.

We also considered the mesoscale eddies that have affected the BATS site in the Sargasso Sea (NASG). These features have been identified through previous studies (Mouriño-Carballido, 2009; Sweeney et al., 2003) and indicate that while MWE support diatom populations, cyclonic eddies in the Sargasso Sea typically support enhanced *Synechococcus* populations; however, as outlined above, the reason for this has remained unknown. In Fig. 3, we present the averaged vertical profiles from 0–400 m (Fig. 3a–c) and from 0–1000 m (Fig. 3d–f) of the relative abundance of silicate over nitrate, Si^*, as well as both silicate concentration $[\text{Si(OH)}_4]$ and nitrate concentration $[\text{NO}^{3-}]$. These results show that the BATS site is affected by different water masses during cyclonic and MWE events (Fig. 3d–f). Despite these data averaging numerous features that affected BATS throughout the year, and that the influence of eddies at the BATS site is inferred remotely from analysis of sea level, the trend observed in mesoscale eddies studied in situ in spring/summer seasons during the EDDIES program is maintained. Si^* is always positive at depths from 0 m to the nutracline (Fig. 3a and c) due to surface non-silicous phytoplankton growth stripping all the available nitrate from the system leaving residual silicate (Fig. 3b). At depths below 100 m, Si* becomes negative (Si* = 0 is shown in Fig. 3a and d as a vertical dotted line), and from the nutracline to ∼500 m Si* is more negative in cyclonic features than MWE features, indicating that the trend observed in the EDDIES program (Fig. 1) is consistent with mesoscale features sampled over the past decade at the BATS site.

4 Discussion

In this paper we identify the tracer Si* (the relative abundance of silicate over nitrate) as a key parameter in determining the character of the phytoplankton community sustained by upwelling mesoscale eddies in the NASG and NPSG. In the Sargasso Sea, mesoscale eddies have been proposed to be an important mechanism by which new nutrients enter the euphotic zone and stimulate primary production and export (Jenkins et al., 1988; McGillicuddy et al., 1999; Oschlies, 2002). While this is clearly the case, there has emerged a clear and consistent trend relating to the nature of the biological response, namely that MWE support diatom populations and cyclonic eddies support prokaryotic populations (Bibby et al., 2008; Mouriño-Carballido, 2009; Sweeney et al., 2003). This has clear implications for the capacity for export within each type of feature and must be considered when deriving mesoscale-resolving models (McGillicuddy et al., 1999; Oschlies, 2002; Oschlies and Garcon, 1998), However, both features can maintain enhanced phytoplankton populations for significant periods (>6 weeks) and the mechanism for the marked biological difference has remained enigmatic (Bibby et al., 2008; McGillicuddy et al., 1999). A method of enhanced nutrient supply in MWE involving the interaction of wind stress on anti-cyclonic features has been suggested (McGillicuddy et al., 2007); however, this does not explain why there is a difference in the phytoplankton community structure or why cyclonic eddies in the NPSG are capable of maintaining communities of large diatoms (Benitez-Nelson et al., 2007).

