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Eddy-driven pulses of respiration in the Sargasso Sea

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1   **Abstract**

2   An analysis of nine years of data from the NW subtropical Atlantic reveals that

3   variability in heterotrophic processes associated with (sub)mesoscale features has a

4   major impact on the balance between photosynthesis and respiration. Higher indirect

5   estimates of net community production (NCPe) are associated with the center of Mode

6   Water Eddies (MWE) and frontal regions between cyclonic and anticyclonic eddies

7   (CA). The increase in NCPe observed at the center of MWE is driven mainly by an

8   increase in autotrophic production, whereas in CA enhanced NCPe rates are the result of

9   an important reduction in bacterial respiration. Both features also exhibit a decrease in

10   nitrate concentration, consistent with nutrient consumption, and relative increases in

11   oxygen anomaly and particulate and dissolved organic carbon in the upper 200 m.

12   Plankton community composition in CA and MWE is characterized by the reduction in

13   bacterial biomass, and the dominance of *Prochlorococcus* and *Synechococcus* in CA,

14   and diatoms and dinoflagellates in MWE. Contrary to a common assumption, these

15   results show for the first time that in ecosystems influenced by (sub)mesoscale

16   dynamics, respiration can be as variable as photosynthesis.

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20

1 **Introduction**

2   Net community production, the balance between gross primary production and

3 total respiration, defines the metabolic state of the euphotic zone and sets a constraint on

4 the amount of organic carbon sinking to the deep ocean (del Giorgio and Duarte, 2002).

5 The relative constancy of organic matter decomposition (respiration) with respect to

6 variable production due to photosynthesis has been a major assumption in contemporary

7 oceanography (Karl et al., 2003). One of the reasons ocean respiration is considered less

8 variable than photosynthesis is that planktonic microbes, particularly heterotrophic

9 bacteria, utilize a diverse array of organic matter, and not just that derived from local

10 primary production (Karl et al., 1998).

11   Over the last several years an intense research effort has been focused on

12 investigating the enigmatic observation that respiration can exceed photosynthesis in

13 large areas of the subtropical ocean (Duarte et al., 1999; Williams, 1998), where

14 geochemical estimates indicate that these regions are in balance or behave as net sinks

15 for CO_2 (Hansell et al., 2004; Najjar and Keeling, 2000; Riser and Johnson, 2008). One

16 of the hypotheses proposed to explain this discrepancy postulates the existence of short

17 intensive bursts of photosynthesis, which charge the organic reservoir, and which

18 respiration slowly and steadily discharges (Karl et al., 2003). Mesoscale phenomena are

19 a mechanism that could generate high-frequency increases of photosynthesis to support

20 this hypothesis (Gonzalez et al., 2001; Maixandeau et al., 2005).

21   The ocean's subtropical gyres have been considered as relatively constant and

22 low productivity ecosystems (Eppley et al., 1973). However, recent studies in these

23 regions report important temporal and spatial variability in photosynthesis (Maranon et

24 al., 2000). A number of methodological issues associated with respiration measurements

25 in systems with low productivity (Williams and Jenkinson, 1982), has severely

1 hampered the development of a global database. In fact, the global dataset of

2 respiration, when compared to that of ^{14}C-based primary production, is about 1%

3 (Williams and Del Giorgio, 2005). As a result, respiration remains the least constrained

4 term in most models of ocean-atmosphere gas exchange (Balkanski et al., 1999).

5   The Bermuda Atlantic Time-series Study (BATS) site is located in the

6 subtropical gyre of the Atlantic Ocean, in the northwest corner of the Sargasso Sea.

7 BATS is designed to measure seasonal and interannual variability in biogeochemical

8 parameters (Steinberg et al., 2001), and measurements taken since 1988 are available at

9 http://bats.bios.edu/. The station is in an area of weak Gulf Stream recirculation with a

10 net flow towards the southwest and intense hydrographic mesoscale activity throughout

11 the region (Cianca et al., 2007). Three different types of mesoscale eddies have been

12 identified in the Sargasso Sea (McGillicuddy et al., 1999): cyclones, anticyclones, and

13 mode-water eddies (MWE). Cyclones and MWE tend to displace upper-ocean

14 isopycnals toward the surface, causing nutrient input into the euphotic zone and the

15 stimulation of photosynthesis. There is growing evidence that primary production

16 occurring both at the scale of mesoscale eddies, with characteristic spatial scales of 10-

17 100 km and temporal scales of weeks to months, and at the scale of submesoscale

18 dynamics contributes significantly to global carbon budgets (Levy, 2007). However,

19 because of the costs and logistics involved in sampling high frequency events in the

20 open ocean, direct observations at submesoscale range are scarce (Strass, 1992).

