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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 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; Maixandau 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 ^{14}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; Maixandeu 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/>

mccillic/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, ^{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 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

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

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

$$\text{BR} = (\text{BG} \times \text{ICF} \times \text{CCF}) \left(\frac{1}{\text{BGE}} - 1 \right)$$

where BG is the bacterial growth rate measured by the {3H-methyl}-thymidine ($^3\text{H-TdR}$) technique (Steinberg et al., 2001). Thymidine incorporation was converted to BR using the commonly reported isotope (ICF, 1.5×10^{18} 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 the more recent BGE reported for open ocean regions (0.08; Robinson, 2008). However, I used the BGE reported by Carlson and Ducklow (1996) because it is derived from experiments carried out in the same location as the study presented here. Mourino-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 BR, I also computed BR using the empirical BGE models reported by del Giorgio and Cole (1998), BP being bacterial production:

$$\text{BGE}_1 = \left(\frac{0.037 + 0.65\text{BP}}{1.8 + \text{BP}} \right)$$

and Lopez-Urrutia and Moran (2007):

$$\text{BGE}_2 = \left(1 - \frac{1}{0.727 \frac{\text{chl}}{\text{chl} + 4.08} + 1.02} \right)$$

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 PP, 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 PP (gross PP – 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–>90%; Rivkin and Legendre, 2001; Robinson and Williams, 2005). Del 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 PP 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.

3. Results and discussion

3.1. 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 and bacterial respiration rates computed for the 1993–2002 period at the BATS site (Fig. 1). To compute BR, I used the mean bacterial growth efficiency, 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 Lopez-Urrutia and Moran (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, 2008), which results in high, and probably unrealistic, rates of BR (Fig. 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

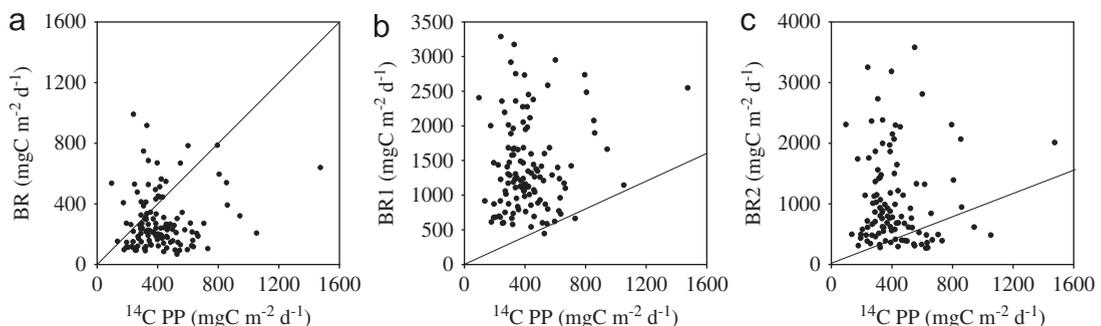


Fig. 1. Depth-integrated (0–100 m) ^{14}C primary production versus depth-integrated bacterial respiration (BR) estimated for the 1993–2002 period at the BATS site. BR was calculated assuming a constant BGE = 0.13 (A). BR $_1$ (B) and BR $_2$ (C) were computed using the empirical models for BGE reported by del Giorgio and Cole (1998) and Lopez-Urrutia and Moran (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.