The results presented here suggest that mesoscale eddy features in the Sargasso Sea are chemically preconditioned to support different types of phytoplankton community and that the potential for export from different features can therefore be predicted. Nitrate supplied to the euphotic zone is completely utilized within the DCM, resulting in undetectable surface concentrations (Figs. 1 and 3). As a result, both the rate of supply and ratio of supplied nutrients will be important in determining the magnitude and structure of the phytoplankton community. In MWE, where silicate and nitrate are both supplied and utilized at the DCM with high Si^*, diatoms can and do become a significant fraction of the community. However, in cyclonic eddies where silicate and nitrate are supplied at lower Si^*, and hence can only both be fully utilized at the DCM at a lower overall silicate/nitrate ratio, diatoms are restricted and comprise a smaller fraction of the community. Although complete nutrient depletion within the DCM thus drives the community structure to be dependent on the ratio of silicate to nitrate supply, the physical rate of supply will then determine the overall magnitude of biomass sustained in each eddy. This rate can vary during the lifetime of a particular feature but, as described by McGillicuddy, et al., is lower in cyclonic eddies than MWE (McGillicuddy et al., 2007). Therefore, MWE are characterized by high phytoplankton biomass, a significant fraction of which comprises diatoms, whereas cyclonic eddies in the Sargasso Sea are characterized by lower phytoplankton biomass dominated by smaller prokaryotes. Moreover, cyclonic eddies in the NPSG have a higher Si^* and hence appear to be able to support diatom populations even with a potentially low rate of nutrient supply (Benitez-Nelson et al., 2007). Interestingly, the residual silicate concentration above the DCM is similar in both cyclonic and MWE features (~1 µM, Fig. 3); this may be indicative of the concentration at which diatoms are out-competed for any remaining nitrate (Egge and Aksnes, 1992) Hence, we suggest that it is only within NASG MWE (and NPSG cyclonic eddies) that nutrient inputs at relative high Si^* can result in higher diatom standing stocks within the DCM.

The observation that cyclonic eddies in the NPSG support diatom populations (Benitez-Nelson et al., 2007; Bibby et al., 2008) clearly indicates that the mechanism responsible for governing the dominance or not of diatoms in oligotrophic eddy communities is not a cyclonic-specific physical mechanism. The nature of the biological response to eddy activity in oligotrophic systems therefore appears to be predetermined by the characteristic waters uplifted by each eddy feature. In Fig. 4, we outline the potential sources for these waters in cyclonic and MWE features in the Atlantic. Cyclonic eddies contain water with a low Si^* that is characteristic of SAMW and has recently been used as a tracer of this water mass (Sarmiento et al., 2004). The low Si^* in SAMW is the result of the selective silicate pump in the Sub-Antarctic in which iron-limited phytoplankton populations, dominated by diatoms, are heavily silicified (have a Si:N ratio >1), resulting in relatively more silicate than nitrate being exported and leaving a low Si^* signature (Sarmiento et al., 2004; Boyd et al., 2001; Hutchins and Bruland, 1998; Takeda, 1998). We suggest that this mechanism caused by iron-limitation in the Southern Ocean predetermines the biological effects of cyclonic eddies in the Sargasso Sea some 6000 miles and 50–100 years away (Naveira-Garabato, personal communication). MWE however contain Sub-Tropical Mode-Water (STMW) that is formed during winter mixing in the northern boundary of the NASG (Palter et al., 2005, 2010; McCartney, 1982; Talley and Raymer, 1982). Surface waters in the NASG have a high Si^* owing to the preferential removal of nitrate over silicate by non-silicifying phytoplankton over the summer. During winter in the STMW formation region, these surface waters will mix with deeper waters with a lower Si^* (the SAMW), forming STMW with a higher Si^* than SAMW. Consequently, when a MWE lens impacts the euphotic zone it is has the capacity to maintain significant diatom growth, in excess of the background community defined at BATS (Mouriño-Carballido, 2009). Our proposed mechanism likely explains the observed increase in biogeogenic silicate production at BATS when mode waters influence the site (Krause, 2010). It also suggests that the extent of winter mixing to the north could have a direct effect on the Si^* of STMW and therefore the biological response to MWE in this region. We believe this is the first demonstration of how mechanisms such as the selective silicate pump in the Southern Ocean, which are temporally and spatially separate from the Sargasso Sea, can affect biology and export in this region. The study further illustrates how large-scale circulation patterns can govern differences in biogeochemical responses between the North Atlantic and Pacific sub-tropical gyres.

