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Microbial dynamics in cyclonic and anticyclonic mode-water eddies in the northwestern Sargasso Sea

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ABSTRACT

The EDdy Dynamics, mixing, Export, and Species composition (EDDIES) project provided a unique opportunity to evaluate the response of the microbial community and further understand the biological and biogeochemical consequences of mesoscale perturbation events in an oligotrophic system. In order to characterize microbial dynamics, we performed measurements of bacterial biomass (BB) and production (BP) and phytoplankton pigment analyses in two upwelling eddies in the Sargasso Sea sampled in 2004 and 2005. We also observed a 3-fold increase in BP at the Bermuda Atlantic Time-series Study (BATS) site during the passage of a cyclonic eddy in 2003. Although the integrated BB and BP over 140 m in 2004 and 2005 eddies remained within the climatological range measured at the BATS site, there was systematic variability in bacterioplankton dynamics across both eddies. Cyclonic eddy C1 demonstrated decreased BP at the feature's center relative to its periphery, and BP was not correlated with total chlorophyll *a* (TChl *a*) variability. However, BP correlated with prymnesiophyte pigments throughout the feature. In contrast, mode-water eddy A4 showed an enhancement in BP at the eddy center (EC) relative to its edges and was coincident with elevated TChl *a*, high primary production measurements, and a high concentration of diatoms. In eddy A4, the tight relationship between enhanced BP, TChl *a* and specific phytoplankton taxa implies that the phytoplankton community structure was an important factor influencing BP variability. While the heterotrophic bacterial response in C1 and A4 was not enhanced relative to BATS summer climatology, these data and the presence of similar nutrient fields across both eddies suggest that BP and BB were influenced by the eddy perturbations and responded to changes in the phytoplankton community.

1. Introduction

Traditional mechanisms of nutrient supply, such as winter mixing, do not provide enough nutrients to the euphotic zone to balance geochemical estimates of new production in the oligotrophic regions such as the Sargasso Sea (Jenkins and Goldman, 1985). Eddy pumping has been proposed as an important mechanism of nutrient supply to the surface of the open sea (Falkowski et al., 1991; McGillicuddy et al., 1998; Siegel et al., 1999). In a cyclonic eddy, both the seasonal and permanent thermocline shoal, causing a negative sea-level anomaly (SLA) (McGillicuddy et al., 1999). In a mode-water eddy, the seasonal thermocline is uplifted while the permanent thermocline is depressed, leading to a positive SLA. Both types of eddies can lift isopycnals into the euphotic zone, injecting nutrients into nutrient-depleted surface waters that can be rapidly utilized, resulting in the accumulation of phytoplankton biomass and organic matter (McGillicuddy et al., 1998). The Sargasso Sea is characterized by the relatively frequent passage of eddies, which introduces spatial and temporal variability in the productivity of the North Atlantic subtropical gyre (Sweeney et al., 2003).

Eddies have been shown to enhance nutrient input to the surface ocean, resulting in increases in chlorophyll concentrations (McGillicuddy et al., 1998; Tarran et al., 2001) as well as new production (Falkowski et al., 1991; Harris et al., 1997; Oschlies and Garçon, 1998; Moran et al., 2001). For example, total chlorophyll *a* (TChl *a*) was enhanced in a cyclonic eddy sampled in the Algerian Basin (SW Mediterranean) and was coincident with 2–3-fold enhancement in primary production rates (Moran et al., 2001). In the NE Atlantic, a cyclonic cold-core eddy demonstrated high concentrations of TChl *a* and phytoplankton biomass (Lochte and Pfannkuche, 1987). Another cyclonic eddy in this same region

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showed a 2-fold increase in primary production rates over the mean in the region (Harris et al., 1997). Despite the relatively higher primary productivity and TChl *a* within these mesoscale features, few data exist regarding how heterotrophic prokaryotes respond in mesoscale eddies.

Heterotrophic bacteria play an important role in the planktonic food web. The amount of organic carbon processed daily by heterotrophic bacteria—the bacterial carbon demand (BCD)—can be comparable to local primary production (Ducklow, 1999). Furthermore, bacteria are key remineralizers of dissolved organic matter (DOM) (Azam and Hodson, 1977; Fuhrman, 1992; Ducklow, 2000), and can play a major role in determining the fate of eddy-stimulated new production. If heterotrophic bacterial activities such as particulate organic carbon (POC) solubilization (Smith et al., 1992) and subsequent POC and dissolved organic carbon (DOC) remineralization are high enough, then a significant fraction of the newly produced organic matter may be regenerated in place (Legendre and Le Fèvre, 1995), thereby minimizing the potential carbon flux of eddies. Little is known about the heterotrophic bacterial response associated with eddy-induced upwelling. Several studies have reported elevated bacterial abundance inside NE Atlantic cold-core eddies (Harris et al., 1997; Lochte and Pfannkuche, 1987; Thyssen et al., 2005) while others have reported no difference in depth-integrated bacterial biomass (BB) inside compared to outside a cyclonic eddy (Gonzalez and Anadon, 2001; Tarran et al., 2001). Even less is known about the associated bacterial production (BP) response in an eddy-induced phytoplankton bloom. Bode et al. (2001) found higher BP rates within a cold-core eddy region near the Canary Islands than in surrounding waters.

