Eddy-driven pulses of respiration in the Sargasso Sea

Beatriz Mouriño-Carballido

Applied Physics and Ocean Engineering Department. Woods Hole Oceanographic Institution, Woods Hole, MA 02543-1541, USA.

1Now at Departamento de Ecoloxía e Bioloxía Animal, Universidade de Vigo, Vigo, Pontevedra, 36200, Spain.

Corresponding author. Tel +34 986 812591; Fax +34 986 812551; E-mail: bmourino@uvigo.es
Abstract

An analysis of nine 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 NC Pe 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.

**Keywords:** (sub)mesoscale, photosynthesis, respiration, net community production, Sargasso Sea
Introduction

Net community production, the balance between gross primary production 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 primary production (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 CO₂ (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 measurements in systems with low productivity (Williams and Jenkinson, 1982), has severely...
hampered the development of a global database. In fact, the global dataset of respiration, when compared to that of $^{14}$C-based primary production, 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 towards 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 primary production occurring both at the scale of mesoscale eddies, with characteristic spatial scales of 10-100 km and temporal scales of weeks to months, and at the scale of submesoscale dynamics contributes significantly to global carbon budgets (Levy, 2007). 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 result of a 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 nine 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.
Methods

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° to 38°N and longitude of 75° to 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 mode water eddies (McGillicuddy et al., 1999), and frontal regions of interaction between cyclones and anticyclonic eddies (CA) as described in Mouriño-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 Mouriño-Carballido and McGillicuddy (2006) as: 1) All the CA were identified during the nine-year period (whereas only CA associated with enhancements of net community production were included in Mouriño-Carballido and McGillicuddy (2006)); 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, $^{14}$C incorporation by phytoplankton ($^{14}$C PP), bacterial growth (BG) and vertical carbon flux from sediment traps ($C_{flux}$). 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 traps 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).

*Indirect estimates of NCP (NCPe) derived from BATS data*

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

\[ \text{NCPe} = \text{^{14}C PP} - \text{BR} \]

where \(^{14}\text{C PP}\) is the rate of \(^{14}\text{C}\) incorporation by phytoplankton (particulate primary
production) and \(\text{BR}\) is bacterial respiration. \(\text{BR}\), in turn was estimated as:

\[ \text{BR} = \left( \text{BG} \times \text{ICF} \times \text{CCF} \right) \times \left( \frac{1}{\text{BGE}} - 1 \right) \]
where BG is bacterial growth rate measured by the \( ^{3}\text{H-methyl}\)-thymidine \((^{3}\text{H-TdR})\) technique (Steinberg et al., 2001). Thymidine incorporation was converted to bacterial respiration using the commonly reported isotope (ICF, \(1.5 \times 10^{18} \text{ cell mol}^{-1}\)) and carbon conversion factors (CCF, 15 fgC cell\(^{-1}\)) (Ducklow, 2000), and the mean bacterial growth efficiency (BGE) reported for the Sargasso Sea (ca. 0.13) (Carlson and Ducklow, 1996). This value is higher than more recent BGE reported for open ocean regions (0.08, Robinson et al., (In press)). However, I used the BGE reported by Carlson and Ducklow (1996) because it derives from experiments carried out in the same location as the study presented here. Mouriño-Carballido and McGillicuddy (2006) applied a similar approach but they used bacterial carbon demand instead of BR.

