Regional Differences in the Role of
Eddy Pumping in the North Atlantic Subtropical Gyre
HISTORICAL CONUNDRUMS REVISITED

BY BEATRIZ MOURIÑO-CARBALLIDO AND SUSANNE NEUER

The vast subtropical regions of the ocean account for at least 30% of the carbon export to the deep ocean. It is predicted that these regions will get larger as a consequence of global warming. Traditionally, they have been considered relatively homogeneous, and observations at one site have been extrapolated to the region as a whole. Two main conundrums remain unresolved: (1) in the western province of the subtropical North Atlantic (NASW), direct measurements of nutrient supply have been considerably lower than indirect estimates, and (2) in the eastern province of the subtropical North Atlantic (NASE), instantaneous oxygen production rates by bottle incubations indicate net heterotrophy prevailing throughout large areas. Episodic nutrient inputs into the photic layer and net oxygen production associated with mesoscale activity have been proposed to reconcile both discrepancies. Here, we compare recent findings obtained at the Bermuda Atlantic Time-series Study (BATS) station in NASW, and in a region between ca. 22–35°N and 15–34°W (NASE), including the European Station for Time-series in the Ocean, Canary Islands (ESTOC) located north of the Canary Islands. These findings show how important spatial heterogeneity is in understanding the biogeochemistry of this biome.

THE NORTH ATLANTIC SUBTROPICAL GYRAL PROVINCE (NAST)

Traditionally, the subtropical gyres have been considered the deserts of the ocean. Phytoplankton biomass is low (Figure 1), mainly due to the paucity of nutrients resulting from strong water-column stratification and weak vertical mixing. Yet, despite their low phytoplankton biomass, the subtropical gyres are surprisingly productive based on the export rates of organic carbon from the euphotic zone (Emerson et al., 1997). This fact, combined with their vast areas (ca. 60% of the total ocean surface; Longhurst, 1998), results in their contribution of at least 30% of total marine new production (Emerson et al., 1997; Jin et al., 2007).

Subtropical gyres were also considered relatively constant ecosystems in time and space until the first comprehensive descriptions of biological time-series data obtained in the Sargasso Sea at Hydrostation S (Menzel and Ryther, 1960) and later on at the Bermuda Atlantic Time-series Study (BATS; Michaels and Knap, 1996) became available. Satellite-derived ocean color imagery also allowed large-spatial-scale observations of the seasonal development of phytoplankton biomass. These time-series observations revealed that phytoplankton in subtropical gyres develop with a seasonality comparable to that of the phytoplankton spring blooms in the temperate North Atlantic, except that they begin earlier and produce less biomass (Sathyendranath et al., 1995; McClain et al., 2004a; Ueyama and Monger, 2005). Subtropical gyres also have been considered relatively
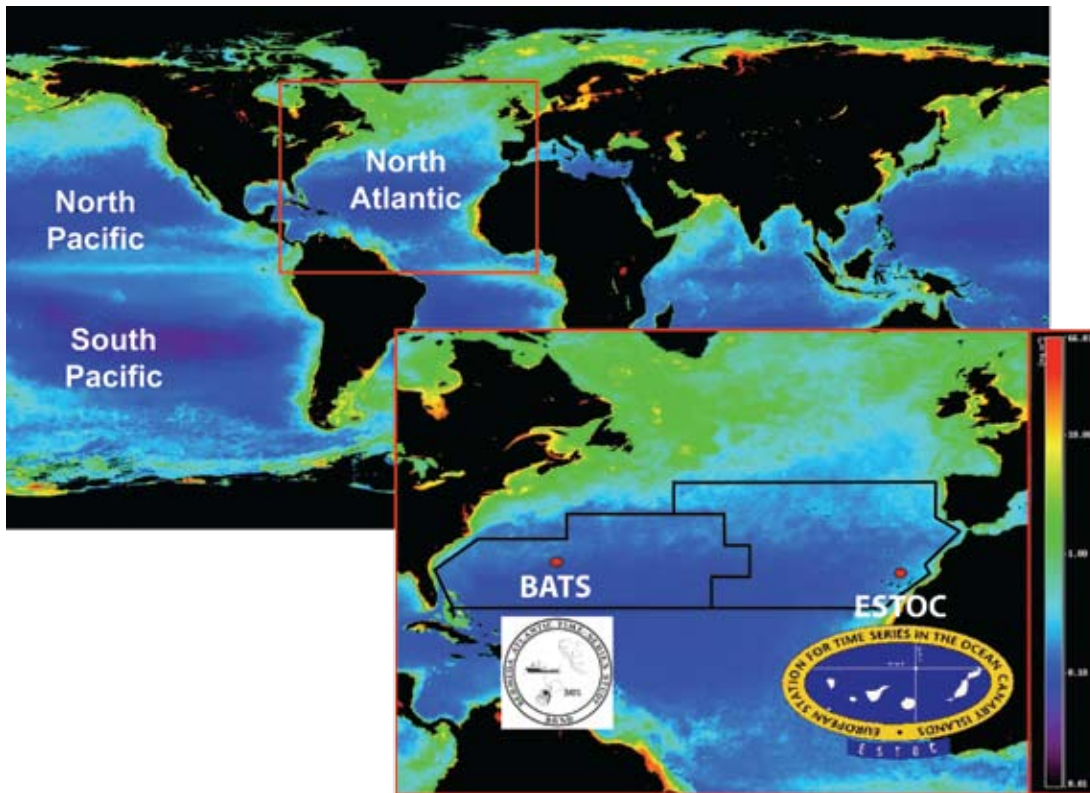
Figure 1. Surface chlorophyll (yearly average for 2007) determined by the MODIS (Moderate Resolution Imaging Spectroradiometer) ocean color sensor. The five subtropical gyres located in the center of each major ocean basin are characterized by low phytoplankton biomass (dark blue). Inset shows the North Atlantic subtropical gyre with time series stations BATS (Bermuda Atlantic Time-series Study) in the western province (NASW) and ESTOC (European Station for Time Series) in the eastern gyre within the eastern province (NASE). *Surface chlorophyll image courtesy of the Goddard Earth Sciences Data and Information Services Center/Distributed Active Archive Center (Code 902) at the Goddard Space Flight Center, Greenbelt, MD 20771*

