1 Mesoscale and Sub-mesoscale Variability in Phytoplankton Community Composition in
2 the Sargasso Sea
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Abstract

The Sargasso Sea is a dynamic physical environment in which strong seasonal variability combines with forcing by mesoscale (~ 100 km) eddies. These drivers determine nutrient, light, and temperature regimes and, ultimately, the composition and productivity of the phytoplankton community. On four cruises (2011 and 2012; one eddy per cruise), we investigated links between water column structure and phytoplankton community composition in the Sargasso at a range of time and space scales. On all cruises, cyanobacteria (*Prochlorococcus* and *Synechococcus*) dominated the phytoplankton numerically, while haptophytes were the dominant eukaryotes (up to 60% of total chl-*a*). There were substantial effects of mesoscale and sub-mesoscale forcing on phytoplankton community composition in both spring and summer. Downwelling (in anticyclones) resulted in *Prochlorococcus* abundances that were 22-66% higher than at 'outside' stations. Upwelling (in cyclones) was associated with significantly higher abundances and POC biomass of nanoeukaryotes. In general, however, each eddy had its own unique characteristics. The center of anticyclone AC1 (spring 2011) had the lowest phytoplankton biomass (chl-*a*) of any eddy we studied and had lower nitrate + nitrite ($N+N < 5 \text{ mmol m}^{-2}$) and eukaryote chl-*a* biomass as compared to its edge and to the Bermuda Atlantic Time-Series station (BATS). At the center of cyclone C1 (summer 2011), we observed uplift of the 26.5 kg m^{-3} isopycnal and high nutrient inventories ($N+N = 74 \pm 46 \text{ mmol m}^{-2}$). We also observed significantly higher haptophyte chl-*a* (non-coccolithophores) and lower cyanobacterial chl-*a* at the center and edge of C1 as compared to outside the eddy at BATS. Cyclone C2 (spring 2012) exhibited a deep mixed layer, yet had relatively low nutrient concentrations. We observed a shift in the

taxonomic composition of haptophytes between a coccolithophore-dominated community in C2 (98% of total haptophyte chl-*a*) and a non-coccolithophore community at BATS. In summer 2012, downwelling associated with anticyclone AC2 occurred at the edge of the eddy (not at the center), where AC2 interacted with a nearby cyclone. At the edge, we found significantly lower *Synechococcus* abundances and higher eukaryote chl-*a* compared to the center of AC2 and BATS. These along-transect nuances demonstrate the significance of small-scale perturbations that substantially alter phytoplankton community structure. Therefore, while seasonality in the North Atlantic is the primary driver of broad-scale trends in phytoplankton community composition, the effects of transient events must be considered when studying planktonic food webs and biogeochemical cycling in the Sargasso Sea.

Keywords: microbe, eddy, picoplankton, community structure, pigment, CHEMTAX, HPLC, *Prochlorococcus*, *Synechococcus*, haptophyte

1. Introduction

The Sargasso Sea is an oligotrophic region of the subtropical western North Atlantic. On a seasonal basis, storm events in winter and early spring mix the water column to as deep as 400 m while thermal stratification in summer reduces the mixed layer to as shallow as 10 m (Michaels and Knap, 1996; Steinberg et al., 2001; Lomas et al., 2013). Overlaying the seasonal pattern of convection are mesoscale eddies (~100 km) (Richardson, 1993). Eddies disrupt the vertical structure of the water column and isolate water masses (Falkowski et al., 1991; McGillicuddy et al., 1998). Anticyclones (warm-core eddies) spin clockwise and are identified by a positive sea level anomaly (SLA) caused by surface convergence of low-density water that drives downwelling in the core (McGillicuddy et al., 1998). As downwelled water is usually low in nutrients, anticyclones are thought to have little to no impact on microbial biomass or biogeochemical cycles (McGillicuddy et al., 1998; Sweeney et al., 2003). Anticyclones harbor microbial food webs with high rates of recycling and low rates of particulate matter export (Mouriño-Carballido and McGillicuddy, 2006). Cyclones (cold-core eddies) spin counter-clockwise and are identified by a negative SLA caused by surface divergence that elevates isopycnals and drives upwelling (McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998). Cyclones may stimulate phytoplankton growth through nutrient injection, thereby leading to biomass accumulation and enhanced productivity (Bibby et al., 2008). Clockwise rotating mode-water eddies (positive SLA) characterized by “lensing” of 18°C mode-water near the surface, result in upwelling (McGillicuddy et al., 1999) that can uplift the permanent thermocline and stimulate blooms of large phytoplankton (McGillicuddy et al., 2007). Blooms of larger phytoplankton, specifically

diatoms, may occur due to eddy mixing and have been estimated to 35-50% of new production in the region (Goldman and McGillicuddy, 2003). These blooms are short-lived, as nutrients are utilized quickly by the resident phytoplankton (Krause et al., 2009; Lomas et al., 2009). The Sargasso Sea EDDIES project found a mode-water induced eddy diatom bloom resulted in lower particulate carbon export than outside, suggesting rapid turnover of the diatom biomass within the euphotic zone (McGillicuddy et al., 2007).

Sub-mesoscale processes, especially along fronts and eddy-eddy interaction zones, also lead to mixing events (Lévy et al., 2001; Klein and Lapeyre, 2009). These events occur on timescales of hours to days (Owen, 1981) and result in upwelling “hot-spots” (Klein et al., 2008). Phytoplankton communities can respond rapidly to the introduced nutrients (Krause et al., 2009) and modify their pigment composition in response to a changing light field on timescales of hours (Lewis and Smith, 1983). Therefore sub-mesoscale mixing events can be associated with increased biological activity (Owen, 1981; Lévy et al., 2001; Klein and Lapeyre, 2009).

Research at the Bermuda Atlantic Time-series Study (BATS) site have provided much information on the structure of the Sargasso Sea phytoplankton community on monthly, annual and multi-year basis (e.g., Michaels and Knap, 1996; Steinberg et al., 2001; Lomas et al., 2013). The most prevalent phytoplankton in the Sargasso Sea are the picophytoplankton (0.2-2 μm) that typically dominate cell abundances, chlorophyll-*a* (chl-*a*) biomass and primary productivity (DuRand et al., 2001). In winter, the cyanobacterium *Synechococcus* dominates cell abundances ($3.3 - 5.6 \times 10^4$ cells ml^{-1} ; Durand et al., 2001) while in summer and fall, the cyanobacterium *Prochlorococcus* is

the most abundant ($1.5 - 2.6 \times 10^5$ cells ml^{-1} ; DuRand et al., 2001). Picoeukaryotes are numerically less abundant than the cyanobacteria, but are larger (Worden et al., 2004) and have cell quotas of carbon (C) that are an order of magnitude greater than the cyanobacteria (2000-6000 fg C cell^{-1} ; Casey et al., 2013). On average, the relative contributions of each of these three picophytoplankton taxa to carbon-based biomass are similar to within a factor of two (DuRand et al., 2001; Casey et al., 2013). Picoeukaryote C biomass is greatest during mixing events, presumably when nutrient inputs are higher (Casey et al., 2013). Picoeukaryotes may be responsible for up to 68% of total primary productivity in the North Atlantic (Li, 1994; Jardillier et al., 2010). These eukaryote communities are largely comprised of non-calcified haptophytes (Cuvelier et al., 2010; Treusch et al., 2012) and prasinophytes (>1000 cells ml^{-1} , DuRand et al., 2001). Observations at BATS have found contributions of eukaryotes (pico- and nano-sized) to total phytoplankton C biomass have increased in association with increased mixing associated with the North Atlantic Oscillation (Casey et al., 2013).

Microbial processes dominate food web dynamics in the Sargasso Sea (Carlson et al., 1996; Steinberg et al., 2001). Recycled nutrients fuel picophytoplankton productivity (Fawcett et al., 2011) though episodic nutrient pulses driven by storms in late winter and spring can stimulate growth of large eukaryotic phytoplankton. Spring blooms are quickly exported and can account for up to 21% of new production (Lomas et al., 2009). Physical forcing by mesoscale eddies has also been shown to result in high rates of nutrient influx to the euphotic zone. An estimated 40 - 70% of the annual nitrate budget may come from eddy-induced upwelling of deep waters (Arístegui et al., 1997; McGillicuddy et al., 1998).