It is known that the conversion factors involved in the calculation of BR from BG are currently poorly constrained (Alonso-Saez et al., 2007). In this study, in order to investigate the effect of a constant BGE in the variability reported for bacterial respiration, I also computed BR using the empirical BGE models reported by del Giorgio and Cole (1998), being BP bacterial production:

\[
BGE_1 = \left( \frac{0.037 + 0.65BP}{1.8 + BP} \right)
\]

and López-Urrutia & Morán (2007):

\[
BGE_2 = \left( 1 - \frac{1}{0.727 \times \frac{\text{chl}}{\text{chl} + 4.08} + 1.02} \right)
\]

where chl is the chlorophyll concentration in mg m\(^{-3}\).
There are two important caveats associated with my estimates of NCP. First the
\(^{14}\)C assimilation technique underestimates gross primary production, and second
estimating respiration on the basis of BR underestimates total respiration. Compilation
of measurements carried out during the Joint Global Ocean Flux Study (JGOFS)
indicated that \(^{14}\)C uptake measures net primary production (gross primary production –
autotrophic respiration) in dawn-dusk incubations (Marra, 2002). Within the euphotic
zone, the existing data further suggest that bacteria are the main contributors to
community respiration (~50 to >90%) (Rivkin and Legendre, 2001; Robinson and
Williams, 2005). Giorgio and Duarte (2002) reviewed the current information on the
contribution of various biotic components and depth layers to respiration in the open
ocean and they assumed that zooplankton respiration represents 5% of the combined
microplankton respiration in the photic and thermocline waters. Mesozooplankton
production at BATS has been estimated to be 2% of primary production at this site
(Roman et al., 2002). Unfortunately, the contribution of bacteria to community
respiration cannot be verified at this site since specific studies about the contribution of
microzooplankton respiration, and their variability, have not been conducted.
Results and discussion

The variability of respiration versus photosynthesis

To determine whether the high variability observed in gross photosynthesis and respiration rates during the EDDIES cruises is a common pattern in this region, I compared depth integrated $^{14}$C primary production (PP) and bacterial respiration (BR) rates computed for the 1993-2002 period at the BATS site (Figure 1). To compute bacterial respiration, I used the mean bacterial growth efficiency (BGE), 0.13, reported for the Sargasso Sea by Carlson and Ducklow (1996). Mean values of BGE computed by using the empirical models reported by del Giorgio and Cole (1998) ($\text{BGE}_1=0.026 \pm 0.005$) and López-Urrutia & Morán (2007) ($\text{BGE}_2=0.05 \pm 0.01$) (see methods) were much lower than the mean BGE value reported for the open ocean (0.08, Robinson et al., (In press)), which results in high, and probably unrealistic, rates of BR (Figure 1). Both empirical models were built from relatively limited data sets culled from diverse ecosystems and they may not be adequate for all environments. No specific empirical models have been reported for highly dynamic ocean ecosystems under the influence of (sub)mesoscale processes. For this reason I decided to use a constant BGE in the estimation of BR and NCPe. This is in agreement with the recent synthesis carried out by Robinson (In press) who reports a median value of 6 mg C m$^{-3}$ d$^{-1}$ for open ocean BR. Variability in depth-integrated BR (reported as the coefficient of variation), computed using BGE=0.013 (Carlson and Ducklow, 1996), $\text{BGE}_1$ and $\text{BGE}_2$ was always similar to or higher than variability in depth-integrated PP (Figure 1). Robinson & Williams (2005) analyzed a large data set of oxygen flux derived gross production and respiration rates available in diverse ocean ecosystems. They reported the variance of photosynthesis to be greater than respiration when volumetric rates computed at different depths were used. However, they found similar variances in photosynthesis
and respiration when they analyzed depth-integrated rates, which are better predictors when regional or temporal differences between stations are analyzed, as they overcome potential separation in depth of photosynthesis and respiration (Robinson and Williams, 2005).

The contribution of mesoscale dynamics to the observed variability in respiration

An important part of the variability observed in the primary production rates measured at BATS has been previously attributed to mesoscale eddies (Sweeney et al., 2003). To investigate how much of the variability in bacterial respiration was driven by (sub)mesoscale forcing, I tracked mesoscale eddies and frontal regions between cyclones and anticyclones, using altimeter and hydrographic data from the BATS station, over the 9-year period. Thirteen cyclones, six anticyclones, 8 MWE, and 17 frontal regions of interaction between cyclonic and anticyclonic eddies (CA) were identified during the 1993 – 2002 period (see Figure 2 and table 1). Cyclones were the (sub)mesoscale features that more frequently affected the area (28% of the samplings were affected by these features), followed by CA (23%), MWE (13%) and anticyclones (8%).

