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# Eddy-driven pulses of respiration in the Sargasso Sea

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#### ABSTRACT

An analysis of 9 years of data from the NW subtropical Atlantic reveals that variability in heterotrophic processes associated with (sub)mesoscale features has a major impact on the balance between photosynthesis and respiration. Higher indirect estimates of net community production (NCPe) are associated with the center of Mode Water Eddies (MWE) and frontal regions between cyclonic and anticyclonic eddies (CA). The increase in NCPe observed at the center of MWE is driven mainly by an increase in autotrophic production, whereas in CA enhanced NCPe rates are the result of an important reduction in bacterial respiration. Both features also exhibit a decrease in nitrate concentration, consistent with nutrient consumption, and relative increases in oxygen anomaly and particulate and dissolved organic carbon in the upper 200 m. Plankton community composition in CA and MWE is characterized by the reduction in bacterial biomass, and the dominance of Prochlorococcus and Synechococcus in CA, and diatoms and dinoflagellates in MWE. Contrary to a common assumption, these results show for the first time that in ecosystems influenced by (sub)mesoscale dynamics, respiration can be as variable as photosynthesis.

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#### 1. Introduction

Net community production, the balance between gross primary production (PP) and total respiration, defines the metabolic state of the euphotic zone and sets a constraint on the amount of organic carbon sinking to the deep ocean (del Giorgio and Duarte, 2002). The relative constancy of organic matter decomposition (respiration) with respect to variable production due to photosynthesis has been a major assumption in contemporary oceanography (Karl et al., 2003). One of the reasons ocean respiration is considered less variable than photosynthesis is that planktonic microbes, particularly heterotrophic bacteria, utilize a diverse array of organic matter, and not just that derived from local PP (Karl et al., 1998).

Over the last several years an intense research effort has been focused on investigating the enigmatic observation that respiration can exceed photosynthesis in large areas of the subtropical ocean (Duarte et al., 1999; Williams, 1998), where geochemical estimates indicate that these regions are in balance or behave as net sinks for CO<sub>2</sub> (Hansell et al., 2004; Najjar and Keeling, 2000; Riser and Johnson, 2008). One of the hypotheses proposed to explain this discrepancy postulates the existence of short intensive bursts of photosynthesis, which charge the organic reservoir, and which respiration slowly and steadily discharges (Karl et al., 2003). Mesoscale phenomena are a mechanism that could generate high-frequency increases of photosynthesis to support this hypothesis (Gonzalez et al., 2001; Maixandeau et al., 2005).

The ocean's subtropical gyres have been considered as relatively constant and low-productivity ecosystems (Eppley et al., 1973). However, recent studies in these regions report important temporal and spatial variability in photosynthesis (Maranon et al., 2000). A number of methodological issues associated with respiration

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measurements in systems with low productivity (Williams and Jenkinson, 1982) have severely hampered the development of a global database. In fact, the global dataset of respiration, when compared to that of <sup>14</sup>C-based PP, is about 1% (Williams and Del Giorgio, 2005). As a result, respiration remains the least constrained term in most models of ocean–atmosphere gas exchange (Balkanski et al., 1999).

The Bermuda Atlantic Time-series Study (BATS) site is located in the subtropical gyre of the Atlantic Ocean, in the northwest corner of the Sargasso Sea. BATS is designed to measure seasonal and interannual variability in biogeochemical parameters (Steinberg et al., 2001), and measurements taken since 1988 are available at http:// bats.bios.edu/. The station is in an area of weak Gulf Stream recirculation with a net flow toward the southwest and intense hydrographic mesoscale activity throughout the region (Cianca et al., 2007). Three different types of mesoscale eddies have been identified in the Sargasso Sea (McGillicuddy et al., 1999): cyclones, anticyclones, and mode-water eddies (MWE). Cyclones and MWE tend to displace upper-ocean isopycnals toward the surface, causing nutrient input into the euphotic zone and the stimulation of photosynthesis. There is growing evidence that PP occurring both at the scale of mesoscale eddies, with characteristic spatial scales of 10-100 km and temporal scales of weeks-months, and at the scale of submesoscale dynamics contributes significantly to global carbon budgets (Levy, 2008). However, because of the costs and logistics involved in sampling high-frequency events in the open ocean, direct observations at submesoscale range are scarce (Strass, 1992).