This work was part of a larger study of carbon cycling within Sargasso Sea food webs (see http://www.msci.sc.edu/trophic_bats). Our first step towards constructing models of Sargasso Sea food webs was to examine the scales of variability of phytoplankton community composition within the Sargasso Sea, recognizing that the presence of mesoscale eddies results in a high degree of heterogeneity in phytoplankton community composition. In this manuscript we characterize phytoplankton community composition along transects from the center of an eddy to the BATS station, using the physical environment as a natural laboratory for studying scales of variability in community structure. We also assessed temporal variability by sampling in different seasons (spring, summer) for two successive years. We hypothesized that along-transect differences in community composition could be as great within a cruise as between cruises in different seasons.

2. Material and Methods

2.1. Study Site Description

Data were collected on four cruises in the Sargasso Sea (Table 1) and four eddies sampled in total (2 anticyclones and 2 cyclones). Eddies were identified using satellite-derived SLA data provided by Drs. Valery Kosnyrev and Dennis McGillicuddy of Woods Hole Oceanographic Institution. On all but one cruise (AE1206), sampling was conducted at three stations: at the center of a mesoscale eddy, the approximate edge of an eddy, and the BATS site (Table 1). Target eddies (one per cruise) were initially identified on the day of departure and the ship's position within the eddy (in the center or at the edge, as appropriate) was confirmed by daily checks of SLA data. The

identification of eddy edges and centers was by eye using SLA maps. Coordinates for the center of eddies were identified as the latitude and longitude of the center of the “bulls eye” of a cyclone or anticyclone as seen in the satellite altimetry data. As the altimetry data are interpolated in areas between satellite passes, the identification of ‘center’ was always approximate. Similarly, we defined the edge of an eddy as a station as far as possible from the eddy ‘center’, but still within the interpolated structure/color code of the altimetry. In all cases, we targeted stations for which ‘real data’ existed from a satellite pass through the target area. In each year, both an anticyclone (AC) and cyclone (C) were sampled: AC1 (Feb-March 2011), C1 (July-Aug 2011), C2 (March 2012), and AC2 (July 2012).

2.2. Sampling and measurements

At each station, high-resolution “core” CTD casts (to either 500 m or 2000 m depending on the day’s required sampling) were performed at mid-day to measure core physical, chemical and biological parameters of the water column. Casts were also performed before dawn at each station for size-fractionated biomass and primary productivity experiments, complete results of which will be presented in a separate publication. Additional “deep” casts (>1000 m) were performed when sampling time permitted at each station. All casts measured vertical profiles of chl-a fluorescence (Chelsea-MkIII Aquatracka), temperature (SBE 3-02/F) and salinity (SBE 4-02/0) using a Sea Bird CTD (Sea-Bird Electronics, SBE-09 *plus*). Irradiance profiles on daytime casts were collected with a 2π PAR sensor (Biospherical Instruments QSP-2350) mounted to the upper frame of the rosette. For core and deep casts, water samples

were taken from four to six depths (generally 1, 20, 50, 100, 150, 200 m) and from the fluorescence maximum (generally 75, 80 or 90 m) using 12-liter Niskin bottles mounted on a 24-bottle CTD rosette (General Oceanics Model 1016-24). Discrete samples for pre-dawn “productivity” casts were taken from 3-4 depths (20, 50, 80 and 100 m).

Water samples were gravity-filtered through a 0.8 μm polycarbonate filter for measurements of inorganic nutrients (nitrite + nitrate (N+N), phosphate, and soluble reactive phosphorus (SRP)). Samples preserved in paraformaldehyde (0.5% final concentration) were used for enumeration of picophytoplankton abundance by flow cytometry. In general, all sample collections were performed using BATS methods (http://bats.bios.edu/bats_methods.html; see also Lomas et al., 2013). Samples (1 - 2 liters) for determination of diagnostic photosynthetic pigments by HPLC were collected from discrete depths during all casts (core, deep, and productivity) and filtered under gentle vacuum onto 0.7 μm Whatman GF/F filters (Pinckney et al., 1996). Each filter was folded and placed into a 1.5 ml cryotube and immediately frozen at -80° C. Filters were stored at -80° C until analysis as described in section 2.3.2.

2.3. Analytical Methods

2.3.1. *Nutrients*

Inorganic nutrient analyses (nitrate + nitrite, N+N) were performed by Continuous Flow Analysis on a Technicon Auto Analyzer III at the Bermuda Institute of Ocean Sciences (Dore et al., 1996). SRP concentrations were analyzed using the Magnesium Induced Co-precipitation (MAGIC) method (Karl and Tien, 1992; Rimmelin and Moutin, 2005; modified as described in Lomas et al., 2010).

2.3.2. HPLC and CHEMTAX analysis

Samples for HPLC analysis were lyophilized for 24 h at -50° C, placed in 90% acetone (0.45-0.55 ml), sonicated, and extracted at -20° C for 24 h. Filtered extracts (350 µl) were injected into a Shimadzu HPLC equipped with a monomeric (Rainin Microsorb-MV, 0.46 x 10 cm, 3 µm) and a polymeric (Vydac 201TP54, 0.46 x 25 cm, 5 µm) reverse-phase C18 column in series. A nonlinear binary gradient consisting of the solvents 80% methanol: 20% 0.50 M ammonium acetate and 80% methanol: 20% acetone was used for pigment separations (Pinckney et al., 1996). Absorption spectra and chromatograms (440 ± 4 nm) were acquired using a Shimadzu SPD-M10av photodiode array detector. Pigment peaks were identified by comparison of retention times and absorption spectra with pure standards (DHI, Denmark). The synthetic carotenoid β-apo-8'-carotenal (Sigma) was used as an internal standard.

HPLC pigments were used for taxonomic identification of phytoplankton groups using CHEMTAX software (Mackey et al., 1996). Initial pigment ratios used in the CHEMTAX matrix were compiled using Higgins et al. (2011) (Table S1). Prior to CHEMTAX analyses a cluster analysis procedure based on 15 photopigment variables was used to define homogeneous groups for separate bins in CHEMTAX analyses (SPSS v. 22.0). Two clusters, each containing 139 (8%) and 1572 (92%) of samples were constructed. The program was run with an iteration limit of 500. The groups were then analyzed using two bins in CHEMTAX to provide estimates of the abundances of seven algal groups according to the method developed by Latasa (2007). The initial pigment ratio matrix (from Higgins et al., 2011; Table S1) was applied to each set of

binned data, the generated matrix was then applied to the data and run again. A minimum of 10 runs was performed on each set of binned data in this manner and was continued until an RMS error of <10% was achieved.

2.3.3. Flow cytometry

Samples fixed with paraformaldehyde were analyzed on a Becton-Dickinson Influx cytometer using 488 nm blue excitation laser with chl-a (692 nm) and phycoerythrin (580 nm) emission bands. The number of *Prochlorococcus* (*Pro*), *Synechococcus* (*Syn*), picoeukaryotes and nanoeukaryotes were enumerated and converted to cell abundances (cells ml⁻¹) by the volume-analyzed method (Sieracki et al., 1993). Cell abundance and size data were then converted to carbon biomass (fg cell⁻¹) using published relationships between cell size and carbon (Casey et al., 2013).

2.4 Statistical Analyses

We determined whether total phytoplankton chl-a biomass (integrated to 100 m) varied significantly by location along each transect (center, edge, and the BATS station) using a single-factor analysis of variance (ANOVA). For these analyses, we combined data from the core casts, productivity casts, and deep casts performed at each station. We also tested whether phytoplankton community composition varied significantly by location (center, edge, and the BATS station) using a multivariate analysis of variance (MANOVA). As with the ANOVA, data was pooled from core casts, productivity casts and deep casts at each station. A MANOVA was performed on integrated relative and absolute chl-a community composition data for each cruise. Flow cytometry data

(replicate casts for statistical analyses) were only available for 3 cruises (summer 2011, spring 2012 and summer 2012). Group abundances (cells m⁻²) and POC data (mg m⁻²) of the picophytoplankton (*Pro*, *Syn* and picoeukaryotes) and nanoeukaryotes were tested. Statistical analyses were performed using routines in SPSS Software 22.0 (IBM Corporation, Armonk, New York). Differences were considered significant when $p < 0.05$.