The impact of the (sub)mesoscale features on PP, BR, and NCPE, is more noticeable when the seasonal signal in these parameters (see Figure 8 in Mouriño-Carballido and McGillicuddy (2006)) is filtered out by computing anomalies relative to monthly averages (Figure 3). Anomalies are rescaled to values between 1 and 10, where 10 is the largest value for each parameter. Positive (negative) values represent enhancements (decreases) with respect to typical background conditions for the sampling month. It is important to bear in mind that this region is populated by closely packed eddies that are constantly evolving and interacting with each other (Cianca et al.,
2007). As such, background conditions (anomalies close to zero) represent the mean stage that results from the influence of the different types of mesoscale features affecting this region. The anomaly record shows pulses in the magnitude of both PP and BR, some of them in close connection with the (sub)mesoscale field. The use of different parameterizations in the calculation of BGE (see methods) does not have a significant effect on the variability in BR and the connection with the (sub)mesoscale field (Figure 3). Nine out of the eighteen large (>2.5) NCPe anomalies occur during periods when BATS is influenced by CA, four are associated with cyclonic eddies, two with MWE, and one with an anticyclone. Six out of the nine high NCPe anomalies found at CA are associated with small negative (< -2.5) anomalies in BR.

The fixed-point time-series data generated by BATS create some inherent difficulties to compare statistically the effects among eddy types. The impact of the mesoscale forcing on the upper-ocean biochemistry at BATS includes variability induced by the type of the mesoscale eddy, the section of the mesoscale eddy going through the site (i.e. center versus edge), and also the variability induced by the stage of the biological response (i.e. initial versus decaying stage). These factors are expected to impact the robustness of statistics calculated from the time-series, in the sense that very long time series would be needed in order to have a representative number of the different stages. However, interesting patterns arise when the seasonal signal of several biogeochemical parameters sampled at BATS site along the 1993 – 2002 period (Steinberg et al., 2001) is filtered by means of anomalies with respect to monthly averages, and when these anomalies are grouped based on the influence of cyclones, anticyclones, MWE, and CA (Figure 4). Again, positive (negative) values represent enhancements (decreases) relative to typical background conditions for the sampling month.
CA are the (sub)mesoscale features associated with the highest anomaly in NCPe, as a result of relative enhanced PP and a strong reduction in BR (Figure 4). These features are also characterized by a decrease of nitrate, consistent with nutrient consumption though photosynthesis, and the increase of oxygen anomaly and particulate organic carbon (POC) in the upper 200 m. Plankton community composition is characterised by the dominance of Prochlorococcus and Synechococcus and a slight decrease in bacterial biomass. The lowest NCPe anomaly is found in anticyclonic eddies, as a result of a substantial increase in BR. These features are also characterized by an increase in nitrate and silicate, a decrease in oxygen anomaly and POC and a noticeable enhancement in bacterial biomass in the upper 200 m. Cyclones and MWE are initially both associated with negative anomalies in NCPe.

