



# Mesoscale and sub-mesoscale variability in phytoplankton community composition in 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  $26.5 \text{ kg m}^{-3}$  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.

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## 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

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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 drive 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 ( $3.3\text{--}5.6 \times 10^4$  cells ml<sup>-1</sup>; DuRand et al., 2001) while in summer and fall, the cyanobacterium *Prochlorococcus* is the most abundant ( $1.5\text{--}2.6 \times 10^5$  cells ml<sup>-1</sup>; 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<sup>-1</sup>; 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<sup>-1</sup>, 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 (Aristegui 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](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 “bull's 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

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