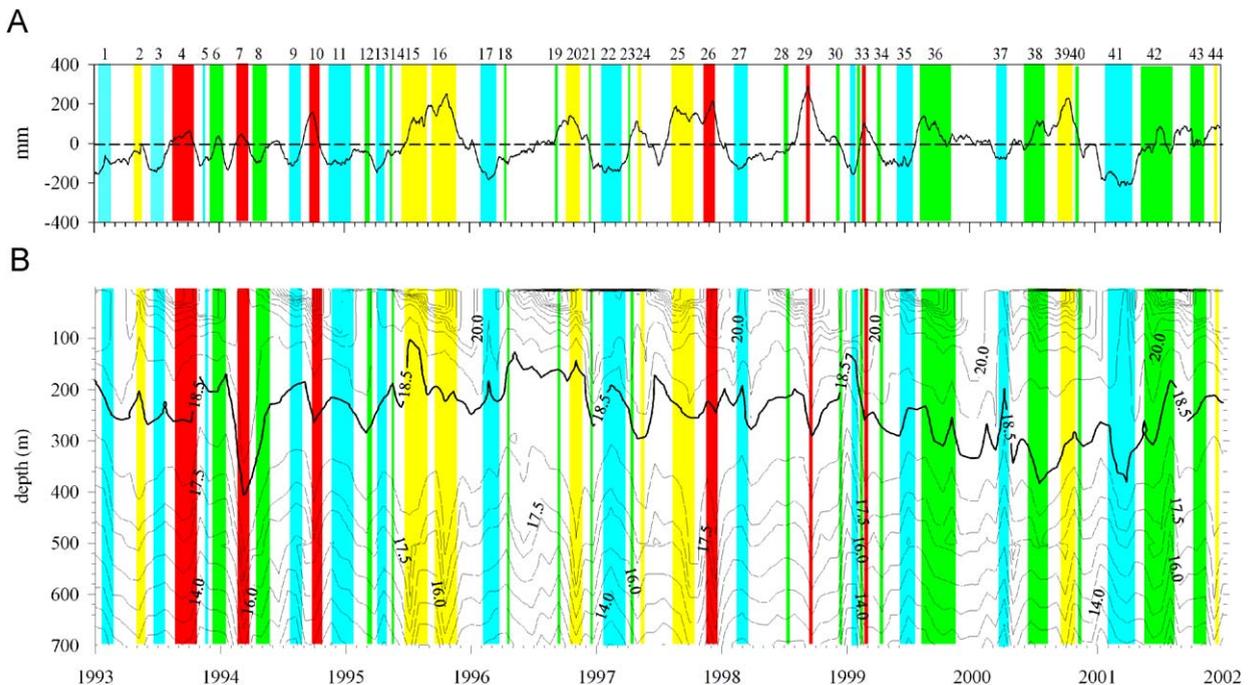


Fig. 2. (A) Sea level anomalies (SLA) estimated for the 1993–2002 period at the BATS site. (B) Temperature in the upper 700 m for the 1993–2002 period at BATS site. Coloured bars indicate periods under the influence of cyclones (blue), anticyclones (red), mode water eddies (yellow), and frontal regions 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). (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Robinson (2008), who reports a median value of $6 \text{ mg C m}^{-3} \text{ d}^{-1}$ for open ocean BR. Variability in depth-integrated BR (reported as the coefficient of variation), computed using $\text{BGE} = 0.013$ (Carlson and Ducklow, 1996), BGE_1 , and BGE_2 was always similar to or higher than variability in depth-integrated PP (Fig. 1). Robinson and Williams (2005) analyzed a large dataset 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).

3.2. The contribution of mesoscale dynamics to the observed variability in respiration

An important part of the variability observed in the PP rates measured at BATS has been previously attributed to mesoscale eddies (Sweeney et al., 2003). To investigate how much of the variability in BR 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, 6 anticyclones,

8 MWE, and 17 frontal regions of interaction between cyclonic and anticyclonic eddies were identified during the 1993–2002 period (see Fig. 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 Fig. 8 in Mourino-Carballido and McGillicuddy, 2006) is filtered out by computing anomalies relative to monthly averages (Fig. 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 (Fig. 3). Nine out of the eighteen large (>2.5) NCPe anomalies occur during periods when BATS is

Table 1

Details of mesoscale features identified at BATS site for the 1993–2002 period.