However, substantial differences between both features arise when the BATS samplings are divided into those influenced by the center of the eddy features and those affected by eddy uplifting but not located at the eddy center (Ce and MWEe). Centers of MWE are characterized by a noticeable increase in NCPe rates, as a result of the estimated enhancement in PP. Drops in nitrate and silicate concentration, consistent with nutrient consumption, as well as enhancements in oxygen anomaly, POC and dissolved organic carbon (DOC) in the upper 200 m are also associated with the center of MWE. Phytoplankton composition is dominated by dinoflagellates and a conspicuous increase in diatoms, whereas bacterial biomass is noticeably reduced. An increase in bacterial respiration is observed at MWEe, where bacterial biomass is slightly enhanced. Centers of cyclonic eddies are associated with low NCPe values, as the result of a noticeable increase in BR. Enhanced nitrate and silicate concentrations, but also oxygen anomaly, and relatively reduced POC and DOC in the upper 200 m are associated with these features. Plankton composition is dominated by Prochlorococcus.
and *Synechococcus* and slightly enhanced bacterial biomass. In agreement with the
patterns observed in NCPe, higher carbon flux inferred from sediment traps was
observed at the center of MWE, whereas the lowest carbon flux was computed at the
center of cyclonic eddies. Differences between particular eddy types are statistically
significant for oxygen anomaly (p=0.015), diatom abundance (p=0.021), and net
community production (p=0.011), once the distinction of those samplings influenced by
eddy center and those affected by eddy uplifting but not located at the eddy center is
made (see Table 2).

This study confirms previous results regarding differences between eddy types.
The analysis of three years of data (1993-1995) from the BATS site reported noticeable
enhancements in primary production associated with two MWE, whereas the 1994
spring bloom was suppressed by the passage of an anticyclone (Sweeney et al., 2003).
The same authors described an increased percentage of diatoms and dinoflagellates in
MWE, whereas cyclones exhibited an increased percentage of *Synechococcus*. The
pattern described in this study in anticyclones and CA is in agreement with *in vitro*
gross photosynthesis and respiration rates reported in summer 2004 by Mouriño-
Carballido and McGillicuddy (2006). The variability reported inside the cyclone
intensively investigated in summer 2004 (C1) highlights the relevance of considering
the time history of mesoscale eddies when interpreting the biological responses
associated with these features. For this reason, patterns observed at each eddy feature
from the retrospective analysis of the BATS data should be considered cautiously as
they may not include a representative number of all the possible eddy life stages. In
agreement with the retrospective analysis of BATS data presented in this study,
plankton composition was dominated by *Prochlorococcus spp.* in cyclone C1 whereas a
diatom bloom was found in MWE A4, the mode water eddy investigated in summer
2005 (McGillicuddy et al., 2007). Based on the assumption that the O₂ minimum found in the central eddy stations at C1 (200-400 m) and A4 (800-1000 m) was a consequence of high particle export from eddy induced blooms, carbon export inferred from the O₂ anomalies was one to three times as much as annual new production for the region (McGillicuddy et al., 2007). The retrospective analysis from the BATS data show a noticeably enhanced deep (200-800 m) oxygen anomaly associated with the center of MWE (see Table 2). Other depth intervals (200-400 m, 400-600 m and 600-800 m) show similar results (data not shown). However, the BATS sampling probably misses the smaller and more variable O₂ anomalies found at C1 and A4 cores. Modeling experiments based on the results from summer 2004 and 2005 EDDIES cruises suggest that diatom blooms are sustained by interactions with the surface wind field at MWE, whereas wind-eddy interactions dampen upwelling in cyclones (McGillicuddy et al., 2007). Details on the mechanisms responsible for the reduced bacterial respiration described at CA remain unknown. The influence of changes in bacterial populations associated with different hydrodynamic regimes (Morris et al., 2005) can not be discounted.

Conclusions

Respiration represents the largest sink of organic carbon in the biosphere. On a global scale, excluding external sources of organic matter (Dachs et al., 2005), respiration must be balanced by the input of organic matter via autotrophic production. Based on the assumption of its relative constancy, respiration has the potential to be a more accurate measure of time-integrated net organic production than photosynthesis, particularly for under-sampled, highly dynamic systems (Carlson et al., 2007). My results show for the first time that, contrary to previous assumptions, in highly dynamic
ecosystems influenced by (sub)mesoscale dynamics, respiration can be as variable as photosynthesis. Pulses in respiration driven by (sub)mesoscale forcing need to be considered in order to quantify the balance between synthesis and consumption of organic matter. Future sampling strategies should be designed in order to resolve higher-frequency, smaller-scale variability in both photosynthesis and respiration, which is crucial to comprehend the potential for carbon export to the deep ocean.