21   Previous studies have reported some evidence of variability in respiration rates

22 associated with different types of mesoscale features. Enhanced respiration rates have

23 been associated with anticyclonic eddies in the Canary Islands region (Aristegui and

24 Montero, 2005). In the NE subtropical Atlantic several observations have reported net

25 autotrophic balances associated with cyclonic eddies as result of a reduction in

1 respiration rates (Gonzalez et al., 2001; Maixandeau et al., 2005). In the summer of

2 2004, during the first year of field work of the Eddy Dynamics, Mixing Export, and

3 Species composition (EDDIES) project, an important variability in gross

4 photosynthesis and respiration rates was reported associated with three mesoscale

5 eddies investigated in the Sargasso Sea (Mourino-Carballido and McGillicuddy, 2006).

6 In this study I combine nine years (1993 – 2002) of altimeter data with data from the

7 BATS program in order to verify the hypothesis that respiration is as variable as

8 photosynthesis and equally influenced by (sub)mesoscale dynamics.

9

1   **Methods**

2   *Retrospective analysis of altimeter and BATS data*

3   Eddy field animations for the 1993 – 2002 period generated from the objective

4   analysis of satellite altimetry for the domain spanning latitude 28° to 38ºN and

5   longitude   of   75°   to   45°W   (available   at

6   http://science.whoi.edu/users/mcgillic/tpd/anim.html) combined with hydrographic

7   profiles at BATS (31.16°N – 64.5°W) were used to assess the influence of the three

8   eddy types described in the Sargasso Sea: cyclones, anticyclones, and mode water

9   eddies (McGillicuddy et al., 1999), and frontal regions of interaction between cyclones

10   and anticyclonic eddies (CA) as described in Mouriño-Carballido and McGillicuddy

11   (2006). Other types of (sub)mesoscale activity that sporadically affect the BATS site

12   were not considered. Only those features that exhibited a strong signal and affected the

13   BATS site for relatively long periods of time were included in the analysis. This study

14   extends the retrospective analysis included in Mouriño-Carballido and McGillicuddy

15   (2006) as: 1) All the CA were identified during the nine-year period (whereas only CA

16   associated with enhancements of net community production were included in Mouriño-

17   Carballido and McGillicuddy (2006)); 2) eddy field animations and hydrographic data

18   were used to identify BATS samplings influenced by the center of the eddy features and

19   those affected by eddy uplifting but not located at the eddy center.

20   BATS data from the same period (1993-2002) were also used to study

21   distributions of nitrate, phosphate, silicate, oxygen, particulate and dissolved organic

22   carbon (POC and DOC, respectively), particulate and dissolved organic nitrogen (PON

23   and DON), pigments, bacterial biomass, ^{14}C incorporation by phytoplankton (^{14}C PP),

24   bacterial growth (BG) and vertical carbon flux from sediment traps (C_{flux}). Changes in

25   community structure composition were investigated by computing the percent

1   chlorophyll-a contributed by different phytoplankton groups by using the algorithms

2   developed for the oligotrophic Pacific by Letelier et al. (1993) and previously used for

3   the BATS site (Boyd and Newton, 1999; Sweeney et al., 2003). Details of the BATS

4   sampling scheme, analytical methods, data quality control, and inter-calibration

5   procedures appear in the BATS Methods Manual (Knap et al., 1993). Data are available

6   from the BATS web site at http://bats.bios.edu/. After much deliberation following

7   different tries with depth intervals, depth range selection was based on the vertical

8   distribution of properties at BATS site (Steinberg et al., 2001). Rates were integrated

9   down to the depth of the euphotic layer (ca. 100 m). Percent chlorophyll-a contributed

10   by different phytoplankton groups was integrated deeper (0-160 m), to cover the deep

11   chlorophyll maximum feature. The deeper level of the sediment traps deployments at

12   BATS (300 m) was chosen to quantify the export of carbon from the upper layer. All

13   the other parameters were integrated down to the winter mixed layer depth (ca. 200 m).

14   One-way analysis of variance (one-way ANOVA) was used to compare parameters

15   between different mesoscale features (cyclones, anticyclones, MWE and CA).

16

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

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

19   according to:

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

21

22   where ${}^{14}C\,PP$ is the rate of ${}^{14}C$ incorporation by phytoplankton (particulate primary

23   production) and BR is bacterial respiration. BR, in turn was estimated as:

24

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

1   where BG is bacterial growth rate measured by the {3H-methyl}-thymidine (^{3}H-TdR)

2   technique (Steinberg et al., 2001). Thymidine incorporation was converted to bacterial

3   respiration using the commonly reported isotope (ICF, 1.5×10^{18} cell mol^{-1}) and carbon

4   conversion factors (CCF, 15 fgC cell^{-1}) (Ducklow, 2000), and the mean bacterial

5   growth efficiency (BGE) reported for the Sargasso Sea (ca. 0.13) (Carlson and

6   Ducklow, 1996). This value is higher than more recent BGE reported for open ocean

7   regions (0.08, Robinson et al., (In press)). However, I used the BGE reported by

8   Carlson and Ducklow (1996) because it derives from experiments carried out in the

9   same location as the study presented here. Mouriño-Carballido and McGillicuddy

10   (2006) applied a similar approach but they used bacterial carbon demand instead of BR.