homogeneous, with observations at one site extrapolated to the larger region (Ledwell et al., 1993; Michaels et al., 1994; Emerson et al., 1997).

This article synthesizes observations from recently published work showing how important spatial heterogeneity is in understanding the biogeochemistry of this biome. We focus on the North Atlantic subtropical gyre, which is undoubtedly one of the best-studied open ocean regions and, in past decades, has been a major contributor to the development of our understanding of biogeochemical cycles in subtropical regions. In defining ecological geographical biomes and provinces for the global ocean, Longhurst (1998) termed this region the North Atlantic Subtropical Gyral Province (NAST) and divided

it into western and eastern portions that we reference as NASW and NASE, respectively (Figure 1).

The two time-series stations, BATS (31.16°N, 64.5°W) and ESTOC (European Station for Time series, Canary Islands; 29.16°N, 15.5°W), are located at about the same latitude in NASW and NASE (Figure 1). BATS is situated within the recirculation of the Gulf Stream with a net flow toward the southwest; ESTOC is located within the southward-flowing Canary Current. An overview of the biogeochemistry and oceanography at BATS is presented in Michaels and Knap (1996) and Steinberg et al. (2001), and more recently at ESTOC (González-Dávila et al., 2003; Cianca et al., 2007; Neuer et al., 2007; Santana-Casiano et al., 2007). BATS and

ESTOC exhibit similar phytoplankton biomass, both in terms of surface as well as integrated chlorophyll, and primary production (Table 1), with a pronounced winter maximum in phytoplankton development (Steinberg et al., 2001; Neuer et al., 2007). In addition to observations at these two time-series stations,

Beatriz Mouriño-Carballido (*bmourino @uvigo.es) was Fulbright Postdoctoral Fellow, Applied Ocean Physics and Engineering Department, Woods Hole, MA, USA, and is now Parga-Pondal Research Fellow at the Departamento de Ecología y Biología Animal, Universidad de Vigo, Vigo, Spain.* **Susanne Neuer** (*susanne. neuer@asu.edu) is Associate Professor, School of Life Sciences, Arizona State University, Tempe, AZ, USA.*

we also include in our comparison measurements obtained on 13 cruises carried out in the NASE province within 22–35°N and 15–34°W from March 1992 to November 2001 (Marañón et al., 2007). Although ESTOC is located within the NASE box, it exhibits the higher end of productivity inside the NASE region (see Table 1).

HISTORICAL CONUNDRUMS

We present here two historical conundrums regarding the biogeochemistry of these regions, each one traditionally characterizing the biogeochemistry of NASW versus NASE. The first conundrum can be termed that of the "missing nutrients": in NASW, geochemically based estimates of new production (NP) determined from dissolved gas inventories (~ 0.5 mol N m^{-2} y^{-1}) are one order of magnitude higher than can be explained by a simple one-dimensional balance where vertical turbulent diffusion supplies the new nitrate into the euphotic zone (Doney, 1997). The second conundrum can be termed the "missing organic carbon": in NASE, measurements of net community production (NCP) based on instantaneous net oxygen production by bottle incubations indicate that net heterotrophy prevails across large areas (Duarte et al., 2001; Robinson et al., 2002; Williams et al., 2004). These observations contradict positive NCP reported at ESTOC based on the biologically driven net change of dissolved inorganic carbon in the euphotic zone (Neuer et al., 2007). They also disagree with geochemical evidence of net oxygen production (Najjar and Keeling, 2000; Riser and Johnson, 2008) and calculated organic matter transports (Hansell et al., 2004) which suggests the upper layer of the subtropical ocean is net autotrophic. But, if true for the larger NASE, the negative NCP values reported by the in vitro oxygen technique (see Table 1) would amount to an organic carbon deficit in this region of ca. 0.3 Gt C yr^{-1} (Mouriño et al., 2003).