Acknowledgments

I am grateful to people involved in the collection, preparation and analysis of the data from the BATS program. I thank D. McGillicuddy and V. Kosnyrev for the elaboration and public access of the dynamical interpolation of mesoscale flows in the Topex/Poseidon diamond surrounding the BATS site. I am also grateful to X. Irigoien, E. Marañón, S. Neuer, T. Bibby, F. Tapia, X.A. Morán, K. Buesseler & the Café Thorium for their valuable comments on this manuscript. Comments by three anonymous reviewers are also acknowledged. I was supported by a Fulbright postdoctoral fellowship and the Juan de la Cierva program from the Spanish Ministry of Science and Education. Support of this activity by the U.S. National Science Foundation and the National Aeronautics and Space Administration is greatly appreciated.
References


8 Cianca, A., Helmke, P., Mourino, B., Rueda, M.J., Llinas, O., and Neuer, S. 2007. Decadal analysis of hydrography and in situ nutrient budgets in the western and


Table 1. Details of mesoscale features identified at BATS site for the 1993 – 2002 period. C is cyclone, A anticyclone and MWE mode water eddy. CA corresponds to areas of interaction between cyclone and anticyclone eddies. Beginning and end periods of mesoscale feature presence at BATS are indicated. Independent features were tracked back in time in order to determine their age at the time they influenced BATS sampling.