3. Results

For presentation of results, we grouped physical, chemical, and biological data for each eddy: AC1 (Figs. 1, 2), C1 (Figs. 3, 4), C2 (Figs. 5, 6), and AC2 (Figs. 7, 8).

3.1 General trends

The water column was well mixed with MLD 65-340 m (Table 1) in the spring, especially in 2011 (Fig. 1b-d) when high winds and rough sea state forced a halt to CTD operations. The water column was strongly stratified, MLD < 35 m at all stations in summer (Table 1). Surface water temperatures did not exceed 20.5°C in spring, but were greater than 26°C in the summer of both years (Figs. 3, 7a). Euphotic zone depths (defined as the depth of 1% surface irradiance) ranged between 93 and 176 m in the spring, and 102 to 148 m in the summer of both years. In general, N+N and SRP concentrations were low to undetectable at the surface with concentrations increasing with depth at all stations and all cruises. For brevity, we show data from three representative depths (1 m, chlorophyll maximum, and 150 m).

Phytoplankton biomass and community composition varied with distance along each transect and with season (Table 2). Overall, the dominant phytoplankton groups

were the cyanobacteria and haptophytes (Figs. 5a-g, 6a-g, 7a-g and 8a-g) with *Prochlorococcus* and *Synechococcus* dominating picophytoplankton abundances (in cells ml^{-1}) on each cruise (Figs. 5h-i, 6h-i, 7h-i and 8h-i). Due to the low abundance of pico- and nanoeukaryotes compared to the cyanobacteria they are reported as a total (“Euks”) in our figures. In addition to cyanobacteria and haptophytes, we observed variable contributions by prasinophytes and dinoflagellates (Figs. 5a-g, 6a-g, 7a-g and 8a-g). Together, these four algal groups comprised 70 - 100% of total integrated chl-a biomass on all cruises. Cryptophytes were identified (by CHEMTAX) at multiple depths on both spring cruises (Figs. 5a-g and 7a-g). Overall, the highest values for integrated chl-a biomass were observed at the edge of eddy AC1 and at BATS in spring 2011 (Fig. 5f), and at the center of eddy C2 in spring 2012 (Fig. 7f; Table 2).

3.2. Spring 2011 Eddy AC1

In spring 2011, anticyclone (AC1) was sampled and the eddy center was located 215 km south of BATS (Fig. 1a). In AC1 surface waters were warmer at the center and edge of the eddy (20.5°C) and these warm waters extended to 200 m (MLD) as compared to the BATS station (19.5 °C) (Fig. 1b). This mixing is also apparent in the salinity profile where less saline water was found at depth (Fig. 1c). Mixed layer depths in the eddy center were 192-201 m and highly variable at the edge (between 38-190m) and BATS (between 77-340 m) (Table 1). In spring 2011, N+N was undetectable to 150 m at the center station (0 km) (Fig. 1e-g, left panels). At the edge of eddy AC1 (83 km), N+N was low but detectable at 80 m the chlorophyll “maximum” ($\sim 0.2 \mu\text{mol l}^{-1}$) and increased to $1.4 \mu\text{mol l}^{-1}$ at BATS (Fig. 1 e-g; left panels). SRP was barely detectable at

the center of the eddy, but concentrations at all depths increased along the transect to a maximum of $0.04 \mu\text{mol l}^{-1}$ at 150 m at BATS (Fig. 1e-g; right panels). The deepest mixed layer depth of 340 m (cast 17; Table 1) occurred during a storm event that terminated ship operations at BATS. Overall, nutrient inventories were lowest at the center of AC1, increased at the edge and were greatest at BATS (Table 2).

Vertical mixing resulted in there being no strong chlorophyll maximum at any station (Fig. 2a-e). Cyanobacteria and haptophytes comprised the majority of total chl-*a* at all depths and stations (Fig. 2a-e). Prasinophytes, cryptophytes, and pelagophytes all increased significantly ($p = 0.012$) in their absolute and relative contributions to total chl-*a* at BATS as compared to the center of the eddy (Fig. 2f-g). At the center of AC1, *Prochlorococcus* was the most abundant of the cyanobacteria (Fig. 2h-i; Table 2), but *Synechococcus* dominated at the edge station and BATS (Fig. 2h-i; Table 2) and comprised the majority of cyanobacteria POC in all cases (Fig. 2j-k; Table 2). Cell abundances of the pico- and nanoeukaryotes (Euks) were minimal compared to those of the cyanobacteria (Fig. 2h-i), while the less numerous nanoeukaryotes contributed more to integrated Euk POC at all stations (Table 2). Overall, both cell abundances and POC biomass for all groups were highly variable among casts but followed a similar distribution pattern as chl-*a* biomass at the surface and chlorophyll “maximum” (Fig. 2h-k). Total integrated phytoplankton chl-*a* biomass was significantly lower ($p = 0.013$) at the center of eddy AC1 (Fig. 2f, Table 2) compared to the other stations (Fig. 2f). Also of note, casts 4 and 5 (Table 1), while still in the eddy center, were just outside the area of maximum SLA displacement. This may explain the increase in chl-*a* biomass from the initial cast at the center of AC1 (cast 3) to the successive casts (Fig. 2f).

3.3. Summer 2011 Eddy C1

In summer 2011, we sampled in a cyclone (C1), the center of which was located 178 km southwest of BATS (Fig. 3a). The water column was stratified to ~ 75 m at all stations as shown by temperature and density profiles (Fig. 3b-d) with MLD < 25 m at all stations (Table 1). N+N was barely detectable (detection limit = $0.05 \mu\text{mol l}^{-1}$) in surface waters at the at all stations (Fig. 3e; left panel) and concentrations increased substantially with depth to a maximum of $3\text{--}4 \mu\text{mol l}^{-1}$ at 150 m (Fig. 3g, left panel). At the eddy center and BATS stations 18°C water penetrated to 200 and 250 m, respectively, but was below 300 m at the edge station (Fig. 3b). SRP concentrations (detection limit = 1 nmol l^{-1}) showed vertical and along-transect trends that were similar to those of nitrate (Fig. 3e-g; right panels). Integrated nutrient inventories (both N and P) were greatest at the eddy center (0 km) and progressively decreased at the edge (95 km) and BATS (178 km) (Table 2).

In summer 2011, vertical profiles showed low chl-*a* biomass ($< 0.2 \text{ mg m}^{-3}$) in the upper 50 m and these communities were nearly exclusively comprised of cyanobacteria and haptophytes (Fig. 4a-c). With the exception of cast 14 (C1 edge), chl-*a* concentrations at discrete depths varied by $< 0.1 \text{ mg m}^{-3}$ between casts at each station (Fig. 4a-e) and integrated biomass varied by $< 5 \text{ mg chl-}a \text{ m}^{-2}$ (Fig. 4f). Broad and distinct deep chlorophyll maxima (DCM) extended between 80 and 100 m on each cast (Fig. 4d-e). *Prochlorococcus* dominated the cyanobacteria community throughout the water column (Fig. 4h-i, Table 2) and were most abundant at the DCM where *Synechococcus* was rarely observed (Fig. 4i). Eukaryote communities at the DCM were

largely comprised of haptophytes and prasinophytes at the center and edge of eddy C1 (Fig. 4d-e). We observed significantly greater nanoeukaryote cell abundances ($p = 0.004$) in C1 and greater haptophyte chl-*a* biomass ($p = 0.007$) as compared to BATS (Table 2). At BATS, where eukaryote abundances were lowest, we observed a significant increase ($p = 0.001$) in absolute and relative integrated cyanobacteria chl-*a* biomass (Figs. 4a-b). Overall, total integrated phytoplankton biomass (as chl-*a*) did not differ significantly ($p = 0.056$) along the transect (Fig. 4f; Table 2).