Note that both "conundrums" rely on two different ecological production terms—that of NP and of NCP. Both should be comparable if the assumption of steady state applies (Quiñones and Platt, 1991), and over large temporal and spatial scales, these terms should provide information about the capacity of the ocean to remove carbon from the upper

Table 1. Summary of phytoplankton biomass (as chlorophyll *a*, mg m^{-3} and depth integrated, mg m^{-2}), primary production (PP), net community production (NCP), respiration (R), and new production at BATS, ESTOC, and from cruises carried out in a larger region within NASE. Rates are in mgC m^{-2} d^{-1}. Unless otherwise noted, values for BATS from Mouriño and McGillicuddy (2006) and for ESTOC from Neuer et al. (2007).

Variable	BATS	ESTOC	NE subtropical gyre
Surface chl-*a*	0.13 ± 0.12 [1]	0.14 ± 0.12	0.08 ± 0.01 (Teira et al., 2005)
Photic layer integrated chl-*a*	24 ± 2 [2]	27 ± 12 [2]	16 ± 1 (Teira et al., 2005)
Photic layer integrated PP	382 ± 37 [3]	397 ± 32 [4]	227 ± 20 [3] (Teira et al., 2005)
Photic layer integrated NCP	46 ± 87 [5] 73 ± 31 [6] (Gruber et al., 1998)	111 ± 34 [7]	-694 ± 171 [8] (Marañón et al., 2007)
Photic layer integrated R	336 ± 78 [9] 587 ± 398 [10]	ND	1324 ± 142 [11] (Marañón et al., 2007)
New production	96 ± 20 (Cianca et al., 2007)	71 ± 23 (Cianca et al., 2007)	42 ± 13 [12] (Varela et al., 2005)

[1] Analyses of 1993–2002 BATS data set.
[2] Integrated down to 160 m for BATS and to 200 m for ESTOC.
[3] ^{14}C – method.
[4] Bio-optical model.
[5] From difference of ^{14}C phytoplankton production and bacterial carbon demand rates.
[6] Mean value for the summary of estimates of net production in the Sargasso Sea reported in Gruber et al (1998).

[7] From dissolved inorganic carbon drawdown due to biological processes in mixed layer.
[8] From in vitro oxygen technique.
[9] From bacterial carbon demand rates using 1993–2002 BATS data set.
[10] From in vitro oxygen technique. Data from spring and summer 2004.
[11] From in vitro oxygen technique. Data collected over a 10-yr period.
[12] From nitrate uptake during the 2000 summer-to-autumn transition period.

layers to the deep ocean (also termed export production) (see Figure 2). However, logistical considerations and the different spatial and temporal time scales involved in these measurements, as well as the lack of concomitance, often compromise the comparison between both rate measurements. Even if the same vertical integration ranges are used, horizontal and vertical decoupling of NCP and NP due to a time lag between biological uptake and regeneration (Platter et al., 2005; Wang et al., 2005; Williams and Del Giorgio, 2005) may affect the comparison of these terms.

Regular cruises and even time-series programs generally undersample the oceanic system and miss episodic nutrient inputs and net oxygen production generated by events that are heterogeneous over temporal and/or spatial scales (McGillicuddy and Robinson, 1997; Karl et al., 2003; Mouriño et al., 2003). One of the mechanisms that can be responsible for this episodicity is the uplift of the isopycnals and nutricline into the euphotic zone by mesoscale eddies, which leads to an enhancement of new and net production (see review by Garçon et al., 2001).

We attempt to reconcile the imbalance postulated above for the western and eastern basins of the subtropical North Atlantic during the past by looking for a common mechanism. We switch the traditional perspectives presented earlier by the "historical conundrums" between NASW and NASE by investigating the following questions: (1) What is the relevance of mesoscale variability as a new nutrient input mechanism in the NASE? and (2) What is the contribution of mesoscale variability to the metabolic balance in NASW?

A. New Production (NP)

$$NP = TP - RP$$

N_2-fixation / Other N-inputs

Total Production (TP)

I_0

$$CO_2 + H_2O \rightleftharpoons CH_2O + O_2$$

NH_4 — Regenerated Production (RP)

1% I_0

$NO_3^-, PO_4^{-3}, SiO_4^{-4}$

CH_2O

Export Production

B. Net Community Production (NCP)

$$NCP = GP - R$$

I_0

Gross Photosynthesis (GP)

$$CO_2 + H_2O \rightleftharpoons CH_2O + O_2$$

Respiration (R)