<table>
<thead>
<tr>
<th>Number</th>
<th>Type</th>
<th>Influence at BATS (beginning)</th>
<th>Influence at BATS (end)</th>
<th>Age (months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>C</td>
<td>12 Jan 1993</td>
<td>11 Feb 1993</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>MWE</td>
<td>27 Apr 1993</td>
<td>11 May 1993</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>C</td>
<td>13 Jun 1993</td>
<td>16 Jul 1993</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>A</td>
<td>17 Aug 1993</td>
<td>14 Oct 1993</td>
<td>7</td>
</tr>
<tr>
<td>5</td>
<td>C</td>
<td>8 Nov 1993</td>
<td>12 Nov 1993</td>
<td>11</td>
</tr>
<tr>
<td>6</td>
<td>CA</td>
<td>6 Dec 1993</td>
<td>18 Jan 1994</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>A</td>
<td>15 Feb 1994</td>
<td>21 Mar 1994</td>
<td>2.5</td>
</tr>
<tr>
<td>8</td>
<td>CA</td>
<td>5 Apr 1994</td>
<td>20 May 1994</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>A</td>
<td>19 Sep 1994</td>
<td>21 Oct 1994</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>C</td>
<td>14 Nov 1994</td>
<td>13 Jan 1995</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>CA</td>
<td>1 Mar 1995</td>
<td>16 Mar 1995</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>C</td>
<td>29 Mar 1995</td>
<td>27 Apr 1995</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>CA</td>
<td>10 May 1995</td>
<td>13 May 1995</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>MWE</td>
<td>12 Jun 1995</td>
<td>22 Aug 1995</td>
<td>1</td>
</tr>
<tr>
<td>16</td>
<td>MWE</td>
<td>12 Sep 1995</td>
<td>11 Nov 1995</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>C</td>
<td>30 Jan 1996</td>
<td>16 Mar 1996</td>
<td>6</td>
</tr>
<tr>
<td>18</td>
<td>CA</td>
<td>8 Apr 1996</td>
<td>13 Apr 1996</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>CA</td>
<td>3 Sep 1996</td>
<td>5 Sep 1996</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>MWE</td>
<td>8 Oct 1996</td>
<td>13 Nov 1996</td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>CA</td>
<td>12 Dec 1996</td>
<td>14 Dec 1996</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>C</td>
<td>13 Jan 1997</td>
<td>19 Mar 1997</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>CA</td>
<td>8 Apr 1997</td>
<td>9 Apr 1997</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>MWE</td>
<td>5 May 1997</td>
<td>8 May 1997</td>
<td>4</td>
</tr>
<tr>
<td>26</td>
<td>A</td>
<td>12 Nov 1997</td>
<td>12 Dec 1997</td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>CA</td>
<td>6 Jul 1998</td>
<td>10 Jul 1998</td>
<td></td>
</tr>
<tr>
<td>29</td>
<td>A</td>
<td>8 Sep 1998</td>
<td>11 Sep 1998</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>CA</td>
<td>8 Dec 1998</td>
<td>11 Dec 1998</td>
<td></td>
</tr>
<tr>
<td>31</td>
<td>C</td>
<td>14 Jan 1999</td>
<td>27 Jan 1999</td>
<td>5.5</td>
</tr>
<tr>
<td>32</td>
<td>CA</td>
<td>11 Feb 1999</td>
<td>13 Feb 1999</td>
<td></td>
</tr>
<tr>
<td>33</td>
<td>A</td>
<td>24 Feb 1999</td>
<td>24 Feb 1999</td>
<td></td>
</tr>
<tr>
<td>34</td>
<td>CA</td>
<td>7 Apr 1999</td>
<td>9 Apr 1999</td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>C</td>
<td>1 Jun 1999</td>
<td>9 Jul 1999</td>
<td>6.5</td>
</tr>
<tr>
<td>36</td>
<td>CA</td>
<td>2 Aug 1999</td>
<td>12 Nov 1999</td>
<td></td>
</tr>
<tr>
<td>37</td>
<td>C</td>
<td>14 Mar 2000</td>
<td>13 Apr 2000</td>
<td></td>
</tr>
<tr>
<td>38</td>
<td>CA</td>
<td>9 Jun 2000</td>
<td>9 Aug 2000</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>CA</td>
<td>13 Nov 2000</td>
<td>17 Nov 2000</td>
<td></td>
</tr>
<tr>
<td>41</td>
<td>C</td>
<td>30 Jan 2001</td>
<td>20 Apr 2001</td>
<td></td>
</tr>
<tr>
<td>42</td>
<td>CA</td>
<td>14 May 2001</td>
<td>18 Aug 2001</td>
<td></td>
</tr>
<tr>
<td>43</td>
<td>CA</td>
<td>9 Oct 2001</td>