Number	Type	Influence at BATS (beginning)	Influence at BATS (end)	Age (months)
1	C	12 Jan 1993	11 Feb 1993	3
2	MWE	27 Apr 1993	11 May 1993	1
3	C	13 Jun 1993	16 Jul 1993	2
4	A	17 Aug 1993	14 Oct 1993	7
5	C	8 Nov 1993	12 Nov 1993	11
6	CA	6 Dec 1993	18 Jan 1994	
7	A	15 Feb 1994	21 Mar 1994	2.5
8	CA	5 Apr 1994	20 May 1994	
9	C	18 Jul 1994	19 Aug 1994	2
10	A	19 Sep 1994	21 Oct 1994	
11	C	14 Nov 1994	13 Jan 1995	
12	CA	1 Mar 1995	16 Mar 1995	
13	C	29 Mar 1995	27 Apr 1995	
14	CA	10 May 1995	13 May 1995	
15	MWE	12 Jun 1995	22 Aug 1995	1
16	MWE	12 Sep 1995	11 Nov 1995	
17	C	30 Jan 1996	16 Mar 1996	6
18	CA	8 Apr 1996	13 Apr 1996	
19	CA	3 Sep 1996	5 Sep 1996	
20	MWE	8 Oct 1996	13 Nov 1996	
21	CA	12 Dec 1996	14 Dec 1996	
22	C	13 Jan 1997	19 Mar 1997	
23	CA	8 Apr 1997	9 Apr 1997	
24	MWE	5 May 1997	8 May 1997	4
25	MWE	11 Aug 1997	8 Oct 1997	
26	A	12 Nov 1997	12 Dec 1997	
27	C	11 Feb 1998	13 Mar 1998	
28	CA	6 Jul 1998	10 Jul 1998	
29	A	8 Sep 1998	11 Sep 1998	
30	CA	8 Dec 1998	11 Dec 1998	
31	C	14 Jan 1999	27 Jan 1999	5.5
32	CA	11 Feb 1999	13 Feb 1999	
33	A	24 Feb 1999	24 Feb 1999	
34	CA	7 Apr 1999	9 Apr 1999	
35	C	1 Jun 1999	9 Jul 1999	6.5
36	CA	2 Aug 1999	12 Nov 1999	
37	C	14 Mar 2000	13 Apr 2000	
38	CA	9 Jun 2000	9 Aug 2000	
39	MWE	11 Sep 2000	21 Oct 2000	
40	CA	13 Nov 2000	17 Nov 2000	
41	C	30 Jan 2001	20 Apr 2001	
42	CA	14 May 2001	18 Aug 2001	
43	CA	9 Oct 2001	13 Nov 2001	
44	MWE	11 Dec 2001	15 Dec 2001	

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.

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 (Fig. 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 (Fig. 4). These features are also characterized by a decrease of nitrate, consistent with nutrient consumption through photosynthesis, and the increase of oxygen anomaly and particulate organic carbon in the upper 200 m. Plankton community composition is characterized 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 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 BR 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

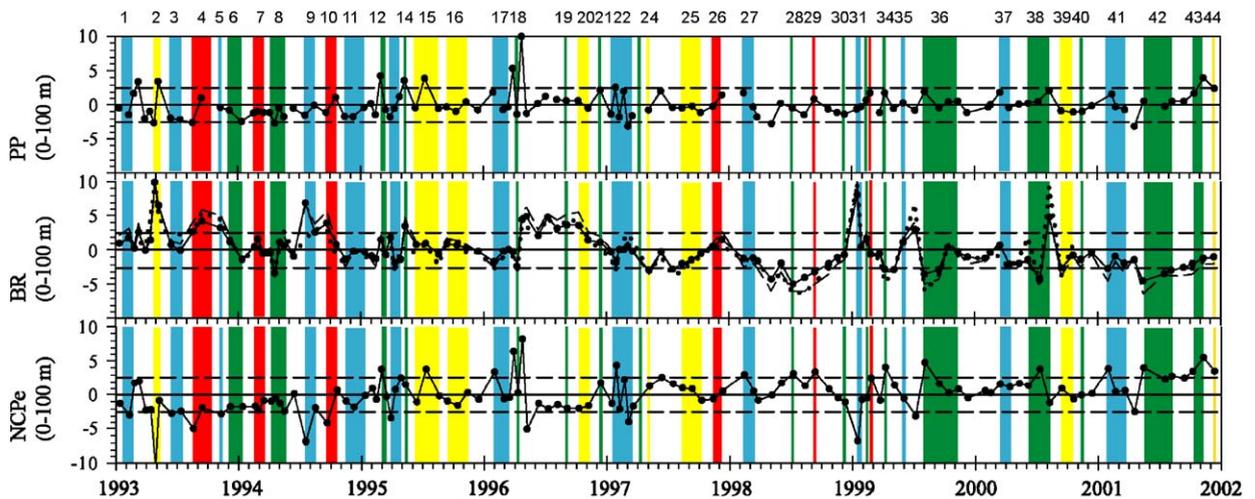


Fig. 3. Anomalies for depth-integrated (0–100 m) primary production (PP), bacterial respiration (BR), and net community production (NCPe) computed with respect to monthly averages and rescaled to values between 1 and 10 for the 1993–2002 period at BATS site. Anomalies for BR computed assuming a constant BGE (0.13; solid line), the empirical model reported by del Giorgio and Cole (1998) (dashed line), and Lopez-Urrutia and Moran (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). (for interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