NCP > 0 — Autotrophic
NCP < 0 — Heterotrophic

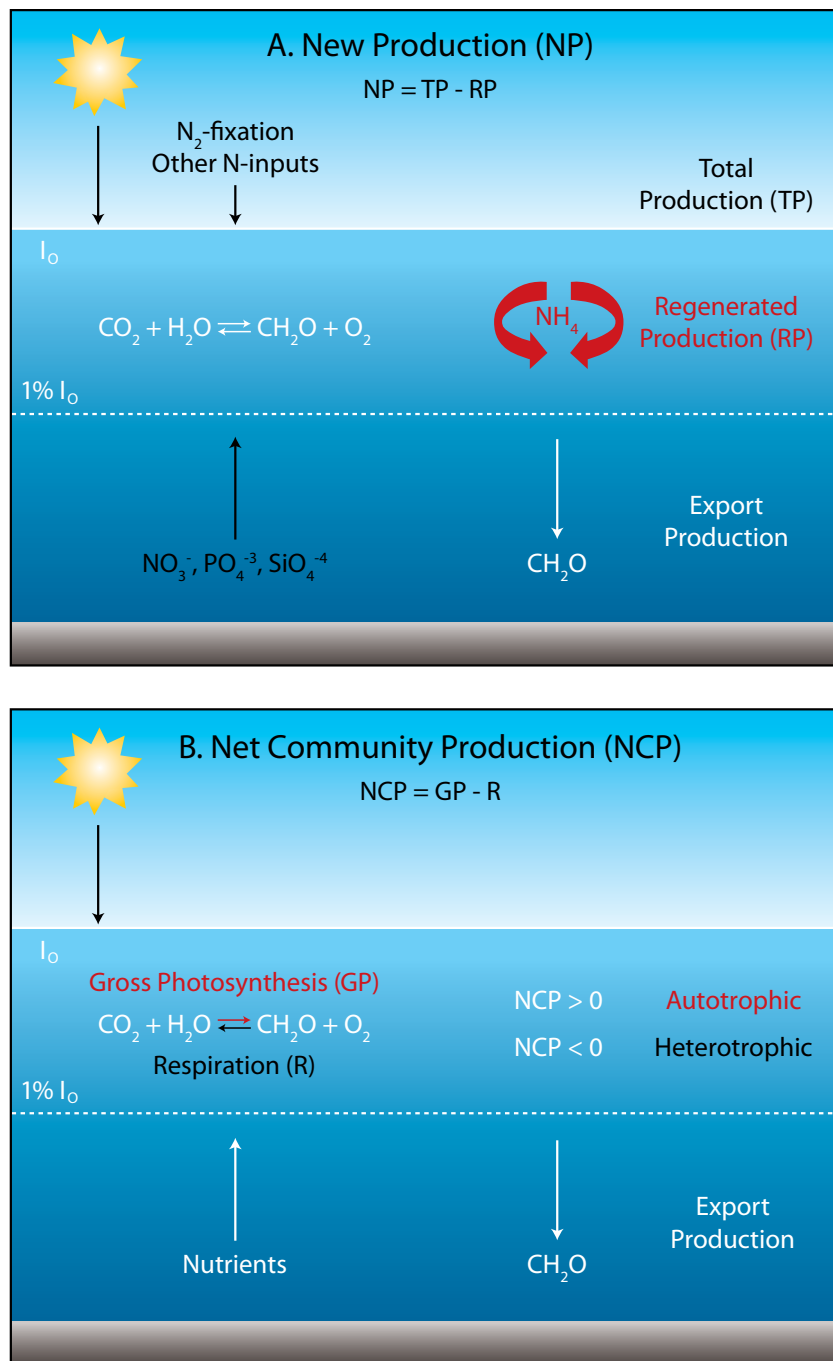1% I_0

Nutrients

CH_2O

Export Production

Figure 2. Simplified scheme of (A) new production (NP) and (B) net community production (NCP). New production refers to the difference between total production and regenerated production; it represents the fraction of primary production fueled by new nutrients (primarily nitrate) that enter the euphotic zone. Net community production refers to the balance between autotrophic (photosynthesis) and heterotrophic (respiration) processes, and defines the metabolic state of the euphotic layer. An excess of production over respiration, referred to as net autotrophic metabolic balance, implies a net synthesis of organic carbon that can be exported vertically to the deep ocean, laterally to other regions, or to higher trophic levels. A negative balance, referred to as net heterotrophic balance, represents a net demand for allochthonous organic carbon, such as dissolved organic matter produced elsewhere. NP and NCP should be equal if integrated over the same temporal and spatial scales.

THE ROLE OF MESOSCALE VARIABILITY IN NUTRIENT SUPPLY AND METABOLIC BALANCE

Mesoscale eddies have been intensively investigated in the Sargasso Sea (McGillicuddy, 1999; McNeil et al., 1999; Sweeney et al., 2003). In this region, three different eddy types have been identified: cyclones, anticyclones, and mode-water eddies (MWEs). Cyclones and MWEs displace isopycnals upward, thereby lifting new nutrients into the euphotic zone and stimulating a biological response. Substantial evidence supports the role of mesoscale eddies in enhancing local photosynthesis (Falkowski et al., 1991; McNeil et al., 1999); however, modeling studies disagree regarding their contribution to regional biogeochemical budgets (Oschlies, 2001; McGillicuddy et al., 2003).

Siegel et al. (1999) estimate that nearly 50% of the new nutrients reaching the euphotic zone at BATS are due to eddy-induced transport. These authors compute the flux of nitrate into the euphotic zone due to eddy pumping by remotely estimating isopycnal displacements using satellite-derived altimetry in conjunction with vertical nutrient distributions determined in situ. In the NASE region,

Mouriño et al. (2003), by using altimeter images, compute the surface area occupied by cyclonic eddies originating from the Azores Current to be less than 2%. Assuming the net primary production measured in one of these cyclonic eddies in April 1999 (Mouriño et al., 2002) to be representative for cyclonic eddies in this region, these authors estimate the contribution of these features to the organic carbon deficit postulated for this region to be lower than 1%. However, differences in these studies should be noted. The fixed-point time-series study (Eulerien approach) of Siegel et al. (1999) focused on determining new production and considered the relevance of the physical forcing and the nutrient background. Mouriño et al (2003) looked at a larger area (Lagrangian approach), determined NCP, and only considered the physical forcing.