3.4. Spring 2012 Eddy C2

In spring 2012, we sampled a cyclone (C2) located 145 km northeast of the BATS station (Fig. 5a); surface water temperatures were cooler at the center of eddy C2 than at the BATS station (19°C vs. 20.5°C) (Fig. 5b). Surface salinities ranged from 36.6 at the center station to 36.7 at BATS (Fig. 5c). Density anomalies followed temperature and salinity profiles; 26.5 kg m⁻³ waters were located at 200 m at the center of the eddy but below 300 m at BATS (Fig. 5d). Concentrations of N+N were <0.1 μmol l⁻¹ at the surface in the center of C2 (Fig. 5e; left panel, shaded) and at the chlorophyll max reached 0.5 μmol l⁻¹ at BATS (Fig. 5f; left panel, no shading). N+N concentrations were highly variable among casts at 150 m at both stations, and ranged between 0.2 and 1.8 μmol l⁻¹ (Fig. 5g; left panel). SRP concentrations showed similar spatial trends as N+N and peaked at 0.08 μmol l⁻¹ at 150 m at BATS (Fig. 5g; right panel, no shading). Overall, nutrient inventories were lower at the center of C2 (0 km) than at BATS (145 km) (Table 2). Mixed layer depths were consistently deeper at the center station (152-166 m) compared with conditions at BATS (65-137 m) (Table 1). At BATS we first observed a

MLD of < 70 m that deepened to 137 m (cast 23) and again shoaled to 65 m by the final day of sampling (Table 1).

Chlorophyll *a* biomass was greater at the surface in the center of C2, as compared to communities at BATS where chl-*a* in the upper 20 m was < 0.2, more reminiscent of summer conditions (Fig. 6a-b). We also observed that between-cast variability in total chl-*a* biomass was high both at discrete sampling depths and integrated throughout the water column (Fig. 6a-f, Table 2). This was particularly evident at BATS where chl-*a* biomass between 40-50 m doubled from cast 17 to 25, and then gradually decreased over subsequent casts (Fig. 6c). Haptophytes dominated eukaryote chl-*a* biomass, while cryptophytes, prasinophytes and diatoms were identified infrequently along the transect (Fig. 6a-g). At the center of C2 we found these groups at shallower depths (<80 m) compared to their vertical distribution at BATS (Fig. 6a-c). At a single cast in the center of C2 (cast 13) we found diatoms in the upper 20 m (Fig. 6a-b) that resulted in diatoms comprising 5% of total integrated chl-*a* (Fig. 6g).

Synechococcus was the most abundant cyanobacterium at all stations and depths (Fig. 6h-i). Integrated picocyanobacteria and eukaryote (pico and nano) POC biomass was significantly greater ($p = 0.012$) at the center of C2 as compared to communities at BATS (Table 2). Eukaryote cell abundances and POC were greatest at the surface and decreased with depth; this trend was most notable at BATS (Fig. 6h-k).

3.5. Summer 2012 Eddy AC2

In summer 2012, we sampled inside of anticyclone AC2 located 205 km northwest of the BATS station (Fig. 7a). We found the water column was well stratified

at all stations (Fig. 7b). There were no strong along-transect variations in surface temperature, except a slight dip in temperature and salinity that coincided with rainfall of $= 25 \text{ mm day}^{-1}$ at the edge of AC2 (Fig. 7b-c). N+N concentrations were just above detection at the surface (Fig. 7e, left panel) and increased with depth at all stations (Fig. 7f-g, left panels). No clear nutrient trends were observed among the three stations at the DCM (Fig. 7f, left panel). At 150 m, N+N concentrations were $1.3 - 1.6 \mu\text{mol l}^{-1}$ at the center of AC2, lower at the edge ($<1 \mu\text{mol l}^{-1}$) and greatest at BATS ($>2 \mu\text{mol l}^{-1}$; Fig. 7g). SRP concentrations showed along-transect trends that were similar to those of N+N at 150 m, with maximum concentrations ($\sim 0.08 \mu\text{mol l}^{-1}$) measured at BATS (Fig. 7g; right panel, no shading). The lowest nutrient inventories (N and P) were measured in the center of AC2 (0 km) as compared to the edge (125 km) and BATS (205 km) (Table 2). The deepest MLD were observed at the edge station (25-34 m) compared with conditions at the center (18-24 m) and BATS (15-22 m) (Table 1).

In summer 2012, cyanobacteria and haptophytes dominated absolute and relative contributions to chl-*a* biomass at all stations and depths (Fig. 8a-e) and *Prochlorococcus* was the most abundant cyanobacterium at all stations and depths (Fig. 8h-i). Integrated *Prochlorococcus* abundances were significantly higher ($p = 0.001$) at the edge of eddy AC2 compared to the center station or BATS, while *Synechococcus* abundances decreased significantly ($p = 0.002$) at the eddy edge (Table 2). Vertical chl-*a* profiles showed a distinct DCM between 80 and 120 m at all stations (Fig. 8d, e). At the edge of AC2 chl-*a* increased at shallower depths relative to the other stations (Fig. 8a-c), and for many casts the DCM was located at 80 m (Fig. 8d). *Prochlorococcus* was most abundant at the DCM (Fig. 8i). Also, at the DCM, prasinophytes and

dinoflagellates made substantial contributions to total chl-*a* at all stations (Fig. 8d-e). Eukaryote (pico- and nanoeukaryote) abundances and POC increased with depth at all stations though between-cast variability was high (Fig. 8h-k). Integrated Euk cell abundances and carbon biomass increased along the transect (Table 2). Despite intra-station variability, integrated chl-*a* biomass was significantly greater ($p = 0.002$) at the edge of AC2 as compared with the center and BATS stations (Fig. 8f, Table 2). Along the transect haptophytes and cyanobacteria comprised ~40% of total chl-*a* biomass each, followed by prasinophytes (10-20%) (Fig. 8g).

4. Discussion

Results of our two-year investigation in the Sargasso Sea showed that eddies significantly affected the biomass of the ambient phytoplankton community and the magnitude and direction of this change varied with season and by eddy. We begin with a discussion of the physical forces that act on a variety of time and space scales.

4.1. Impact of seasonality on water column conditions in the Sargasso Sea

In this study, data collected in spring and summer of both years clearly showed the large-scale (gyre-wide) seasonality that defined the water column structure and has been well described previously for this region (Steinberg et al., 2001; Lomas et al., 2013). In spring 2011 and 2012 we observed cool, well-mixed surface waters that differed from the thermally stratified waters in summer. Cool, high density surface waters in winter drive mixing deepened by episodic storm events throughout spring (Michaels and Knap, 1996; Lomas et al., 2009). High rates of organic matter

remineralization at the surface (Carlson et al., 1996) in summer promote accumulation of nutrients in the permanent thermocline near the base of the euphotic zone (Jenkins and Doney, 2003). In our study, comparisons of vertical nutrient profiles between seasons showed this seasonal effect: during summer N+N exceeded $2 \mu\text{mol l}^{-1}$ between 80 and 150 m but was often $<1 \mu\text{mol l}^{-1}$ at these depths in spring when the MLD was deepest. The physical stratification of the water column results in the development of a well-defined DCM near the base of the euphotic zone where phytoplankton balance their need for sunlight with access to the nutricline (Cullen, 2015). On both summer cruises a DCM persisted between 80 and 100 m where chl-*a* concentrations often exceeded 0.55 mg m^{-3} . The seasonally alternating conditions of mixing and stratification impact phytoplankton community structure on the timescales of months (DuRand et al., 2001).

4.2. Influence of mesoscale and sub-mesoscale forcing on water column conditions

Mesoscale eddies act on shorter timescales and over smaller spatial scales than basin-wide seasonal hydrographic changes, but are important features due to their pervasiveness (Richardson, 1993). Eddy circulation both isolates water parcels and drives downwelling or upwelling of water masses, the impact of which is greatest at the core (Sweeney et al., 2003; Anderson et al., 2011). These effects can last for months, or until interaction with surface winds and other eddies breaks down eddy circulation (Sweeney et al., 2003; Anderson et al., 2011). We found on each cruise that the physical, chemical and biological conditions within each eddy differed from conditions at our “outside of the eddy” station, the BATS station. However, the magnitude and

direction of this impact varied by season and eddy and will be discussed in more detail in sections 4.3.1 and 4.3.2. While mesoscale forcing drives sustained mixing and can have potentially week to month-long effects on microbial communities, phytoplankton respond on short time scales (~1 day) to physical perturbations (Letelier et al., 2004). In summer 2012 we witnessed an increase in phytoplankton chl-*a* biomass ($p = 0.002$) associated with the edge of anticyclone AC2 that was interacting with a nearby cyclone. Though this response was outside of the eddy core where isopycnal displacement should be greatest, we also observed a shift in the composition of the cyanobacteria community at the interaction zone that we infer was due to sub-mesoscale mixing (Klein et al., 2008). Additionally, on space scales of 1 km or less (Owen, 1981) vertical mixing by internal waves can have a notable effect on phytoplankton communities, especially at the DCM (Lomas et al., 2009; Liccardo et al., 2013) and will be discussed in section 4.3.2.