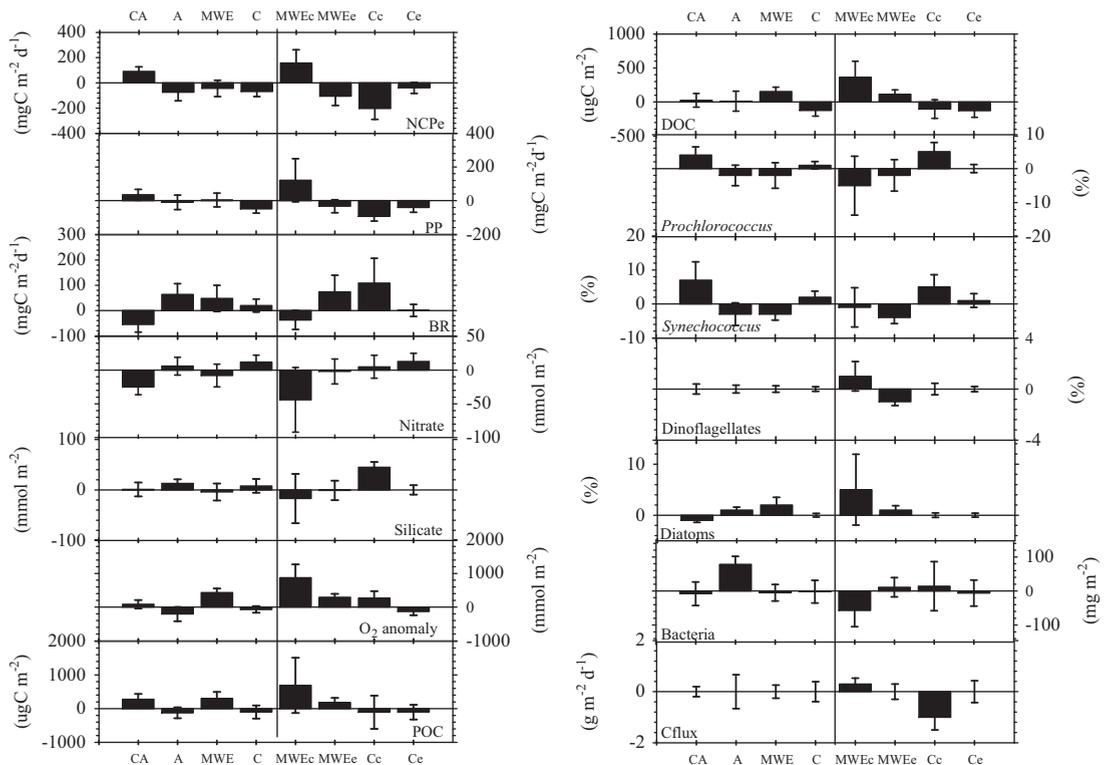


Fig. 4. Anomalies for selected parameters computed with respect to monthly averages for the 1993–2002 period at BATS site. CA corresponds to cyclone–anticyclone interactions. A, MWE, and C correspond to anticyclones, mode water eddies, and cyclones, respectively (c, center; e, edge). NCPe is indirect estimates of net community production; PP, primary production; BR, bacterial respiration (computed assuming BGE = 0.13); O₂ anomaly, O₂ in situ–O₂ saturation; POC (DOC), particulate (dissolved) organic carbon. *Prochlorococcus*, *Synechococcus*, dinoflagellates, and diatoms represent the percent chlorophyll-a contributed by these groups. Bacteria, bacterial biomass; C_{flux}, vertical carbon flux from sediment traps. Error bars represent standard errors. See Table 2 for depth-integration intervals.

Table 2
Anomalies for selected parameters computed with respect to monthly averages for the 1993–2002 period at BATS site.