11   It is known that the conversion factors involved in the calculation of BR from

12   BG are currently poorly constrained (Alonso-Saez et al., 2007). In this study, in order to

13   investigate the effect of a constant BGE in the variability reported for bacterial

14   respiration, I also computed BR using the empirical BGE models reported by del

15   Giorgio and Cole (1998), being BP bacterial production:

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17
$$BGE_1 = \left(\frac{0.037 + 0.65BP}{1.8 + BP} \right)$$

18

19

20   and López-Urrutia & Morán (2007):

21

22
$$BGE_2 = \left(1 - \frac{1}{0.727 \text{ x } \dfrac{chl}{chl + 4.08} + 1.02} \right)$$

23

24

25   where chl is the chlorophyll concentration in mg m^{-3}.

1   There are two important caveats associated with my estimates of NCP. First the

2   ^{14}C assimilation technique underestimates gross primary production, and second

3   estimating respiration on the basis of BR underestimates total respiration. Compilation

4   of measurements carried out during the Joint Global Ocean Flux Study (JGOFS)

5   indicated that ^{14}C uptake measures net primary production (gross primary production –

6   autotrophic respiration) in dawn-dusk incubations (Marra, 2002). Within the euphotic

7   zone, the existing data further suggest that bacteria are the main contributors to

8   community respiration (~50 to >90%) (Rivkin and Legendre, 2001; Robinson and

9   Williams, 2005). Giorgio and Duarte (2002) reviewed the current information on the

10   contribution of various biotic components and depth layers to respiration in the open

11   ocean and they assumed that zooplankton respiration represents 5% of the combined

12   microplankton respiration in the photic and thermocline waters. Mesozooplankton

13   production at BATS has been estimated to be 2% of primary production at this site

14   (Roman et al., 2002). Unfortunately, the contribution of bacteria to community

15   respiration cannot be verified at this site since specific studies about the contribution of

16   microzooplancton respiration, and their variability, have not been conducted.

17

1 **Results and discussion**

2 *The variability of respiration versus photosynthesis*

3   To determine whether the high variability observed in gross photosynthesis and

4 respiration rates during the EDDIES cruises is a common pattern in this region, I

5 compared depth integrated ^{14}C primary production (PP) and bacterial respiration (BR)

6 rates computed for the 1993-2002 period at the BATS site (Figure 1). To compute

7 bacterial respiration, I used the mean bacterial growth efficiency (BGE), 0.13, reported

8 for the Sargasso Sea by Carlson and Ducklow (1996). Mean values of BGE computed

9 by using the empirical models reported by del Giorgio and Cole (1998) (BGE_1=0.026 ±

10 0.005) and López-Urrutia & Morán (2007) (BGE_2=0.05 ± 0.01) (see methods) were

11 much lower than the mean BGE value reported for the open ocean (0.08, Robinson et

12 al., (In press)), which results in high, and probably unrealistic, rates of BR (Figure 1).

13 Both empirical models were built from relatively limited data sets culled from diverse

14 ecosystems and they may not be adequate for all environments. No specific empirical

15 models have been reported for highly dynamic ocean ecosystems under the influence of

16 (sub)mesoscale processes. For this reason I decided to use a constant BGE in the

17 estimation of BR and NCPe. This is in agreement with the recent synthesis carried out

18 by Robinson (In press) who reports a median value of 6 mg C m^{-3} d^{-1} for open ocean

19 BR.Variability in depth-integrated BR (reported as the coefficient of variation),

20 computed using BGE=0.013 (Carlson and Ducklow, 1996), BGE_1 and BGE_2 was

21 always similar to or higher than variability in depth-integrated PP (Figure 1). Robinson

22 & Williams (2005) analyzed a large data set of oxygen flux derived gross production

23 and respiration rates available in diverse ocean ecosystems. They reported the variance

24 of photosynthesis to be greater than respiration when volumetric rates computed at

25 different depths were used. However, they found similar variances in photosynthesis

1   and respiration when they analyzed depth-integrated rates, which are better predictors

2   when regional or temporal differences between stations are analyzed, as they overcome

3   potential separation in depth of photosynthesis and respiration (Robinson and Williams,

4   2005) .

5

6   *The contribution of mesoscale dynamics to the observed variability in respiration*

7   An important part of the variability observed in the primary production rates

8   measured at BATS has been previously attributed to mesoscale eddies (Sweeney et al.,

9   2003). To investigate how much of the variability in bacterial respiration was driven by

10   (sub)mesoscale forcing, I tracked mesoscale eddies and frontal regions between

11   cyclones and anticyclones, using altimeter and hydrographic data from the BATS

12   station, over the 9-year period. Thirteen cyclones, six anticyclones, 8 MWE, and 17

13   frontal regions of interaction between cyclonic and anticyclonic eddies (CA) were

14   identified during the 1993 – 2002 period (see Figure 2 and table 1). Cyclones were the

15   (sub)mesoscale features that more frequently affected the area (28% of the samplings

16   were affected by these features), followed by CA (23%), MWE (13%) and anticyclones

17   (8%).