On each cruise we measured both short-term temporal and small-scale spatial changes in phytoplankton community composition. In eddies we employed Lagrangian sampling where SLA data was used to track a specific location (~center and edge) and multiple casts were performed at these stations. In eddies between-cast variability represented short-term temporal changes in a particular water mass. This differed from our Eulerian sampling at the BATS station; there daily changes demonstrated spatial heterogeneity as water masses moved passed our fixed position. Both our Lagrangian (eddy) and Eulerian (BATS) sampling revealed significant variability in phytoplankton biomass between successive casts. These data support our hypothesis that along-

transect differences in community composition could be as great within a cruise as between cruises in different seasons.

4.3. Phytoplankton community composition in spring and summer in the Sargasso Sea

Data from this study showed that small phytoplankton, with high affinity for nutrients at low concentrations (Chisholm, 1992), dominated the phytoplankton community on all cruises, a condition that is well established in the Sargasso Sea (Lomas et al., 2013). The dominant phytoplankton groups, in terms of cellular abundance, were the cyanobacteria that followed a seasonal oscillation whereby *Prochlorococcus* was numerically dominant on summer cruises and *Synechococcus* in spring, in most cases. Communities of prasinophytes, pelagophytes, dinoflagellates, and cryptophytes (identified by pigment data) were found throughout the water column on spring cruises, and at the DCM in summer. Typically, pigment data from monthly BATS cruises are analyzed by the Letelier et al. (1993) method that does not include the cryptophyte biomarker, alloxanthin. Flow cytometry (DuRand et al., 2001; Cavender-Bares et al., 2001) and RNA analyses (Treusch et al., 2012) have demonstrated the presence of cryptophytes in the region, especially during the spring bloom. Our analyses used CHEMTAX software that employs factor analysis to fit data based on an initial estimation of pigment ratios for specified algal groups (Mackey et al., 1996) (refer to Table S1 for our starting matrix). Alloxanthin was quantified on nearly all cruises, and we found cryptophytes contributed up to 25% of integrated chl-*a* biomass in spring.

Haptophytes were the most dominant eukaryotes, in terms of contribution to chl-*a*, in our samples during both seasons. Haptophyte communities in the Sargasso Sea

are comprised of nanophytoplankton-sized coccolithophores that respond rapidly to convective overturn in winter/spring (Lomas et al., 2009), and non-calcareous picophytoplankton that persist throughout the year (Cuvelier et al., 2010; Jardillier et al., 2010; Treusch et al., 2012). In our study, non-coccolithophorid organisms comprised 60-89% of total integrated haptophyte chl-*a* biomass in summer, while in spring coccolithophores contributed up to 98% of total (data not shown). Recent evidence suggests that non-coccolithophore haptophytes may be responsible for 30-50% of global phytoplankton stocks (Liu et al., 2009). These organisms persist under low nutrient conditions and sub-optimal irradiances through a pairing of photosynthetic and mixotrophic lifestyles (Zubkov and Tarran, 2008). Our CHEMTAX data suggests that haptophyte community composition varies between stations within an eddy and outside, and specific examples will be described in the following sections.

As much of this discussion relies on our CHEMTAX analyses we performed a first-order check of our results by dividing pigment data by flow cytometry cell abundances. We performed this analysis for *Prochlorococcus* and *Synechococcus*. The average chl-*a* per cell for *Prochlorococcus* was 1.0 fg chl-*a*/cell which compared well with published values of 0.88-1.76 fg chl-*a*/cell (Morel et al., 1993). Additionally, values of chl-*a*/cell increased for both groups at the DCM as would be expected due to photoacclimation. We found these patterns of chl-*a*/cell matched those of C/cell for *Synechococcus* that increased substantially at the DCM, from 200 fg C/cell at depths above 50 m to >400 fg C/cell below. We also considered the potential for loss of *Prochlorococcus* cells (average size 0.6 μ m; Morel et al., 1993) through 0.7 μ m GF/F filters used for pigment samples. Researchers in David Karl's lab at the University of

Hawaii regularly process filtrates of pre-sorted samples on their flow cytometer. Based on their unpublished analyses, up to 5% of *Prochlorococcus* may pass through a 0.7 μm filter (Ken Doggett, pers. comm.). Using our estimates of 1.0 fg chl-*a*/*Prochlorococcus* this would result in an average underestimate of 0.0037 mg chl-*a* m^{-3} , or 1-2% of total. We also present data collected during both day and night periods, which may present a source of error, particularly for chl-*a* measurements. Integrated chl-*a* biomass from night casts was often, but not always, lower by 0.2-6.6 mg chl-*a* m^{-2} as compared to values from day casts at the same station. These values corresponded to 1-44% of total chl-*a*. Ideally, all casts would be performed at equivalent time points, though in our case maximizing replication at each station required this sampling scheme.

4.3.1. Impact of mesoscale and sub-mesoscale activity on phytoplankton communities under seasonally mixed conditions

In spring 2011, we visited an anticyclone (AC1) that was ‘typical’ with respect to its physical and biological features: downwelling and low nutrients. We observed deepening of the MLD in the center of eddy AC1 coincident with a reduction in overall nutrient concentrations, as compared to variable MLD and higher concentrations of nutrients (two orders of magnitude greater) at BATS. We contend that the downwelling of warm, low-density surface waters to 200 m (MLD) resulted in the transport of nutrient-poor surface waters to depth, a common feature of anticyclones (Sweeney et al., 2003). Downwelling anticyclones in the Sargasso Sea have garnered little attention as their effect on chl-*a* biomass is expected to be minor (McGillicuddy et al., 1998; Sweeney et al., 2003; Ewart et al., 2008). However, we observed anticyclones could be associated

538 with significant changes in cyanobacteria community structure in both spring and
539 summer. In spring 2011 we observed a reduction of total and eukaryote integrated chl-a
540 biomass ($p = 0.012$) in the center of AC1 as compared to the eddy edge and BATS
541 while *Prochlorococcus* was highly abundant in the center of the feature. Typically,
542 *Prochlorococcus* dominates the cyanobacteria community in the summer while
543 *Synechococcus* is more prevalent in spring (DuRand et al., 2001). Associated with this
544 anomalous spring *Prochlorococcus* community, temperatures at the center of AC1 were
545 1° C warmer and N+N inventories an order of magnitude lower than at BATS. DuRand
546 et al. (2001) found the two groups of cyanobacteria were nearly equal in abundance at
547 BATS in spring 1990 when N+N did not exceed $0.1 \mu\text{mol l}^{-1}$ at the surface.
548 *Prochlorococcus* is well adapted to oligotrophic conditions and they use the limiting
549 nutrient resources with high efficiency (Lomas et al., 2014). Light and temperature are
550 the main controls on *Prochlorococcus* growth and they are constrained to warmer
551 waters than *Synechococcus* (Chisholm et al., 1992).

552 At the edge of AC1 and at BATS, the diversity of phytoplankton communities
553 resembled spring bloom conditions, when larger eukaryotes are more abundant
554 (Bidigare et al., 1990; Lomas et al., 2009). Cryptophyte chl-a biomass was greater ($p =$
555 0.012) at BATS in spring 2011 as compared with the center of AC1. We also measured
556 the greatest nanoeukaryote abundances ($2 \pm 0.4 \times 10^{10} \text{ cells m}^{-2}$) of any cruise at
557 BATS. The presence of cryptophytes and abundance of larger cells indicated the spring
558 bloom was progressing outside the eddy center. Traditionally, the spring bloom begins
559 after the winter mixed period when the water column begins to stratify and initially
560 promotes the growth of larger eukaryotes (Sverdrup, 1953). Evidence for the

561 suppression of the *Synechococcus* and eukaryote-dominated community by AC1
562 included the numerical dominance of *Prochlorococcus* and the greater ($p = 0.007$)
563 contributions by cyanobacteria to total chl-*a* biomass observed in the downwelling
564 center of the anticyclone. Unfortunately, we were not able to re-occupy the eddy to
565 determine how long this community was sustained.