Variable (units)	C		Cc		Ce		A		MWE		MWEc		MWEe		CA		One way ANOVA	
	Mean ± STD	n	Mean ± STD	n	Mean ± STD	n	Mean ± STD	n	Mean ± STD	n	Mean ± STD	n	Mean ± STD	n	Mean ± STD	n	p-value	
Nitrate (0–200 m) (mmol m ⁻²)	12 ± 62	37	5 ± 38	6	13 ± 66	31	6 ± 44	12	-8 ± 63	15	-44 ± 48	2	-2 ± 64	13	-25 ± 61	29	0.224	
Phosphate (0–200 m) (mmol m ⁻²)	1 ± 4	36	2 ± 2	6	1 ± 4	30	1 ± 3	12	-1 ± 5	15	-4 ± 1	2	0 ± 5	13	-1 ± 4	29	0.281	
Silicate (0–200 m) (mmol m ⁻²)	8 ± 51	37	45 ± 23	6	0 ± 52	31	13 ± 27	12	-4 ± 65	16	-17 ± 69	3	-1 ± 67	13	1 ± 73	29	0.706	
ΔO ₂ (0–200 m) (mmol m ⁻²)	-70 ± 601	38	266 ± 460	6	-133 ± 609	32	-207 ± 700	12	431 ± 492	17	874 ± 683	4	295 ± 347	13	85 ± 686	31	0.015* MWEc > Ce, A	
ΔO ₂ (200–800) (mmol m ⁻²)	-2883 ± 4311	26	-4856 ± 2517	4	-2524 ± 4615	1721 ± 4670	9	5706 ± 5552	15	9214 ± 9899	3	4830 ± 4149	12	-1165 ± 3902	25	< 0.001** MWE > C, CA		
POC (0–200 m) (μg m ⁻²)	-104 ± 1149	36	-107 ± 1105	6	-104 ± 1176	30	-124 ± 510	11	300 ± 780	17	691 ± 1420	4	180 ± 491	13	279 ± 881	31	0.428	
DOC (0–200 m) (μg m ⁻²)	-124 ± 428	27	-103 ± 238	4	-128 ± 457	23	11 ± 415	9	155 ± 209	12	364 ± 234	2	114 ± 189	10	25 ± 470	23	0.465	
PON (0–200 m) (μg m ⁻²)	-43 ± 168	36	14 ± 73	6	-54 ± 180	30	20 ± 123	11	26 ± 147	17	43 ± 227	4	21 ± 126	13	41 ± 141	31	0.349	
DON (0–200 m) (μg m ⁻²)	-2 ± 86	26	-35 ± 77	5	6 ± 88	21	-28 ± 47	9	-19 ± 47	14	19 ± 44	3	-29 ± 44	11	23 ± 81	25	0.307	
<i>Prochlorococcus</i> (0–160 m) (%)	1 ± 6	32	5 ± 6	6	0 ± 6	26	-2 ± 10	12	-2 ± 15	17	-5 ± 15	4	-2 ± 16	13	4 ± 12	26	0.167	
<i>Synechococcus</i> (0–160 m) (%)	2 ± 10	32	5 ± 8	6	1 ± 10	26	-3 ± 11	12	-3 ± 7	17	-1 ± 10	4	-4 ± 6	13	7 ± 27	26	0.486	
Prymnesiophytes (0–160 m) (%)	0 ± 6	32	-1 ± 6	6	1 ± 6	26	1 ± 3	12	-2 ± 6	17	1 ± 9	4	-3 ± 5	13	0 ± 10	26	0.895	
Prasinophytes (0–160 m) (%)	0 ± 3	32	-1 ± 1	6	0 ± 3	26	-1 ± 2	12	0 ± 2	17	2 ± 3	4	-1 ± 2	13	1 ± 5	26	0.316	
Pelagophytes (0–160 m) (%)	0 ± 2	32	-1 ± 1	6	0 ± 3	26	0 ± 2	12	1 ± 4	17	1 ± 3	4	0 ± 4	13	0 ± 5	26	0.973	
Dinoflagellates (0–160 m) (%)	0 ± 1	32	0 ± 1	6	0 ± 1	26	0 ± 1	12	0 ± 1	17	1 ± 2	4	-1 ± 1	13	0 ± 2	26	0.137	
Diatoms (0–160 m) (%)	0 ± 2	32	0 ± 1	6	0 ± 2	26	1 ± 2	12	2 ± 6	17	5 ± 12	4	1 ± 3	13	-1 ± 2	26	0.030* MWEc > Ce, CA	
Bacterial biomass (0–200 m) (mg m ⁻²)	-2 ± 197	36	14 ± 161	6	-6 ± 205	30	78 ± 75	11	-5 ± 97	17	-57 ± 83	4	11 ± 98	13	-8 ± 189	31	0.722	
PP (0–100 m) (mg C m ⁻² d ⁻¹)	-49 ± 141	34	-94 ± 60	6	-40 ± 152	28	-10 ± 136	11	4 ± 165	17	121 ± 222	4	-33 ± 134	13	35 ± 172	29	0.147	
BR (0–100 m) (mg C m ⁻² d ⁻¹)	20 ± 147	34	109 ± 220	6	1 ± 124	28	64 ± 134	11	48 ± 207	17	-37 ± 65	4	74 ± 230	13	-55 ± 158	29	0.111	
NCPe (0–100 m) (mg C m ⁻² d ⁻¹)	-69 ± 227	34	-203 ± 194	6	-40 ± 226	28	-74 ± 216	11	-44 ± 259	17	158 ± 181	4	-106 ± 251	13	90 ± 195	29	0.011* CA > Cc	
C _{flux} (0–300 m) (g m ⁻² d ⁻¹)	0 ± 2	28	-1 ± 1	5	0 ± 2	23	0 ± 2	10	0 ± 1	16	0.3 ± 0.4	4	0 ± 1	12	0 ± 1	27	0.887	