18   The impact of the (sub)mesoscale features on PP, BR, and NCPe, is more

19   noticeable when the seasonal signal in these parameters (see Figure 8 in Mouriño-

20   Carballido and McGillicuddy (2006)) is filtered out by computing anomalies relative to

21   monthly averages (Figure 3). Anomalies are rescaled to values between 1 and 10, where

22   10 is the largest value for each parameter. Positive (negative) values represent

23   enhancements (decreases) with respect to typical background conditions for the

24   sampling month. It is important to bear in mind that this region is populated by closely

25   packed eddies that are constantly evolving and interacting with each other (Cianca et al.,

1   2007). As such, background conditions (anomalies close to zero) represent the mean

2   stage that results from the influence of the different types of mesoscale features

3   affecting this region. The anomaly record shows pulses in the magnitude of both PP and

4   BR, some of them in close connection with the (sub)mesoscale field. The use of

5   different parameterizations in the calculation of BGE (see methods) does not have a

6   significant effect on the variability in BR and the connection with the (sub)mesoscale

7   field (Figure 3). Nine out of the eighteen large (>2.5) NCPe anomalies occur during

8   periods when BATS is influenced by CA, four are associated with cyclonic eddies, two

9   with MWE, and one with an anticyclone. Six out of the nine high NCPe anomalies

10   found at CA are associated with small negative (< -2.5) anomalies in BR.

11   The fixed-point time-series data generated by BATS create some inherent

12   difficulties to compare statistically the effects among eddy types. The impact of the

13   mesoscale forcing on the upper-ocean biochemistry at BATS includes variability

14   induced by the type of the mesoscale eddy, the section of the mesoscale eddy going

15   through the site (i.e. center versus edge), and also the variability induced by the stage of

16   the biological response (i.e. initial versus decaying stage). These factors are expected to

17   impact the robustness of statistics calculated from the time-series, in the sense that very

18   long time series would be needed in order to have a representative number of the

19   different stages. However, interesting patterns arise when the seasonal signal of several

20   biogeochemical parameters sampled at BATS site along the 1993 – 2002 period

21   (Steinberg et al., 2001) is filtered by means of anomalies with respect to monthly

22   averages, and when these anomalies are grouped based on the influence of cyclones,

23   anticyclones, MWE, and CA (Figure 4). Again, positive (negative) values represent

24   enhancements (decreases) relative to typical background conditions for the sampling

25   month.

1   CA are the (sub)mesoscale features associated with the highest anomaly in

2   NCPe, as a result of relative enhanced PP and a strong reduction in BR (Figure 4).

3   These features are also characterized by a decrease of nitrate, consistent with nutrient

4   consumption though photosynthesis, and the increase of oxygen anomaly and

5   particulate organic carbon (POC) in the upper 200 m. Plankton community composition

6   is characterised by the dominance of *Prochlorococcus* and *Synechococcus* and a slight

7   decrease in bacterial biomass. The lowest NCPe anomaly is found in anticyclonic

8   eddies, as a result of a substantial increase in BR. These features are also characterized

9   by an increase in nitrate and silicate, a decrease in oxygen anomaly and POC and a

10   noticeable enhancement in bacterial biomass in the upper 200 m. Cyclones and MWE

11   are initially both associated with negative anomalies in NCPe.

12   However, substantial differences between both features arise when the BATS

13   samplings are divided into those influenced by the center of the eddy features and those

14   affected by eddy uplifting but not located at the eddy center (Ce and MWEe). Centers of

15   MWE are characterized by a noticeable increase in NCPe rates, as a result of the

16   estimated enhancement in PP. Drops in nitrate and silicate concentration, consistent

17   with nutrient consumption, as well as enhancements in oxygen anomaly, POC and

18   dissolved organic carbon (DOC) in the upper 200 m are also associated with the center

19   of MWE. Phytoplankton composition is dominated by dinoflagellates and a conspicuous

20   increase in diatoms, whereas bacterial biomass is noticeably reduced. An increase in

21   bacterial respiration is observed at MWEe, where bacterial biomass is slightly

22   enhanced. Centers of cyclonic eddies are associated with low NCPe values, as the result

23   of a noticeable increase in BR. Enhanced nitrate and silicate concentrations, but also

24   oxygen anomaly, and relatively reduced POC and DOC in the upper 200 m are

25   associated with these features. Plankton composition is dominated by *Prochlorococcus*

1 and *Synechococcus* and slightly enhanced bacterial biomass. In agreement with the

2 patterns observed in NCPe, higher carbon flux inferred from sediment traps was

3 observed at the center of MWE, whereas the lowest carbon flux was computed at the

4 center of cyclonic eddies. Differences between particular eddy types are statistically

5 significant for oxygen anomaly (p=0.015), diatom abundance (p=0.021), and net

6 community production (p=0.011), once the distinction of those samplings influenced by

7 eddy center and those affected by eddy uplifting but not located at the eddy center is

8 made (see Table 2).