566 In spring 2012 we sampled cyclone C2 that exhibited upwelling at the core, as
567 evidenced by cooler water temperatures as compared to conditions at BATS. While total
568 chl-*a* did not differ significantly ($p = 0.96$) between the center of C2 and BATS, we
569 measured higher nanoeukaryote POC ($p = 0.012$) in C2 as compared to the BATS
570 station. Coincident with the increased carbon biomass of these larger cells, our
571 CHEMTAX data revealed coccolithophores (Hapto6; Table S1) comprised 98% of
572 haptophyte chl-*a* in C2, but just 6% at BATS (data not shown). The upwelling of cold,
573 dense water is a feature of cyclones that results in an increased nutrient supply (Bibby
574 et al., 2008), though nutrient inventories were lower at the center of C2 than at BATS.
575 As described previously, eddies can be described as “natural laboratories” as they trap
576 and move water throughout the gyre, so conditions within differ from those outside their
577 circulation (Bibby et al., 2008). Eddies mature and eventually decay so that nutrient
578 injection decreases and nutrients become exhausted within the eddy core (Sweeney et
579 al., 2003). Cyclones greater than four months of age are shown to exhibit little to no
580 biological response due to removal of resources through increased particle export that
581 occurs in young cyclones (Buesseler et al., 2008). Our post-cruise analyses of time-
582 course SLA data showed eddy C2 was ~6 months old and had well-defined eddy
583 circulation over its entire lifetime, indicating little potential for mixing from outside. The

low nutrient inventories in C2 indicated age was a factor in the phytoplankton response we observed that included no difference in total chl-a and eukaryote abundances ($p = 0.08$) as compared to communities at BATS. These data suggest that the higher nanophytoplankton C biomass and greater contributions of coccolithophores to chl-a were evidence of a bloom that occurred earlier in the life cycle of C2. In the EDDIES study, where multiple occupations of a cyclone occurred, they found the chemical and biological conditions associated with upwelling decayed within weeks (McGillicuddy et al., 2007). The implications these changes in phytoplankton community composition have for planktonic food webs and carbon flux will be discussed in section 4.4.

4.3.2. Impact of mesoscale and sub-mesoscale activity on phytoplankton communities under seasonally stratified conditions

When surface stratification is strong in summer, mesoscale and sub-mesoscale effects are more intense due to wind forcing and flow perturbations (Alonso-González et al., 2013). Uplift of deep isopycnals into the euphotic zone by mesoscale eddies in summer have a large impact specifically at the DCM as these communities lie on specific density surfaces that become vertically displaced by eddy motion (Bibby et al., 2008). We observed that on both summer cruises the DCM followed a narrow range of density surfaces ($25.43 - 26.36 \text{ kg m}^{-3}$). Between-cast variability of chemical and biological parameters was most apparent at the DCM at both eddy and BATS stations on both summer cruises. The actions of internal waves occur on the timescales of hours to days and they mobilize communities through a vertical gradient of light, temperature and nutrient conditions (Owen, 1981). Diatoms have been shown to grow rapidly by

accessing new nitrogen introduced by episodic upwelling events associated with the bottom 50 m of the euphotic zone in cyclones and mode-water eddies (Goldman, 1993). Despite evidence for upwelling in the center of both summer eddies, we did not observe a substantial diatom presence at the DCM in either eddy.

Eddies access deep nutrient stores below the seasonal thermocline; in our study we observe this build-up of nutrients at depths below the DCM, greater than 100 m. In summer 2011 cyclone C1 was associated with uplift of the 26.5 kg m^{-3} isopycnal to between 80 and 100 m at the eddy center as compared to where it lay outside the eddy (at 300 m). These data indicate eddy-induced nutrient upwelling occurred in C1 (McGillicuddy et al., 1998). In our study, N+N and SRP concentrations were highest at the center of C1, decreased somewhat at the edge and were lowest at BATS. Our data indicate nutrients upwelled by C1 stimulated the growth of nanoeukaryotes whose abundances and POC biomass were greater ($p = 0.004$) in the cyclone as compared to conditions at BATS. Considering age is a factor in defining the chemical and biological conditions of an eddy, these data are indicative of a young eddy as compared to spring C2. This was supported by SLA data that showed C1 was ~2 months at time of sampling. We also considered whether the significant increase in nanoeukaryotes and concomitant increase in haptophyte chl-*a* biomass ($p = 0.001$) was indicative of a shift towards a more coccolithophore-based community, as we found in C2 (spring 2012). Our CHEMTAX data revealed that non-coccolithophores contributed >80% of total haptophyte chl-*a* biomass at all stations (data not shown). In our study, we also observed the dominant picophytoplankton communities (*Pro* + *Syn* + picoeukaryotes) exhibited increased C:chl-*a* ratios in C1 as compared to BATS (data not shown).

Cyclones in the Sargasso Sea are associated with increased biomass of the dominant picophytoplankton community coincident with influx of nutrients (McGillicuddy et al., 1998; Ewart et al., 2008; Bibby et al., 2008; Mouriño-Carballido, 2009), though these studies measured chl-a rather than carbon biomass.

The youngest eddy we sampled was anticyclone AC2 in summer 2012 (aged <1 month). This anticyclone was atypical in that it exhibited slight upwelling at the center ($\sim 0.16 \text{ m d}^{-1}$) that appeared to be wind induced (McGillicuddy, pers. comm.). Eddy/wind interactions have been shown previously to cause upwelling in the center of anticyclones (Sweeney et al., 2003; Anderson et al., 2011) and due to heating of surface waters can result in cross-isopycnal flux (Ledwell et al., 2008). Wind and current data from the Sargasso Sea suggests mode-water eddies (not studied by us) can be an initial stage in the life cycle of an anticyclone (McGillicuddy, pers. comm.). Effects of anticyclones and mode-water eddies on phytoplankton communities (as measured by chl-a) are remarkably different (McGillicuddy et al., 1998, 2007; Siegel et al., 1999). Due to the brevity of our sampling period we were unable to determine whether AC2 developed into a mode-water eddy. However we did observe physical perturbations at the edge of AC2 unique in our study. A slight reduction in temperature and salinity in surface waters, possibly caused by rain events that deepened the MLD were coincident with displacement of the 26.5 kg m^{-3} isopycnal to $\sim 140 \text{ m}$, compared to 100 m at the other stations. The physical features included a cyclonic eddy to the southeast (at BATS), the edge of which was interacting with the edge of AC2. Eddy-eddy interactions are common phenomenon in the region (Mouriño-Carballido and McGillicuddy, 2006)

that exacerbate sub-mesoscale turbulence at frontal zones and mix waters by horizontal stirring (Klein and Lapeyre, 2009).

At the edge of AC2 we observed greater *Prochlorococcus* cell abundances ($p = 0.001$) compared to the center and BATS stations. Though integrated nutrient inventories did not differ substantially along the transect, deepening of the 26.5 kg m^{-3} isopycnal shifted the nitracline deeper in the water column at the edge station, below the euphotic zone ($131 \pm 11 \text{ m}$; data not shown). *Prochlorococcus* biomass, dominated by low-light adapted ecotypes, is strongly correlated with nitracline depths (Moore et al., 1995; Moore and Chisholm, 1999) where new nitrogen sources comprise up to 10% of their N requirements (Casey et al., 2007). While we found the nitracline was below the depth of the euphotic zone, recent ^{14}C -tracer experiments in the North Atlantic show primary production occurs several 10's of meters below the depth of 1% surface PAR (Marra et al., 2014). In the Sargasso Sea, *Prochlorococcus* contributes significantly more to total picophytoplankton C biomass when the depth of the nitracline is suppressed (DuRand et al., 2001) and *Synechococcus* is out-competed under the low light, low nutrient conditions (Moore et al., 1995). Decreased *Synechococcus* ($p = 0.002$) and increased *Prochlorococcus* abundances ($p = 0.001$) at the edge of AC2, concurrent with deepening of the nitracline support this competition scenario.

We also observed an increase in integrated haptophyte and prasinophyte chl-*a* ($p = 0.002$) at the edge of AC2. Eukaryote biomass is positively correlated with N+N concentrations (Cavender-Bares et al., 2001) and picoeukaryotes at the DCM receive more than half of their N requirements from upwelled nitrate (Fawcett et al., 2011). Phytoplankton communities at the DCM are comprised of low light adapted organisms

that harvest light with high efficiency (Bouman et al., 2011). Using unpublished size-fractionated chl-a data we found pico- and nanoeukaryote chl-a per cell increased by an order of magnitude from the surface to the DCM (data in prep). As Euk abundances did not differ significantly along the transect ($p = 0.1$) the increased haptophyte and prasinophyte chl-a demonstrated photoacclimation to lower irradiances associated with downwelling rather than an accumulation of biomass.