Depth integration intervals are shown. C, A, and MWE correspond to cyclones, anticyclones, and mode water eddies, respectively (c, center; e, edge). CA corresponds to cyclones–anticyclones interactions. ΔO₂ is oxygen anomaly (O₂ in situ – O₂ saturation); POC (DOC) is particulate (dissolved) organic carbon; PON (DON) is particulate (dissolved) organic nitrogen. *Prochlorococcus*, *Synechococcus*, prymnesiophytes, prasinophytes, pelagophytes, dinoflagellates, and diatoms represent the percent chlorophyll-a contributed by these groups. PP, primary production; BR, bacterial respiration (computed assuming BGE = 0.13); NCPe, net community production. C_{flux} is carbon flux estimated from sediment traps. STD is standard deviation; *p* statistic probability, *n* number of samples. The multiple comparison Bonferroni test was applied *a posteriori* to analyse the differences between every pair of groups.

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 3 years of data (1993–1995) from the BATS site reported noticeable enhancements in PP 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 Mourino-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 MWE 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 shows a noticeably enhanced deep (200–800 m) oxygen anomaly associated with the center of MWE (see Table 2). Other depth intervals (200–400, 400–600, 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 BR described at CA remain unknown. The influence of changes in bacterial populations associated with different hydrodynamic regimes (Morris et al., 2005) cannot be discounted.

4. 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.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2009.03.001.

References

- Alonso-Saez, L., Gasol, J.M., Aristegui, J., Vilas, J.C., Vaque, D., Duarte, C.M., Agusti, S., 2007. Large-scale variability in surface bacterial carbon demand and growth efficiency in the subtropical northeast Atlantic Ocean. *Limnology and Oceanography* 52 (2), 533–546.
- Aristegui, J., Montero, M.F., 2005. Temporal and spatial changes in plankton respiration and biomass in the Canary Islands region: the effect of mesoscale variability. *Journal of Marine Systems* 54 (1–4), 65–82.
- Balkanski, Y., Monfray, P., Battle, M., Heimann, M., 1999. Ocean primary production derived from satellite data: an evaluation with atmospheric oxygen measurements. *Global Biogeochemical Cycles* 13 (2), 257–271.
- Boyd, P.W., Newton, P.P., 1999. Does planktonic community structure determine downward particulate organic carbon flux in different oceanic provinces? *Deep Sea Research I: Oceanographic Research Papers* 46 (1), 63–91.
- Carlson, C., Del Giorgio, P.A., Herndl, G.J., 2007. Microbes and the dissipation of energy and respiration: from cells to ecosystems. *Oceanography* 20 (2), 89–100.
- Carlson, C.A., Ducklow, H.W., 1996. Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquatic Microbial Ecology* 10 (1), 69–85.