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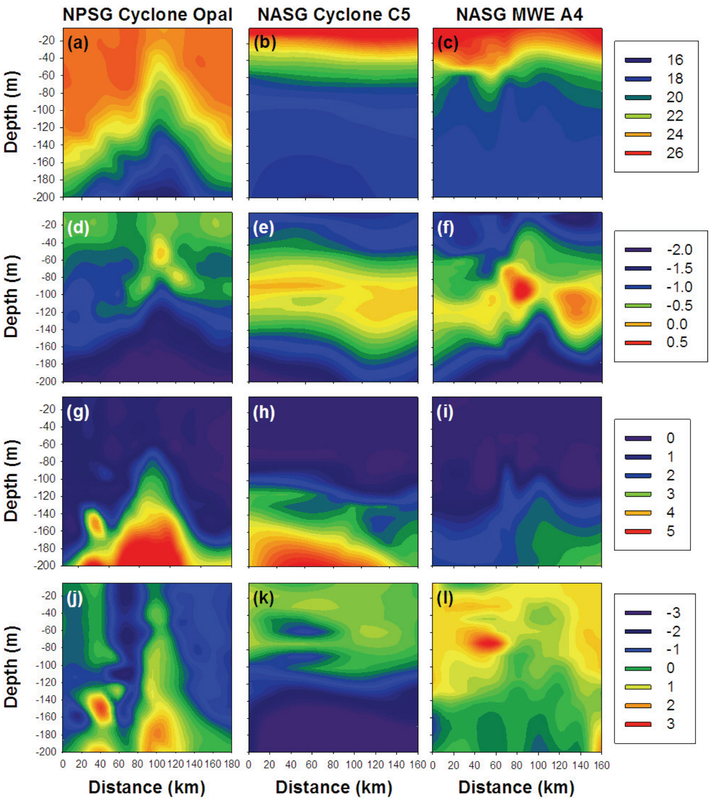

Fig. 1. Comparison of physical and chemical features in transects of vertical profiles (0–200 m) through the physical centre of three eddies. **(a–c)** show transects of temperature (°C), **(d–f)** transects of total chlorophyll-*a* (mg m^{-3}; shown on a log scale), **(g–i)** transects of total dissolved nitrate (µM), and **(j–l)** Si*. Cyclonic eddy Opal was sampled close to Hawai'i in the NPSG, while cyclonic eddy C5 and MWE A4 were sampled in the Sargasso Sea NASG, at similar times of year.

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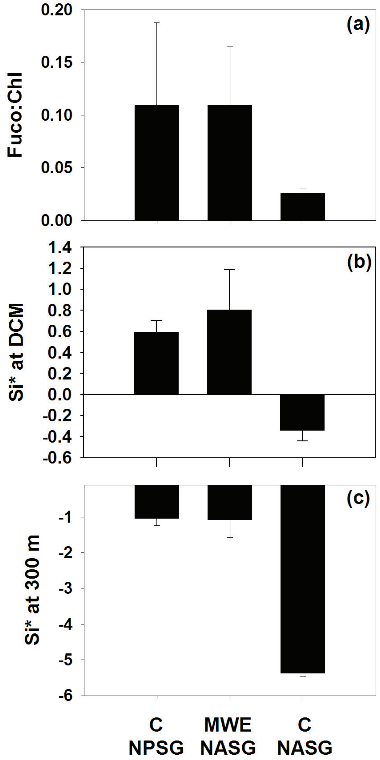

Fig. 2. The biological community sustained at the deep-chlorophyll maximum (DCM) at the central station of the three eddy types described in the paper, two from the Sargasso Sea (NASG) (MWE, $n = 2$, and cyclonic eddy, C, $n = 4$) and one from the Hawai'i region of the NPSG (cyclonic eddy, C, $n = 2$). The DCM at the eddy centre station from each feature was sampled multiple times; averages are shown for each eddy type. The y-axis represents the ratio of fucoxanthin:chlorophyll-*a* **(a)**, Si* at the DCM **(b)**, and Si* at 300 m **(c)**. Standard error bars are shown.