9 This study confirms previous results regarding differences between eddy types.

10 The analysis of three years of data (1993-1995) from the BATS site reported noticeable

11 enhancements in primary production associated with two MWE, whereas the 1994

12 spring bloom was suppressed by the passage of an anticyclone (Sweeney et al., 2003).

13 The same authors described an increased percentage of diatoms and dinoflagellates in

14 MWE, whereas cyclones exhibited an increased percentage of *Synechococcus*. The

15 pattern described in this study in anticyclones and CA is in agreement with *in vitro*

16 gross photosynthesis and respiration rates reported in summer 2004 by Mouriño-

17 Carballido and McGillicuddy (2006). The variability reported inside the cyclone

18 intensively investigated in summer 2004 (C1) highlights the relevance of considering

19 the time history of mesoscale eddies when interpreting the biological responses

20 associated with these features. For this reason, patterns observed at each eddy feature

21 from the retrospective analysis of the BATS data should be considered cautiously as

22 they may not include a representative number of all the possible eddy life stages. In

23 agreement with the retrospective analysis of BATS data presented in this study,

24 plankton composition was dominated by *Prochlorococcus spp.* in cyclone C1 whereas a

25 diatom bloom was found in MWE A4, the mode water eddy investigated in summer

1   2005 (McGillicuddy et al., 2007). Based on the assumption that the O_2 minimum found

2   in the central eddy stations at C1 (200-400 m) and A4 (800-1000 m) was a consequence

3   of high particle export from eddy induced blooms, carbon export inferred from the O_2

4   anomalies was one to three times as much as annual new production for the region

5   (McGillicuddy et al., 2007). The retrospective analysis from the BATS data show a

6   noticeably enhanced deep (200-800 m) oxygen anomaly associated with the center of

7   MWE (see Table 2). Other depth intervals (200-400 m, 400-600 m and 600-800 m)

8   show similar results (data not shown). However, the BATS sampling probably misses

9   the smaller and more variable O_2 anomalies found at C1 and A4 cores. Modeling

10   experiments based on the results from summer 2004 and 2005 EDDIES cruises suggest

11   that diatom blooms are sustained by interactions with the surface wind field at MWE,

12   whereas wind-eddy interactions dampen upwelling in cyclones (McGillicuddy et al.,

13   2007). Details on the mechanisms responsible for the reduced bacterial respiration

14   described at CA remain unknown. The influence of changes in bacterial populations

15   associated with different hydrodynamic regimes (Morris et al., 2005) can   not be

16   discounted.

17

18   **Conclusions**

19   Respiration represents the largest sink of organic carbon in the biosphere. On a

20   global scale, excluding external sources of organic matter (Dachs et al., 2005),

21   respiration must be balanced by the input of organic matter via autotrophic production.

22   Based on the assumption of its relative constancy, respiration has the potential to be a

23   more accurate measure of time-integrated net organic production than photosynthesis,

24   particularly for under-sampled, highly dynamic systems (Carlson et al., 2007). My

25   results show for the first time that, contrary to previous assumptions, in highly dynamic

1 ecosystems influenced by (sub)mesoscale dynamics, respiration can be as variable as

2 photosynthesis. Pulses in respiration driven by (sub)mesoscale forcing need to be

3 considered in order to quantify the balance between synthesis and consumption of

4 organic matter. Future sampling strategies should be designed in order to resolve

5 higher-frequency, smaller-scale variability in both photosynthesis and respiration,

6 which is crucial to comprehend the potential for carbon export to the deep ocean.

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14

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.

Number	Type	Influence at BATS (begining)	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	

Table 2. Anomalies for selected parameters computed with respect to monthly averages for the 1993 – 2002 period at BATS site. 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. ΔO_2, is oxygen anomaly (O_2 in situ – O_2 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. The 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.

Variable (units)	C Mean ± STD	n	Cc Mean ± STD	n	Ce Mean ± STD	n	A Mean ± STD	n	MWE Mean ± STD	n	MWEc Mean ± STD	n	MWEe Mean ± STD	n	CA Mean ± STD	n	One way ANOVA *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) (ug 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) (ug 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) (ug 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) (ug 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
Prochlorococcus (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
Synechococcus (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) (mgC 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) (mgC 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) (mgC 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
Cflux (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

1   **Figure legends**

2   Figure 1. Depth-integrated (0-100 m) ^{14}C primary production versus depth-integrated

3   bacterial respiration (BR) estimated for the 1993-2002 period at the BATS site. BR was

4   calculated assuming a constant BGE=0.13 (A). BR_1 (B) and BR_2 (C) were computed using

5   the empirical models for BGE reported by del Giorgio and Cole (1998) and López-Urrutia

6   & Morán (2007) (see methods). Coefficient of variation for ^{14}C PP, BR, BR_1 and BR_2 are

7   45, 66, 46 and 71%, respectively. Median values for BR, BR_1 and BR_2 are 226, 1238 and

8   790 mgC m^{-2} d^{-1}, respectively. The black lines are the 1:1 lines.