4.4. Impact of phytoplankton community composition on food webs in the Sargasso Sea

Our results demonstrate how phytoplankton communities in the Sargasso Sea are impacted by multiple environmental factors over a variety of time and space scales. Seasonal differences in temperature and solar insolation regulate the distribution of resources throughout the water column, driving species succession. Previous research demonstrates how eddy-induced shifts in phytoplankton community composition influence the productivity of the ecosystem (Mouriño-Carballido and McGillicuddy, 2006; Mouriño-Carballido, 2009). Positive net community production rates are associated with young cyclones and at eddy-eddy interaction zones (Mouriño-Carballido and McGillicuddy, 2006) while blooms in mode-water eddies result in high rates of primary productivity (Sweeney et al., 2003; McGillicuddy et al., 2007). Anticyclones and decaying cyclones are associated with decreased primary productivity (Sweeney et al., 2003) and negative net community production rates (Mouriño-Carballido and McGillicuddy, 2006). The effects of mesoscale and sub-mesoscale activity propagate through the ecosystem, as phytoplankton regulate the magnitude and pathways of carbon flow through planktonic food webs.

In this study, both cyclones (C1 and C2) were associated with increased abundances and/or POC biomass of nanoeukaryotes. We also found haptophyte chl-a biomass was greater in both cyclones as compared to outside, and a shift to a coccolithophore-dominated community occurred in spring (C2). While cell size plays a role in how an organism passes through the food web, there are also taxonomic differences. Calcifying organisms found in sediment traps are less degraded compared to diatom biomass that is rapidly turned-over in the water column (Klaas and Archer, 2002). The largest POC flux event recorded in the Northeast Atlantic was associated with a coccolithophore bloom at the center of a cyclone; indicating these organisms contribute substantially to export flux by escaping remineralization (Alonso-González et al., 2010). Therefore while both cyclones sampled in this study were associated with an increase in haptophytes, the coccolithophore-dominated community in C2 represented greater export potential. However, the export of this material is also dependent on the age of C2 (6 months); eddies older than 4 months have not been associated with significant carbon export events (Sweeney et al., 2003).

While both cyclones were associated with larger phytoplankton, in the two anticyclones (AC1 and AC2) we found *Prochlorococcus* was 22-66% more abundant than outside stations. In the case of spring eddy AC1 this community was found at the center of the eddy, while in summer 2012 we found increased *Prochlorococcus* at the edge of AC2. While picophytoplankton-derived carbon is traditionally considered to be turned-over within the microbial loop we now know that these small cells can contribute to export (Richardson and Jackson, 2007). Picophytoplankton are shown to be present in fecal pellets and aggregates at depth (Lomas and Moran, 2011; Amacher et al.,

2013). There may be differences in the fate of the two groups of cyanobacteria, *Prochlorococcus* and *Synechococcus*. *Synechococcus* is more heavily grazed upon by ciliates while *Prochlorococcus* is first consumed by smaller nanoflagellates and therefore mineralized in the microbial food web (Christaki et al., 1999). DNA analyses of trap material at BATS find *Prochlorococcus* sequences are underrepresented in traps compared to the water column (Amacher et al., 2013). Unpublished DNA analyses from this study found *Prochlorococcus* was rarely present in fecal pellets or sediment traps (Wilson, Neuer, and de Martini, pers comm.). Therefore, a shift in the cyanobacteria population favoring *Prochlorococcus* in anticyclones may result in lower carbon export due to their higher remineralization rates in the euphotic zone.

The timescales of the biological response associated with eddies remain poorly constrained. Eddies propagate for months in the Sargasso Sea, undergoing a series of strengthening and weakening periods. During the EDDIES project, repeated occupations of a cyclone (June-Aug 2004) and mode-water eddy (June - Aug 2005) found much of eddy-stimulated biological responses degraded two weeks after initial sampling (McGillicuddy et al., 2007; Bibby et al., 2008; Ewart et al., 2008). Increased temporal resolution of eddies is required to understand their impact as compared to seasonal forces. In this work we are limited to speculation on the role the food web has on the fate of phytoplankton biomass. However, the data presented here is part of the Trophic-BATS collaborative research project; in future publications we will provide evidence for how differences in the phytoplankton communities described here propagate through the food web.

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Table 1. Sargasso Sea sampling locations and dates in 2011 and 2012. The abbreviations AC1, C1, C2 and AC2 are used in the text to refer to eddies sampled on cruises AE1102, AE1118, AE1206, AE1219, respectively. Mixed layer depths were calculated by $\Delta\sigma_t = 0.125 \text{ kg m}^{-3}$ (Levitus, 1982). Dashed lines are used to separate data collected from the center and edge of each eddy from data collected at BATS that was outside of eddy influence in most cases (the exception was AE1219 where BATS was at the edge of a cyclone).

Cruise Number, Season	Eddy Type	Station	Latitude	Longitude	Distance Along Transect (km)	Cast number	Dates	Time deployed (Local)	Mixed Layer Depth (m)
AE1102 Spring 2011	Anticyclone (AC1)	Center	29° 42' N	64° 06' W	0	3	2/24/2011	15:25	198
						4	2/25/2011	02:14	192
						5	2/27/2011	12:03	201
		Edge	30° 30' N	64° 08' W	85	8	2/27/2011	02:01	86
						9	2/27/2011	13:55	38
		BATS	31° 66' N	64° 17' W	215	11	2/28/2011	12:28	190
						13	3/2/11	02:05	77
						14	3/2/11	11:37	181
						16	3/4/11	02:43	93
						17	3/4/11	05:39	340
AE1118 Summer 2011	Cyclone (C1)	Center	30° 49' N	65° 47' W	0	2	7/23/2011	02:15	19
						3	7/23/2011	12:08	13
						4	7/24/2011	09:00	12
						7	7/25/2011	02:11	18
		Edge	31° 17' N	64° 55' W	95	8	7/25/2011	12:05	7
						12	7/27/2011	08:04	13
						14	7/28/2011	02:12	12

						15	7/28/2011	09:59	12
						17	7/29/2011	10:01	12
		BATS	31° 66	64° 21	178	21	7/31/2011	03:01	16
						22	7/31/2011	10:01	21
						24	8/1/2011	09:58	20
						27	8/2/2011	02:57	17
						28	8/2/2011	10:04	24
						30	8/3/2011	10:04	22
AE1206	Cyclone	Center	32° 50' N	63° 29' W	0	1	3/15/2012	01:06	166
Spring	(C2)					4	3/15/2012	12:07	165
2012						10	3/17/2012	02:15	158
						13	3/17/2012	12:30	152
		BATS	31° 67' N	64° 17' W	145	17	3/19/2012	02:28	68
						20	3/19/2012	13:07	65
						23	3/20/2012	12:05	137
						25	3/21/2012	02:25	82
						27	3/21/2012	12:02	85
						29	3/22/2012	12:45	65
AE1219	Anticyclone	Center	33° 30' N	64° 27' W	0	5	7/20/2012	01:32	19
Summer	(AC2)					7	7/20/2012	13:01	18
2012						9	7/21/2012	11:58	18
						11	7/22/2012	01:30	23
						13	7/22/2012	12:03	24
		Edge	32° 23' N	64° 22' W	125	16	7/24/2012	01:32	34
						18	7/24/2012	13:00	28
						21	7/25/2012	12:28	31
						23	7/26/2012	01:31	25

BATS	31° 67' N	64° 17' W	205	25	7/26/2012	12:07	27
				28	7/27/2012	12:33	18
				29	7/28/2012	01:29	22
				31	7/28/2012	13:15	15
				35	7/29/2012	12:13	15
				37	7/30/2012	01:29	17
				39	7/30/2012	07:34	19

Euphotic zone depths (defined as depth of 1% surface irradiance) ranged from 93 to 176 meters in the spring and 102 to 148 meters in summer (data not shown).