These observations clearly point to regional differences in the biogeochemical role of eddy pumping in the subtropical North Atlantic. These differences also become apparent in maps of eddy kinetic energy that show a clear asymmetry across NAST, with higher energy levels in NASW compared to NASE (Smith et al., 2000). In order to investigate the role of eddy pumping as a mechanism to produce episodic nutrient inputs and/or

net oxygen production in both NASW and NASE, we compare in the next section findings obtained at BATS and in the region that includes the time-series station ESTOC (between ~ 22–35°N and 15–34°W).

Cianca et al. (2007) used 10 years of hydrography and satellite altimeter data from BATS and ESTOC to budget the new nutrient input into the euphotic zone at both sites. The sea-level anomaly (SLA) computed at both stations indicates a much lower mesoscale variability at ESTOC (Figure 3A). Also, winter mixing was shallower at ESTOC compared to BATS (data not shown), consistent with greater wind forcing in the western region (Ueyama and Monger, 2005). Another important distinction between the stations became apparent when comparing the depth of the nutricline, which is significantly shallower at the NASE station compared to the NASW (Figure 3B)(Cianca et al., 2007). The importance of higher physical forcing, deeper mixed layer depths, and higher mesoscale variability at BATS compared to ESTOC is thus partly compensated for by this shallower nutricline. As a result of the combination of the physical forcing and the nutrient background, NASE receives ~75% of the nutrients available for new production at NASW, although this difference is not statistically significant due to the large interannual variability. However, in the overall budget of new nutrient input at both stations, eddy-induced pumping was significantly greater at BATS compared to ESTOC and constitutes the main new nutrient source in the annual new nutrient budget. In contrast, Cianca et al. (2007) found that wintertime convection is the main nutrient supply mechanism

Subtropical gyres have been considered relatively homogeneous, with observations at one site extrapolated to the larger region.

in the NASE region. This study points to the relevance of considering the nutrient background when computing the nutrient supply to the upper layer through different physical mechanisms. This conclusion is further supported by the importance of the wedge of nutrient-poor subtropical mode water found to dominate the western but not the eastern basin of the subtropical Atlantic (Palter et al., 2005).

The development of a basin-wide database of net community production has been limited by methodological problems associated with measuring respiration in low-productivity regions.

This situation has been particularly severe in the northwest subtropical Atlantic where, until very recently, only one direct estimate of NCP had been reported, with respiration exceeding photosynthesis in summertime surface waters (Williams and Jenkinson, 1982). Several geochemical estimates of net
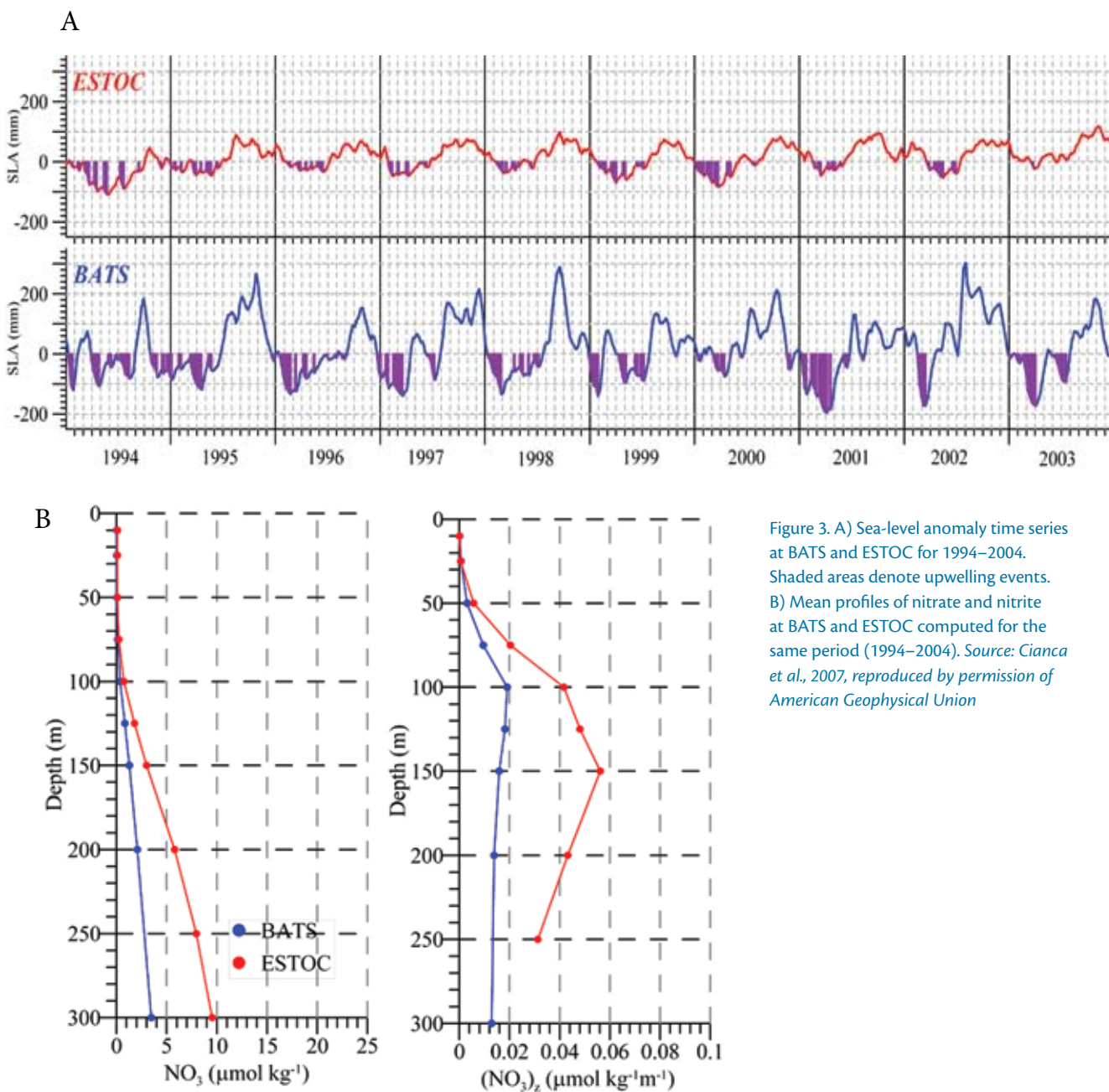