9   Figure 2. (A). Sea level anomalies (SLA) estimated for the 1993-2002 period at the BATS

10   site. (B) Temperature in the upper 700 m for the 1993 – 2002 period at BATS site. Coloured

11   bars indicate periods under the influence of cyclones (blue), anticyclones (red), mode water

12   eddies (yellow), and frontal regions between cyclonic and anticyclonic eddies (green).

13   White sections correspond to other type of (sub)mesoscale activity not included in this

14   analysis. Numbers on the top correspond to mesoscale features identified during the 9-year

15   period (see table 1).

16   Figure 3. Anomalies for depth-integrated (0-100 m) primary production (PP), bacterial

17   respiration (BR) and net community production (NCPe) computed with respect to monthly

18   averages and rescaled to values between 1 and 10 for the 1993 – 2002 period at BATS site.

19   Anomalies for BR computed assuming a constant BGE (0.13) (solid line), the empirical

20   model reported by del Giorgio and Cole (1998) (dashed line) and López-Urrutia & Morán

21   (2007) (dotted line) are represented. Coloured bars indicate periods under the influence of

22   cyclonic (blue), anticyclonic (red), mode water eddies (yellow), and frontal regions between

23   cyclonic and anticyclonic eddies (green). White sections correspond to other type of

1 (sub)mesoscale activity not included in this analysis (see methods). Horizontal dashed lines

2 indicates arbitrary thresholds in the 1–10 scale of 2.5 (i.e., 25% of the largest value) and -

3 2.5 (i.e., -25% of the largest value). Numbers on the top correspond to mesoscale features

4 identified during the 9-year period (see table 1).

5 Figure 4. Anomalies for selected parameters computed with respect to monthly averages for

6 the 1993 – 2002 period at BATS site. CA corresponds to cyclone – anticyclone interactions.

7 A, MWE and C correspond to anticyclones, mode water eddies and cyclones, respectively

8 (c, center; e, edge). NCPe is indirect estimates of net community production; PP, primary

9 production; BR, bacterial respiration (computed assuming BGE=0.13); O_2 anomaly, O_2 in

10 situ – O_2 saturation in the upper 200 m; POC (DOC), particulate (dissolved) organic carbon.

11 *Prochlorococcus, Synechococcus,* dinoflagellates and diatoms represent the percent

12 chlorophyll-a contributed by these groups. Bacteria is bacterial biomass and Cflux vertical