- Cianca, A., Helmke, P., Mourino, B., Rueda, M.J., Llinas, O., Neuer, S., 2007. Decadal analysis of hydrography and in situ nutrient budgets in the western and eastern North Atlantic Subtropical Gyre. *Journal of Geophysical Research C: Oceans* 112, C07025.
- Dachs, J., Calleja, M.L., Duarte, C.M., del Vento, S., Turpin, B., Polidori, A., Herndl, G.J., Agustí, S., 2005. High atmosphere–ocean exchange of organic carbon in the NE subtropical Atlantic. *Geophysical Research Letters* 32 (21), L21807.
- del Giorgio, P.A., Cole, J.J., 1998. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics* 29, 503–541.
- del Giorgio, P.A., Duarte, C.M., 2002. Respiration in the open ocean. *Nature* 420 (6914), 379–384.
- Duarte, C.M., Agustí, S., del Giorgio, P.A., Cole, J.J., 1999. Regional carbon imbalances in the oceans. *Response. Science* 284, 1735b.
- Ducklow, H.W., 2000. Bacterial production and biomass in the oceans. In: Kirchman, D.L. (Ed.), *Microbial Ecology of the Oceans*. Wiley, New York.
- Eppley, R.W., Renger, E.H., Venrick, E.L., Mullin, M.M., 1973. Study of plankton dynamics and nutrient cycling in Central Gyre of North Pacific Ocean. *Limnology and Oceanography* 18, 534–551.
- Gonzalez, N., Anadon, R., Mourino, B., Fernandez, E., Sinha, B., Escanez, J., de Armas, D., 2001. The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: the role of meso-scale instabilities. *Limnology and Oceanography* 46 (4), 946–952.
- Hansell, D.A., Ducklow, H.W., Macdonald, A.M., Baringer, M.O., 2004. Metabolic poise in the North Atlantic Ocean diagnosed from organic matter transports. *Limnology and Oceanography* 49 (4), 1084–1094.
- Karl, D.M., Hebel, D.V., Bjorkman, K., Letelier, R.M., 1998. The role of dissolved organic matter release in the productivity of the oligotrophic North Pacific Ocean. *Limnology and Oceanography* 43 (6), 1270–1286.
- Karl, D.M., Laws, E.A., Morris, P., Williams, P.J.L., Emerson, S., 2003. Metabolic balance of the open sea. *Nature* 426 (6962), 32.
- Knap, A.H., Michaels, A.F., Dow, R.L., Johnson, R.J., Gundersen, K., Sorensen, J.C., Close, A., Howse, F., Hammer, M., Bates, N.R., Doyle, A., Waterhouse, T., 1993. *BATS Methods Manual, Version 3*. US JGOFS Planning Office, Woods Hole, MA, USA.
- Letelier, R.M., Bidigare, R.R., Hebel, D.V., Ondrusek, M., Winn, C.D., Karl, D.M., 1993. Temporal variability of phytoplankton community structure—based on pigment analysis. *Limnology and Oceanography* 38 (7), 1420–1437.
- Levy, M., 2008. The Modulation of Biological Production by Oceanic Mesoscale Turbulence, Transport and Mixing in Geophysical Flows. Springer, Berlin/Heidelberg, pp. 219–261.
- Lopez-Urrutia, A., Moran, X.A.G., 2007. Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. *Ecology* 88 (4), 817–822.
- Maixandeau, A., Lefevre, D., Karayanni, H., Christaki, U., Van Wambeke, F., Thyssen, M., Denis, M., Fernandez, C.I., Uitz, J., Leblanc, K., Queguiner, B., 2005. Microbial community production, respiration, and structure of the microbial food web of an ecosystem in the northeastern Atlantic Ocean. *Journal of Geophysical Research—Oceans* 110 (C7), C07S17.
- Maranon, E., Holligan, P.M., Varela, M., Mourino, B., Bale, A.J., 2000. Basin-scale variability of phytoplankton biomass, production and growth in the Atlantic Ocean. *Deep-Sea Research I: Oceanographic Research Papers* 47 (5), 825–857.