Previous studies have reported some evidence of variability in respiration rates associated with different types of mesoscale features. Enhanced respiration rates have been associated with anticyclonic eddies in the Canary Islands region (Aristegui and Montero, 2005). In the NE subtropical Atlantic several observations have reported net autotrophic balances associated with cyclonic eddies as a result of reduction in respiration rates (Gonzalez et al., 2001; Maixandeau et al., 2005). In the summer of 2004, during the first year of field work of the Eddy Dynamics, Mixing Export, and Species composition (EDDIES) project, an important variability in gross photosynthesis and respiration rates was reported associated with three mesoscale eddies investigated in the Sargasso Sea (Mourino-Carballido and McGillicuddy, 2006). In this study I combine 9 years (1993-2002) of altimeter data with data from the BATS program in order to verify the hypothesis that respiration is as variable as photosynthesis and equally influenced by (sub)mesoscale dynamics.

#### 2. Methods

#### 2.1. Retrospective analysis of altimeter and BATS data

Eddy field animations for the 1993–2002 period generated from the objective analysis of satellite altimetry for the domain spanning latitude 28–38°N and longitude of 75–45°W (available at http://science.whoi.edu/users/

mcgillic/tpd/anim.html) combined with hydrographic profiles at BATS (31.16°N, 64.5°W) were used to assess the influence of the three eddy types described in the Sargasso Sea: cyclones, anticyclones, and MWE (McGillicuddy et al., 1999), and frontal regions of interaction between cyclones and anticyclonic eddies (CA) as described in Mourino-Carballido and McGillicuddy (2006). Other types of (sub)mesoscale activity that sporadically affect the BATS site were not considered. Only those features that exhibited a strong signal and affected the BATS site for relatively long periods of time were included in the analysis. This study extends the retrospective analysis included in Mourino-Carballido and McGillicuddy (2006) as: (1) all the CA were identified during the 9-year period (whereas only CA associated with enhancements of net community production were included in Mourino-Carballido and McGillicuddy, 2006) and (2) eddy field animations and hydrographic data were used to identify BATS samplings influenced by the center of the eddy features and those affected by eddy uplifting but not located at the eddy center.

BATS data from the same period (1993-2002) were also used to study distributions of nitrate, phosphate, silicate, oxygen, particulate and dissolved organic carbon (POC and DOC, respectively), particulate and dissolved organic nitrogen (PON and DON), pigments, bacterial biomass, <sup>14</sup>C incorporation by phytoplankton (<sup>14</sup>C PP), bacterial growth (BG), and vertical carbon flux from sediment traps (C<sub>flux</sub>). Changes in community structure composition were investigated by computing the percent chlorophyll-a contributed by different phytoplankton groups by using the algorithms developed for the oligotrophic Pacific by Letelier et al. (1993) and previously used for the BATS site (Boyd and Newton, 1999; Sweeney et al., 2003). 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 web site at http://bats.bios.edu/. After much deliberation following different tries with depth intervals, depth range selection was based on the vertical distribution of properties at BATS site (Steinberg et al., 2001). Rates were integrated down to the depth of the euphotic layer (ca. 100 m). Percent chlorophyll-a contributed by different phytoplankton groups was integrated deeper (0–160 m), to cover the deep chlorophyll maximum feature. The deeper level of the sediment trap deployments at BATS (300 m) was chosen to quantify the export of carbon from the upper layer. All the other parameters were integrated down to the winter mixed layer depth (ca. 200 m).

One-way analysis of variance (one-way ANOVA) was used to compare parameters between different mesoscale features (cyclones, anticyclones, MWE, and CA).

### 2.2. Indirect estimates of NCP (NCPe) derived from BATS data

Indirect estimates of NCP (NCPe) for the 1993–2002 period were calculated according to

$$NCPe = {}^{14}CPP - BR$$

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