Figure 3. A) Sea-level anomaly time series at BATS and ESTOC for 1994–2004. Shaded areas denote upwelling events. B) Mean profiles of nitrate and nitrite at BATS and ESTOC computed for the same period (1994–2004). *Source: Cianca et al., 2007, reproduced by permission of American Geophysical Union*

production in this region confirm that, despite seasonal variability, photosynthesis exceeds respiration (Jenkins and Goldman, 1985; Gruber et al., 1998). Indirect estimates of the balance between photosynthesis and respiration at BATS can be inferred from the difference between ^{14}C incorporation by phytoplankton and bacterial carbon demand (NCPe; Mouriño-Carballido and McGillicuddy, 2006). This estimate is based on the assumption that bacterial remineralization represents the main component of total respiration. Estimates of NCPe carried out between 1993 and 2002 reveal that on an annual basis, net community production is always positive except during the summer months (Figure 4). In the summertime, when nutrients are not available in the photic layer and eddy pumping contributes more to fertilizing the upper layer, net community production rates are highly variable, ranging from positive to negative values.

HOW MUCH OF THIS VARIABILITY IS EXPLAINED BY MESOSCALE EDDIES?

The answer to that question is provided by the results from experiments based on in vitro changes in oxygen carried out in the summer of 2004 during the first year of fieldwork for the EDDIES (Eddies Dynamics, Mixing Export, and Species composition) project (Mouriño-Carballido and McGillicuddy, 2006). NCP rates derived from these experiments range from negative to positive values, and the age and type of the sampled eddy are important factors responsible for this variability (Figure 4). Positive rates are found in younger cyclones and in areas of eddy-eddy interactions, whereas negative NCP rates occur in anticyclones and older cyclone features that are decaying. When comparing the results from these experiments with the estimates of net community production carried out at BATS, the variability in NCPe values in general

spanned the variability of available direct observations of net community production from the EDDIES cruises. The reported variability in NCP associated with the mesoscale features investigated in summer 2004 was the result of variability in gross photosynthesis (GP) but also respiration (R) (Figure 5). Higher GP was measured in the center of the relatively young cyclonic eddy C2 (see Mouriño-Carballido and McGillicuddy, 2006, for a detailed time history of the eddy features), at the edge of the decaying cyclonic eddy C1 during the first cruise, and at BATS during the first and second cruises. Sea-level anomaly data from altimeter images revealed that the BATS site could have been under the influence of submesoscale processes associated with the interaction of anticyclonic eddies A1 and C1 during both cruises. Lower GP was found in the C1 center during the second cruise. Higher R was measured in anticyclone A1, whereas lower R was determined in the
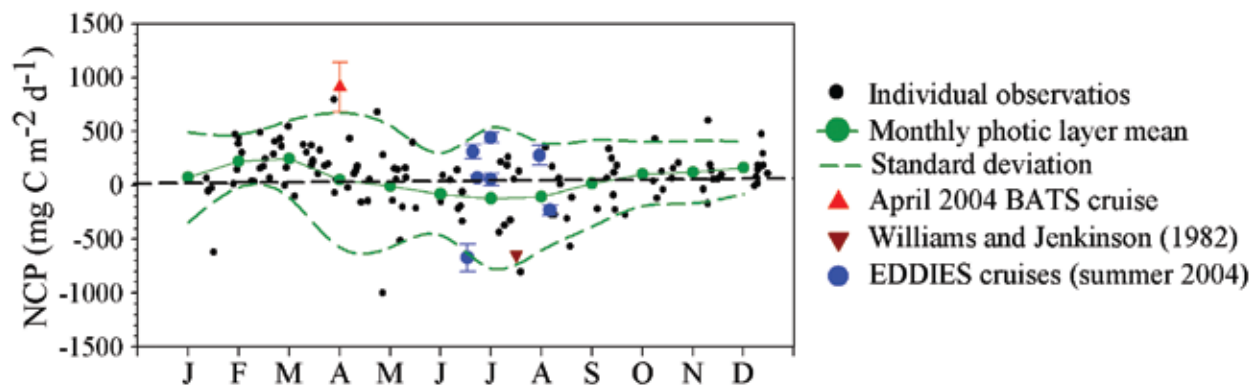