<td>13 Nov 2001</td>
<td></td>
</tr>
<tr>
<td>44</td>
<td>MWE</td>
<td>11 Dec 2001</td>
<td>15 Dec 2001</td>
<td></td>
</tr>
<tr>
<td>Variable (units)</td>
<td>Mean ± STD (n)</td>
<td>Mean ± STD (n)</td>
<td>Mean ± STD (n)</td>
<td>Mean ± STD (n)</td>
</tr>
<tr>
<td>--------------------------</td>
<td>----------------</td>
<td>----------------</td>
<td>----------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Nitrate (0-200 m) (mmol m⁻²)</td>
<td>12 ± 62 (37)</td>
<td>5 ± 38 (6)</td>
<td>6 ± 66 (31)</td>
<td>6 ± 44 (12)</td>
</tr>
<tr>
<td>Phosphate (0-200 m) (mmol m⁻²)</td>
<td>1 ± 4 (36)</td>
<td>2 ± 2 (6)</td>
<td>1 ± 4 (30)</td>
<td>1 ± 3 (12)</td>
</tr>
<tr>
<td>Silicate (0-200 m) (mmol m⁻²)</td>
<td>8 ± 51 (37)</td>
<td>45 ± 23 (6)</td>
<td>0 ± 52 (31)</td>
<td>13 ± 27 (12)</td>
</tr>
<tr>
<td>ΔO₂ (0-200 m) (mmol m⁻²)</td>
<td>-70 ± 601 (38)</td>
<td>266 ± 460 (6)</td>
<td>-133 ± 609 (32)</td>
<td>-207 ± 700 (12)</td>
</tr>
<tr>
<td>ΔO₂ (200-800) (mmol m⁻²)</td>
<td>-2883 ± 4311 (26)</td>
<td>26 ± 2517 (4)</td>
<td>2524 ± 4615 (17)</td>
<td>1721 ± 5552 (9)</td>
</tr>
<tr>
<td>POC (0-200 m) (ug m⁻²)</td>
<td>-104 ± 1149 (36)</td>
<td>-107 ± 1165 (6)</td>
<td>-104 ± 1164 (30)</td>
<td>-124 ± 510 (11)</td>
</tr>
<tr>
<td>DOC (0-200 m) (ug m⁻²)</td>
<td>-124 ± 428 (27)</td>
<td>-103 ± 238 (4)</td>
<td>128 ± 457 (23)</td>
<td>11 ± 415 (9)</td>
</tr>
<tr>
<td>DON (0-200 m) (ug m⁻²)</td>
<td>-43 ± 168 (36)</td>
<td>14 ± 73 (6)</td>
<td>54 ± 180 (30)</td>
<td>20 ± 123 (11)</td>
</tr>
<tr>
<td>Prochlorococcus (0-160 m) (%)</td>
<td>1 ± 6 (32)</td>
<td>5 ± 6 (6)</td>
<td>0 ± 6 (26)</td>
<td>-2 ± 10 (12)</td>
</tr>
<tr>
<td>Synechococcus (0-160 m) (%)</td>
<td>2 ± 10 (32)</td>
<td>5 ± 8 (6)</td>
<td>1 ± 10 (26)</td>
<td>-3 ± 11 (12)</td>
</tr>
<tr>
<td>Prymnesiophytes (0-160 m) (%)</td>
<td>0 ± 6 (32)</td>
<td>-1 ± 6 (6)</td>
<td>1 ± 6 (26)</td>
<td>1 ± 3 (12)</td>
</tr>
<tr>
<td>Prasinophytes (0-160 m) (%)</td>
<td>0 ± 3 (32)</td>
<td>-1 ± 1 (6)</td>
<td>0 ± 3 (26)</td>
<td>-1 ± 2 (12)</td>
</tr>
<tr>
<td>Pelagophytes (0-160 m) (%)</td>
<td>0 ± 2 (32)</td>
<td>-1 ± 1 (6)</td>
<td>0 ± 3 (26)</td>
<td>0 ± 2 (12)</td>
</tr>
<tr>
<td>Dinoflagellates (0-160 m) (%)</td>
<td>0 ± 1 (32)</td>
<td>0 ± 1 (6)</td>
<td>0 ± 1 (26)</td>
<td>0 ± 1 (12)</td>
</tr>
<tr>
<td>Diatoms (0-160 m) (%)</td>
<td>0 ± 2 (32)</td>
<td>0 ± 1 (6)</td>
<td>0 ± 2 (26)</td>
<td>1 ± 2 (12)</td>
</tr>
<tr>
<td>Bacterial biomass (0-200 m) (mg m⁻²)</td>
<td>-2 ± 197 (36)</td>
<td>14 ± 161 (6)</td>
<td>6 ± 205 (30)</td>
<td>78 ± 75 (11)</td>
</tr>
<tr>
<td>PP (0-100 m) (mgC m⁻² d⁻¹)</td>
<td>-49 ± 141 (34)</td>
<td>-94 ± 60 (6)</td>
<td>40 ± 152 (28)</td>
<td>-10 ± 136 (11)</td>
</tr>
<tr>
<td>BR (0-100 m) (mgC m⁻² d⁻¹)</td>
<td>20 ± 147 (34)</td>
<td>109 ± 220 (6)</td>
<td>1 ± 124 (28)</td>
<td>64 ± 134 (11)</td>
</tr>
<tr>
<td>NCPe (0-100 m) (mgC m⁻² d⁻¹)</td>
<td>-69 ± 227 (34)</td>
<td>-203 ± 194 (6)</td>
<td>40 ± 226 (28)</td>
<td>-74 ± 216 (11)</td>
</tr>
<tr>
<td>Cflux (0-300 m) (g m⁻² d⁻¹)</td>
<td>0 ± 2 (28)</td>
<td>-1 ± 1 (5)</td>
<td>0 ± 2 (23)</td>
<td>0 ± 2 (10)</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. Depth-integrated (0-100 m) $^{14}$C primary production versus depth-integrated bacterial respiration (BR) estimated for the 1993-2002 period at the BATS site. BR was calculated assuming a constant BGE=0.13 (A). BR$_{1}$ (B) and BR$_{2}$ (C) were computed using the empirical models for BGE reported by del Giorgio and Cole (1998) and López-Urrutia & Morán (2007) (see methods). Coefficient of variation for $^{14}$C PP, BR, BR$_{1}$ and BR$_{2}$ are 45, 66, 46 and 71%, respectively. Median values for BR, BR$_{1}$ and BR$_{2}$ are 226, 1238 and 790 mgC m$^{-2}$ d$^{-1}$, respectively. The black lines are the 1:1 lines.