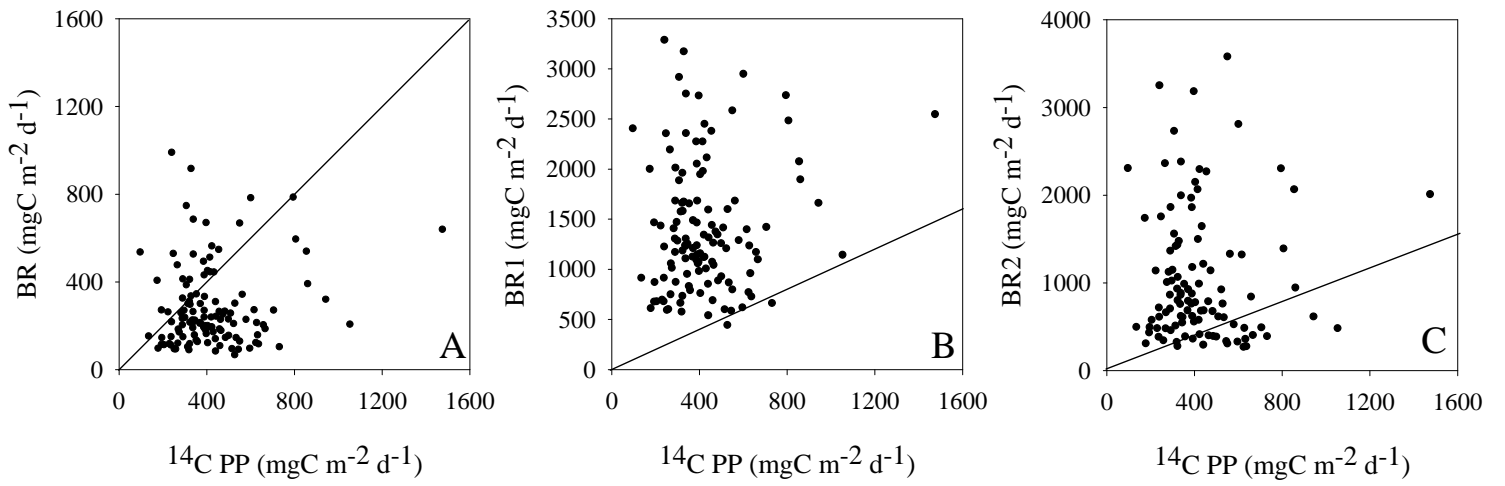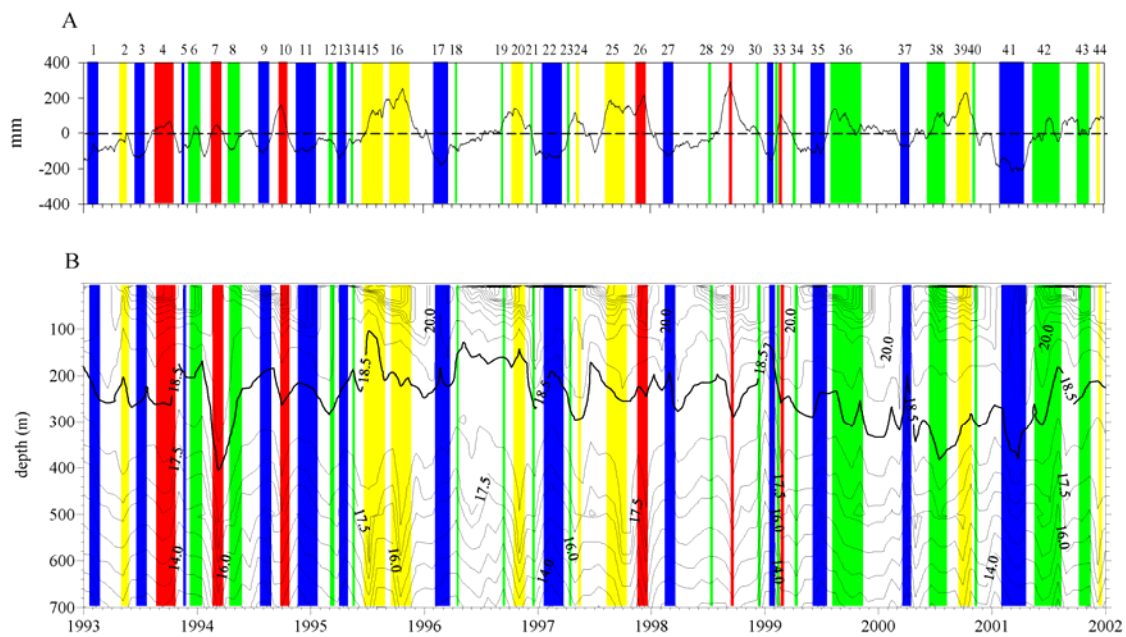13 carbon flux from sediment traps. Error bars represent standard errors. See table 2 for depth-