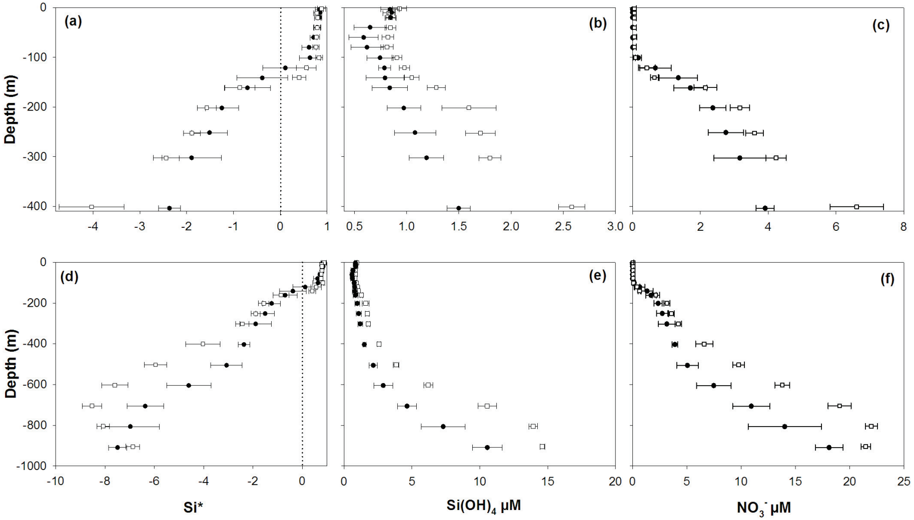

Fig. 3. Depth profiles of Si*, the concentration of silicate (Si(OH)$_4$ µM) and the concentration of nitrate (NO$_3^-$ µM) in eddy features that have affected the Bermuda Atlantic Time Series (BATS) over the past decade. Si*=0 is shown by a dotted line. Averages of six cyclonic (white squares) and four mode-water eddy (black circles) features are shown (standard error bars are shown on the graph). **(a–c)** show the depth profiles to 400 m, while **(d–f)** show profiles to 1000 m.

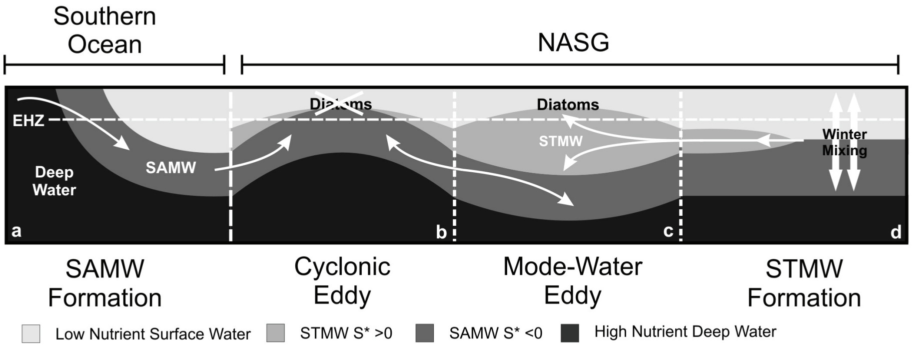

Fig. 4. Proposed model of the source of nutrients that affect the thermocline in the North Atlantic Sub-tropical Gyre (NASG). The figure shows a stylized section of Si^* in both the Southern Ocean and the NASG. Sub-Antarctic Mode-Water (SAMW) where a negative Si^* is formed in Antarctica from upwelling of nutrient-rich deep waters followed by subsequent northward Ekman transport and concurrent preferential silicate removal **(a)**. This water is transported north and can reach the thermocline in the NASG through the action of mesoscale cyclonic eddies **(b)**, but is downwelled by the action of mesoscale mode-water eddies **(c)** and uncoupled from the thermocline. Winter mixing of SAMW and surface water **(d)** on the northern boundary of the NASG leads to the formation of sub-tropical mode water (STMW) with positive Si^* that impacts the base of the euphotic zone (EHZ, dashed horizontal line) in the NASG through the action of mesoscale mode-water eddies (c). This mechanism determines whether the phytoplankton community stimulated by mesoscale eddies can sustain significant diatom populations.