Figure 2. (A). Sea level anomalies (SLA) estimated for the 1993-2002 period at the BATS site. (B) Temperature in the upper 700 m for the 1993 – 2002 period at BATS site. Coloured bars indicate periods under the influence of cyclones (blue), anticyclones (red), mode water eddies (yellow), and frontal regions between cyclonic and anticyclonic eddies (green). White sections correspond to other type of (sub)mesoscale activity not included in this analysis. Numbers on the top correspond to mesoscale features identified during the 9-year period (see table 1).

Figure 3. Anomalies for depth-integrated (0-100 m) primary production (PP), bacterial respiration (BR) and net community production (NCPe) computed with respect to monthly averages and rescaled to values between 1 and 10 for the 1993 – 2002 period at BATS site. Anomalies for BR computed assuming a constant BGE (0.13) (solid line), the empirical model reported by del Giorgio and Cole (1998) (dashed line) and López-Urrutia & Morán (2007) (dotted line) are represented. Coloured bars indicate periods under the influence of cyclonic (blue), anticyclonic (red), mode water eddies (yellow), and frontal regions between cyclonic and anticyclonic eddies (green). White sections correspond to other type of
(sub)mesoscale activity not included in this analysis (see methods). Horizontal dashed lines indicate arbitrary thresholds in the 1–10 scale of 2.5 (i.e., 25% of the largest value) and -2.5 (i.e., -25% of the largest value). Numbers on the top correspond to mesoscale features identified during the 9-year period (see table 1).

Figure 4. Anomalies for selected parameters computed with respect to monthly averages for the 1993 – 2002 period at BATS site. CA corresponds to cyclone – anticyclone interactions. A, MWE and C correspond to anticyclones, mode water eddies and cyclones, respectively (c, center; e, edge). NCPe is indirect estimates of net community production; PP, primary production; BR, bacterial respiration (computed assuming BGE=0.13); O\textsubscript{2} anomaly, O\textsubscript{2} in situ – O\textsubscript{2} saturation in the upper 200 m; POC (DOC), particulate (dissolved) organic carbon. Prochlorococcus, Synechococcus, dinoflagellates and diatoms represent the percent chlorophyll-a contributed by these groups. Bacteria is bacterial biomass and C\textsubscript{flux} vertical carbon flux from sediment traps. Error bars represent standard errors. See table 2 for depth-integration intervals.
Figure 1
Figure 4