- Marra, J., 2002. Approaches to the measurement of plankton production. In: Williams, P.J.L., Thomas, D.N., Reynolds, C.S. (Eds.), *Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater Ecosystems*. Blackwell Publishing, Ltd., Cambridge, Blackwells, pp. 78–108.
- McGillicuddy, D., Laurence, A., Bates, N.R., Bibby, T., Buesseler, K.O., Carlson, C.A., Davis, C.S., Ewart, C., Falkowski, P.G., Goldthwait, S.A., Hansell, D.A., Jenkins, W.J., Johnson, R., Kosnyrev, V.K., Ledwell, J.R., Li, Q.P., Siegel, D.A., Steinberg, D.K., 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. *Science* 316 (5827), 1021–1026.
- McGillicuddy, D.J., Johnson, R., Siegel, D.A., Michaels, A.F., Bates, N.R., Knap, A.H., 1999. Mesoscale variations of biogeochemical properties in the Sargasso Sea. *Journal of Geophysical Research—Oceans* 104 (C6), 13381–13394.
- Morris, R.M., Vergin, K.L., Cho, J.C., Rappe, M.S., Carlson, C.A., Giovannoni, S.J., 2005. Temporal and spatial response of bacterioplankton lineages to annual convective overturn at the Bermuda Atlantic Time-series Study site. *Limnology and Oceanography* 50 (5), 1687–1696.
- Mourino-Carballido, B., McGillicuddy, D.J., 2006. Mesoscale variability in the metabolic balance of the Sargasso Sea. *Limnology and Oceanography* 51 (6), 2675–2689.
- Najjar, R.G., Keeling, R.F., 2000. Mean annual cycle of the air–sea oxygen flux: a global view. *Global Biogeochemical Cycles* 14 (2), 573–584.
- Riser, S.C., Johnson, K.S., 2008. Net production of oxygen in the subtropical ocean. *Nature* 451 (7176), 323–325.
- Rivkin, R.B., Legendre, L., 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. *Science* 291 (5512), 2398–2400.
- Robinson, A.R., Williams, P.J.L., 2005. Respiration and its measurement in surface marine waters. In: Del Giorgio, P.A., Williams, P.J.L. (Eds.), *Respiration in Aquatic Ecosystems*. Oxford University Press, New York, pp. 147–180.
- Robinson, C., 2008. Heterotrophic bacterial respiration. In: Kirchman, D.L. (Ed.), *Advances in Microbial Ecology of the Oceans*. Wiley, New York, pp. 299–334.
- Roman, M.R., Adolf, H.A., Landry, M.R., Madin, L.P., Steinberg, D.K., Zhang, X., 2002. Estimates of oceanic mesozooplankton production: a comparison using the Bermuda and Hawaii time-series data. *Deep-Sea Research II: Topical Studies in Oceanography* 49 (1–3), 175–192.
- Steinberg, D.K., Carlson, C.A., Bates, N.R., Johnson, R.J., Michaels, A.F., Knap, A.H., 2001. Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep-Sea Research II: Topical Studies in Oceanography* 48 (8–9), 1405–1447.
- Strass, V.H., 1992. Chlorophyll patchiness caused by mesoscale upwelling at fronts. *Deep-Sea Research A: Oceanographic Research Papers* 39 (1A), 75–96.
- Sweeney, E.N., McGillicuddy, D.J., Buesseler, K.O., 2003. Biogeochemical impacts due to mesoscale eddy activity in the Sargasso Sea as measured at the Bermuda Atlantic Time-series Study (BATS). *Deep-Sea Research II: Topical Studies in Oceanography* 50 (22–26), 3017–3039.
- Williams, P.J.B., Del Giorgio, P.A., 2005. Respiration in aquatic ecosystems: history and background. In: Del Giorgio, P.A., Williams, P.J.B. (Eds.), *Respiration in Aquatic Ecosystems*. Oxford University Press, New York, pp. 1–17.
- Williams, P.J.L., 1998. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* 394 (6688), 55–57.
- Williams, P.J.L., Jenkinson, N.W., 1982. A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. *Limnology and Oceanography* 27 (3), 576–584.