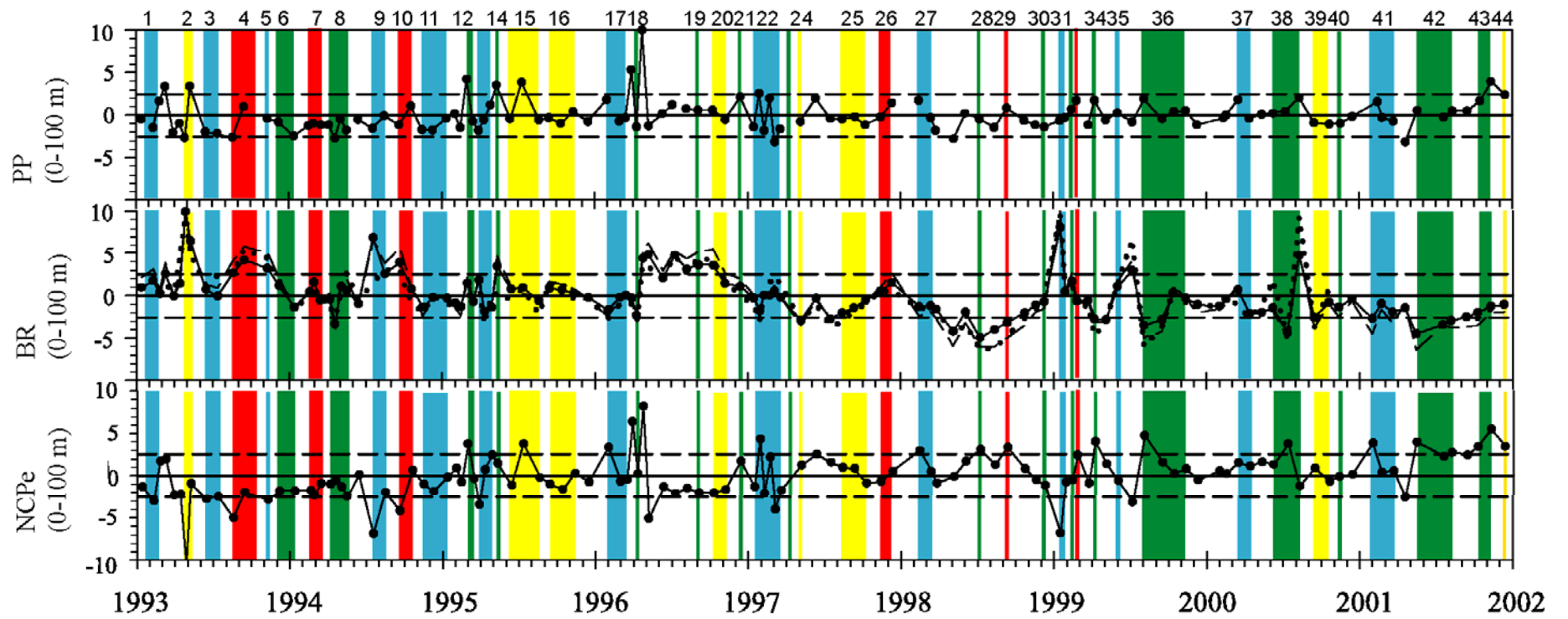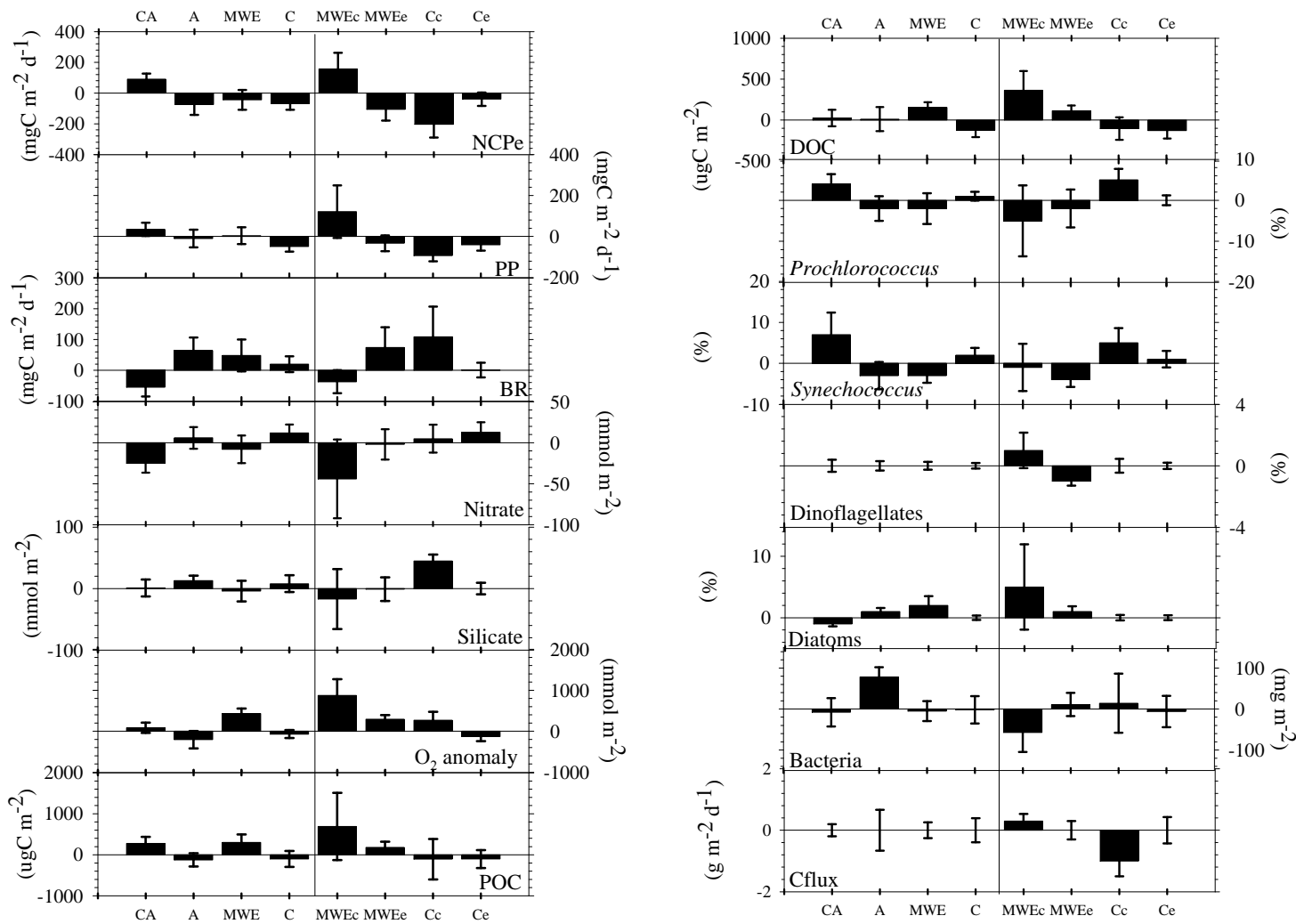14 integration intervals.

Figure 1

Figure 2

Figure 3

Figure 4