Table 2. Integrated concentrations of nitrate+nitrite (N+N), soluble reactive phosphorus (SRP) and phytoplankton abundance and biomass. For station locations see Table 1. All values were integrated to 100 meters. *Pro* = *Prochlorococcus*, *Syn* = *Synechococcus*, P-euk = picoeukaryotes, N-euk = nanoeukaryotes. Data are averages $\pm$ standard deviation of multiple casts per station. Dashed lines are used to separate data collected from the center and edge of each eddy from data collected at BATS that was outside of eddy influence in most cases (the exception was AE1219 where BATS was at the edge of a cyclone).

Cruise Date	Station	N + N (mmol m ⁻²)	SRP (mmol m ⁻²)	Chl-a (mg m ⁻²)	<i>Pro</i> (x 10 ¹⁰ cells m ⁻²)	<i>Syn</i> (x 10 ¹⁰ cells m ⁻²)	P-euk (x 10 ¹⁰ cells m ⁻²)	N-euk (x 10 ¹⁰ cells m ⁻²)	<i>Pro</i> POC (mg m ⁻²)	<i>Syn</i> POC (mg m ⁻²)	P-euk POC (mg m ⁻²)	N-euk POC (mg m ⁻²)
AE1102 Spr '11	Center	3	0.4	11 $\pm$ 8	403	117	2.6	1.2	570	447	138	157
	Edge	17 $\pm$ 19	1 $\pm$ 0	27 $\pm$ 3	315 $\pm$ 155	210 $\pm$ 29	4.6 $\pm$ 0.6	1.4 $\pm$ 0.3	385 $\pm$ 231	607 $\pm$ 78	161 $\pm$ 2	191 $\pm$ 28
	BATS	78 $\pm$ 25	3 $\pm$ 1	31 $\pm$ 3	138 $\pm$ 90	507 $\pm$ 124	6.8 $\pm$ 3.4	2.0 $\pm$ 0.4	144 $\pm$ 101	883 $\pm$ 276	196 $\pm$ 78	262 $\pm$ 56
AE1118 Sum '11	Center	74 $\pm$ 46	4 $\pm$ 3	14 $\pm$ 2	734 $\pm$ 81	133 $\pm$ 63	15 $\pm$ 9	1.8 $\pm$ 0.2	325 $\pm$ 48	256 $\pm$ 125	359 $\pm$ 77	237 $\pm$ 35
	Edge	26 $\pm$ 21	1 $\pm$ 1	21 $\pm$ 7	577 $\pm$ 90	80 $\pm$ 19	8 $\pm$ 1	0.7 $\pm$ 0.2	161 $\pm$ 24	114 $\pm$ 25	209 $\pm$ 16	100 $\pm$ 34
	BATS	8 $\pm$ 15	1 $\pm$ 1	14 $\pm$ 2	804 $\pm$ 11	76 $\pm$ 59	8 $\pm$ 1	0.8 $\pm$ 0.2	178 $\pm$ 22	107 $\pm$ 11	202 $\pm$ 8	109 $\pm$ 30
AE1206 Spr '12	Center	4 $\pm$ 3	0.4 $\pm$ 0.1	30 $\pm$ 4	211 $\pm$ 48	410 $\pm$ 109	18 $\pm$ 3	1.6 $\pm$ 0.3	107 $\pm$ 7	625 $\pm$ 43	364 $\pm$ 45	259 $\pm$ 40
	BATS	7 $\pm$ 7	0.4 $\pm$ 0.1	23 $\pm$ 4	158 $\pm$ 77	177 $\pm$ 77	9 $\pm$ 0.7	0.6 $\pm$ 0.2	72 $\pm$ 34	320 $\pm$ 147	193 $\pm$ 32	105 $\pm$ 30
AE1219 Sum '12	Center	7 $\pm$ 6	1 $\pm$ 1	18 $\pm$ 1	637 $\pm$ 39	61 $\pm$ 3	8 $\pm$ 0.8	0.7 $\pm$ 0.2	188 $\pm$ 45	88 $\pm$ 18	270 $\pm$ 71	111 $\pm$ 22
	Edge	17 $\pm$ 17	1 $\pm$ 1	25 $\pm$ 3	851 $\pm$ 51	32 $\pm$ 5	10 $\pm$ 5	0.8 $\pm$ 0.1	380 $\pm$ 39	75 $\pm$ 11	294 $\pm$ 36	129 $\pm$ 21
	BATS	12 $\pm$ 13	1 $\pm$ 1	16 $\pm$ 6	528 $\pm$ 34	56 $\pm$ 5	12 $\pm$ 5	0.8 $\pm$ 0.4	270 $\pm$ 53	105 $\pm$ 17	308 $\pm$ 96	140 $\pm$ 26

Figure captions.

Fig. 1 Eddy AC1 Cruise track, physical and nutrient data from Cruise AE1102 (24 February – 5 March, 2011) where a) satellite altimetry data depicting location of the study region and sea level anomalies for eddy AC1 where white circles indicate sampling stations. Images created using altimetry data from Dr. Dennis McGillicuddy and Dr. Valery Kosnyrev, data available at <http://science.whoi.edu/users/valery/altimetry/>. Section plots b-d) depict physical features: b) temperature (in °C), c) salinity, and d) density (in kg m^{-3}) where filled circles represent discrete sampling depths. Bar plots of nitrate+nitrite concentrations (N+N; left panels, in $\mu\text{mol l}^{-1}$) and soluble reactive phosphorus (SRP; right panels, in $\mu\text{mol l}^{-1}$) at e) 1 m, f) the chlorophyll maximum, and g) 150 m. Note the 1m depth panels (e) are scaled to $1/10^{\text{th}}$ the value of the other panels due to nearly depleted nutrient concentrations at the surface. Gray background represents “eddy conditions” and white background indicates the BATS station. Cast numbers are presented above each column. The cruise transect began at the eddy center (at 0 km) and progressed to the edge station and BATS.

Fig. 2 Eddy AC1 Phytoplankton community composition from Cruise AE1102 (24 February – 5 March, 2011) where a-e) depicts the phytoplankton community composition, as contributions to chlorophyll biomass (mg chl a m^{-3}) at discrete sampling depths: a) 1 m, b) 20 m, c) 40-50 m, d) 75-80 m, and e) 90-100 m. Phytoplankton groups include: cyanobacteria (cyano), prasinophytes (prasino), cryptophytes (crypto), pelagophytes (pelago), diatoms (diatom), haptophytes (hapto) and dinoflagellates (dino) and f) shows the integrated chlorophyll a biomass (to 100 m) and g) depicts the relative

contributions by algal groups to total integrated chlorophyll *a* biomass (to 100 m). Plots h-k) depict flow cytometry data for the picocyanobacteria groups *Prochlorococcus* (*Pro*), *Synechococcus* (*Syn*), and the sum of pico- and nanoeukaryotes (Euks) where h-i) depict cell abundances (cells ml⁻¹) sampled at h) 1 m, and i) the chlorophyll *a* maximum and j-k) depicts particulate carbon biomass for these groups (POC, in mg m⁻³) sampled at j) 1 m, and k) the chlorophyll *a* maximum. Gray background represents “eddy conditions” and white background indicates the BATS station. Cast numbers are presented above each column. The cruise transect began at the eddy center (at 0 km) and progressed to the edge station and BATS.

Fig. 3 Eddy C1 Cruise track, physical and nutrient data from Cruise AE1118 (22 July – 5 August, 2011) where a) the SLA profile depicts eddy C1. All else as in Figure 1.

Fig. 4 Eddy C1 Phytoplankton community composition from Cruise AE1118 (22 July – 5 August, 2011). All else as in Figure 5.

Fig. 5 Eddy C2 Cruise track, physical and nutrient data from Cruise AE1206 (15-23 March 2012) where a) the SLA profile depicts eddy C2. All else as in Figure 1.

Fig. 6 Eddy C2 Phytoplankton community composition from Cruise AE1206 (15-23 March 2012). All else as in Figure 5.

Fig. 7 Eddy AC2 Cruise track, physical and nutrient data from Cruise AE1219 (19-31 July, 2012) where a) the SLA profile depicts eddy AC2. All else as in Figure 1.

Fig. 8 Eddy AC2 Phytoplankton community composition from Cruise AE1219 (19-31 July, 2012). All else as in Figure 5.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 6

Fig. 7

Fig. 8