Figure 4. Monthly means of net community production (NCPe) estimated for the 1993–2002 period at the BATS site. Black dots represent individual observational points. Green circles are monthly means integrated to the 1% light depth (100 m). Green dashed line represents standard deviations about the monthly means. Black dashed line is NCP =0. NCP rates estimated from in vitro changes in dissolved oxygen after 24-h incubations in the BATS region are also indicated. *From Mouriño and McGillicuddy, 2006, with permission*
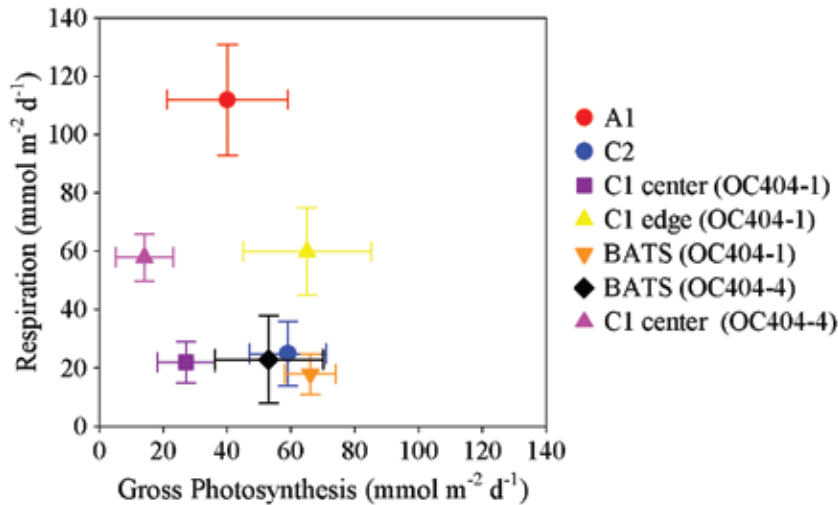
Figure 5. Depth-integrated (0–100 m) gross photosynthesis and respiration rates determined from in vitro changes in dissolved oxygen experiments carried out during the summer 2004 EDDIES cruises (OC404-1 and OC404-4). A1 is an anticyclonic eddy; C1 and C2 are cyclonic eddies. *Data from Mouriño and McGillicuddy, 2006*

centers of cyclones C2 and C1 during the first cruise and at BATS during the first and second cruises. The observation that respiration is as variable as photosynthesis and equally influenced by mesoscale dynamics is confirmed by retrospective analyses of nine years of data from the BATS program (author Mouriño-Carballido has a paper in progress on this study). This study shows increases in NCPe in the center of MWEs and frontal regions between eddies, which are partially driven by differences in bacterial respiration. These results contradict the traditional thinking that assumes the relative constancy of respiration processes compared to variable photosynthesis (Karl et al., 2003). Differences in the biological response associated with MWEs and cyclones have been attributed to interactions with

the wind field. Recent modeling studies suggest that diatom blooms in MWEs are sustained by interactions with the surface wind field, whereas wind-eddy interactions dampen upwelling in cyclones (McGillicuddy et al., 2007).

These studies confirm the greater importance of mesoscale activity as a nutrient supply mechanism in NASW compared to NASE. They also show that NASW is characterized by highly variable NCP values, controlled by the type and age of mesoscale features. No specific study on the role of mesoscale eddies in the balance between photosynthesis and respiration has been conducted at ESTOC; however, the results presented here point to the minor importance of mesoscale eddies for the metabolic balance of NASE compared to wintertime convection.

RECONCILING NEW PRODUCTION AND NET COMMUNITY PRODUCTION

An increase in thermal stratification in the open ocean and, consequently, the spread of subtropical regions, analogous to the expansion of terrestrial deserts, is predicted to occur as a consequence of global warming (Sarmiento et al., 1998; McClain et al., 2004b; Polovina et al., 2008). A prerequisite for understanding the potential effects of those changes is an adequate knowledge of the mechanisms that control the supply of nutrients into the euphotic zone. Recent research indicates that traditional one-dimensional schemes are not adequate, and that more comprehensive three-dimensional models are needed to understand how inorganic nutrients are remineralized within the main thermocline and returned to the ocean surface (Jenkins and Doney, 2003).