The EDdy Dynamics, mixing, Export, and Species composition (EDDIES) project provided a unique opportunity to evaluate the response of heterotrophic prokaryotes to the newly produced organic matter resulting from episodic perturbations in an open-ocean oligotrophic system. In order to characterize the heterotrophic prokaryotic dynamics within the EDDIES program, estimates of BB and BP in two upwelling eddies in the Sargasso Sea were made over two field seasons in 2004 and 2005. Here we compare and contrast the similarities and differences between the heterotrophic bacterial dynamics within and between two eddy types (cyclonic and mode-water) and relative to the phytoplankton community dynamics. We also report findings from a cyclonic eddy that passed over Bermuda Atlantic Time-series Study (BATS) in July 2003.

2. Methods

2.1. Eddy tracking

As part of the EDDIES project, two types of eddies—cyclonic and anticyclonic mode-water—were examined as part of a two-ship operation (see McGillicuddy et al., 2007). The R.V. *Oceanus* provided survey data for several eddies during each year of the study. In an attempt to capture the temporal dynamics in biological and biogeochemical responses to these mesoscale perturbations, a separate set of cruises aboard the R.V. *Weatherbird II* was designed to measure nutrients, vertical flux, primary production and microbial community dynamics. Each eddy type was occupied twice for 10 days within a 1-month period in 2004 and 2005. In 2004, a cyclonic eddy (C1) was surveyed between June 23 and July 2 (C1-1) and again from July 31 to August 9 (C1-2). In 2005, an anticyclonic mode-water eddy, (A4), was surveyed from July 6 to 15 (A4-1) and August 16–25 (A4-2). Near-real-time satellite altimetry (Leben et al., 2002) and shipboard acoustic doppler current profiler (ADCP) data from R.V. *Oceanus* permitted accurate tracking of the eddies throughout the cruises, and allowed for high-resolution sampling across the diameter of each eddy with sampling distances ranging from 10 to 40 km apart aboard R.V. *Weatherbird II* (Fig. 1). The BATS site (31°40′N, 64°10′W) also was sampled during each field season to serve as a control station. To improve comparability, within-eddy data were compared to the BATS summer climatology. All BATS data presented here are available online (http://www.bbsr.edu/cintoo/bats/bats.html). All EDDIES data are also accessible (http://ocb.whoi.edu/jg/dir/OCB/EDDIES/).

2.2. Sample collection

Sample water was collected from the surface 300 m of the ocean via a 24-place CTD rosette equipped with 12-l Niskin bottles containing epoxy-coated springs or from 12-l GoFlo bottles on a Kevlar line. Preliminary experiments showed no significant difference in BP or BB measured in water from GoFlo bottles vs. Niskin bottles. Nitrile gloves were used during sample collection and handling. Only data for the surface 200 m of the ocean are presented in this manuscript, because data below 200 m did not show any appreciable variability.

2.3. Bacterial biomass

2.3.1. Epifluorescence microscopy

Samples for bacterial abundance were collected in 15–50-ml acid-rinsed Falcon tubes, preserved with 0.2-μm-filtered formalin (final concentration 1%) and stored at 4 °C for no more than 48 h before slide preparation. About 5–10-ml samples were filtered onto blackened 0.2-μm polycarbonate filters backed by 0.8-μm mixed ester filters and stained in the dark with 4′,6-diamidino-2-phenylindole (DAPI, final concentration 5 $\mu g\,ml^{-1}$) (Porter and Feig, 1980). Filters were mounted onto slides with Resolve immersion oil (Richard-Allan Scientific) and stored dry at −20 °C until counted on an Olympus BX51 epifluorescence microscope at 1000× magnification. At least 200 cells per slide were counted.

2.3.2. Flow cytometry

Cell abundance also was enumerated using an LSR II flow cytometer (FCM) (BD Biosciences) equipped with a 488-nm excitation laser and standard filter set as described in Campbell (2001) and Marie et al. (1997). This allowed high throughput of samples and was comparable to counts by epifluorescence microscopy (see Section 3). FCM samples were fixed with 0.2-μm-filtered fresh paraformaldehyde (final concentration of 0.5%) and stored at 4 °C for 1–6 h prior to long-term storage in liquid nitrogen (LN) (Vaulot et al., 1989). Cells were stained with SYBR Green I (Molecular Probes) at a final concentration of 1:10,000 (vol:vol) for at least 30 min in the dark and analyzed within 60 min of staining following the protocols of Marie et al. (1997) and Campbell (2001).

The LSR II analytical performance was evaluated for quality control with 3.0-μm Rainbow beads (Spherotech Inc.). Seawater aliquots collected from 80, 100, and 120 m at Hydrostation S (32°10′N, 64°30′W) and stored in LN, were run daily to check the consistency and precision of the system. Flow rate was calibrated by measuring change in weight of 1 ml samples of deionized water before and after 5–10 min flow runs. This flow calibration was assessed before and after each day's run.

Data were acquired in log mode until 20,000 events were recorded, with green fluorescence (GFL) at 200 V set as the discriminator. Gating analysis was performed using FACS Diva software (BD Biosciences). Cell abundance in cells ml^{-1} was calculated from sample flow rates and number of events recorded