Quantification of alternative nutrient sources other than physical supply, such as the fixation of molecular N_2 by cyanobacteria (Capone et al., 1997), is important to constrain global and regional nutrient budgets. The relevance of this process, initially considered a relatively minor supply of new nitrogen in NAST, is expected to increase in global warming scenarios (Levitan et al., 2007). Despite a notable increase in the research effort to estimate nitrogen fixation in the subtropical North Atlantic over the last decade (Gruber and Sarmiento, 1997; Capone et al., 2005; Deutsch et al., 2007; Hansell et al., 2007), measurements based on geochemistry and in situ incubations differ by more than an order of magnitude. Relatively elevated concentrations of *Trichodesmium* spp. have been

reported across the basin at low latitudes (Tyrrell et al., 2003), and high rates of N$_2$ fixation have been measured in the southwest quadrant of the subtropical gyre (Capone et al., 2005). Geochemical proxies point to N$_2$ fixation being of lesser importance in the eastern compared to the western basin (Neuer et al., 2002). To date, the relative contribution of this process to the nutrient budgets at both stations remains unresolved.

Today, respiration is severely underconstrained compared to rates of primary production in models of air-sea O$_2$ fluxes (Balkanski et al., 1999). We need to better quantify respiration and characterize its variability. Understanding the connections between new production and net community production requires a constraint on the temporal and spatial scales controlling nutrient supply and the balance between synthesis and consumption of organic matter. Finally, we need to understand the spatial heterogeneities that exist inside these ecosystems so that we can incorporate them into future models. We should also acknowledge these heterogeneities when extrapolating data from a particular site to the larger province. Comparative studies in both NASW and NASE aimed at reconciling NCP with NP are needed in order to put together all the pieces of this important and currently unsolved puzzle.

REFERENCES

Balkanski, Y., P. Monfray, M. Battle, and M. Heimann. 1999. Ocean primary production derived from satellite data: An evaluation with atmospheric oxygen measurements. *Global Biogeochemical Cycles* 13:257–271.

Capone, D.G., J.A. Burns, J.P. Montoya, A. Subramaniam, C. Mahaffey, T. Gunderson, A.F. Michaels, and E.J. Carpenter. 2005. Nitrogen fixation by *Trichodesmium* spp.: An important source of new nitrogen to the tropical and subtropical North Atlantic Ocean. *Global Biogeochemical Cycles* 19, GB2024, doi:10.1029/2004GB002331.

Capone, D.G., J.P. Zehr, H.W. Paerl, B. Bergman, and E.J. Carpenter. 1997. *Trichodesmium*, a globally significant marine cyanobacterium. *Science* 276:1,221–1,229.

Cianca, A., P. Helmke, B. Mouriño, M. Rueda, O. Llinas, and S. Neuer. 2007. Decadal analysis of hydrography and in situ nutrient budgets in the western and eastern North Atlantic subtropical gyre. *Journal of Geophysical Research* 112, C07025, doi:10.1029/2006JC003788.

Deutsch, C., J.L. Sarmiento, D.M. Sigman, N. Gruber, and J.P. Dunne. 2007. Spatial coupling of nitrogen inputs and losses in the ocean. *Nature* 445:163–167.

Doney, S.C. 1997. The ocean's productive deserts. *Nature* 389:905–906.

Duarte, C.M., S. Agustí, J. Arístegui, N. Gonzalez, and R. Anadón. 2001. Evidence for a heterotrophic subtropical northeast Atlantic. *Limnology and Oceanography* 46:425–428.

Emerson, S., P. Quay, D. Karl, C. Winn, L. Tupas, and M. Landry. 1997. Experimental determination of the organic carbon flux from open-ocean surface waters. *Nature* 389:951–954.

Falkowski, P.G., D. Ziemann, Z. Kolber, and P.K. Bienfang. 1991. Role of eddy pumping in enhancing primary production in the ocean. *Nature* 353:55–58.

Garçon, V.C., A. Oschlies, S.C. Doney, D. McGillicuddy, and J. Waniek. 2001. The role of mesoscale variability on plankton dynamics in the North Atlantic. *Deep-Sea Research Part II* 48:2,199–2,226.

González-Dávila, M., J.M. Santana-Casiano, M. Rueda, O. Llinás, and E.F. González-Dávila. 2003. Seasonal and interannual variability of sea-surface carbon dioxide species at the European Station for Time Series in the Ocean at the Canary Islands (ESTOC) between 1996 and 2000. *Global Biogeochemical Cycles* 17(3), 1076, doi:10.1029/2002GB001993.

Gruber, N., C.D. Keeling, and T.F. Stocker. 1998. Carbon-13 constraints on the seasonal inorganic carbon budget at the BATS site in the northwestern Sargasso Sea. *Deep-Sea Research Part I* 45:673–717.

Gruber, N., and J.L. Sarmiento. 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochemical Cycles* 11:235–266.

Hansell, D.A., H.W. Ducklow, A.M. Macdonald, and M.O. Baringer. 2004. Metabolic poise in the North Atlantic Ocean diagnosed from organic matter transports. *Limnology and Oceanography* 49:1,084–1,094.

Hansell, D.A., D.B. Olson, F. Dentener, and L.M. Zamora. 2007. Assessment of excess nitrate development in the subtropical North Atlantic. *Marine Chemistry* 106:562–579.

Jenkins, W.J., and S.C. Doney. 2003. The subtropical nutrient spiral. *Global Biogeochemical Cycles* 17, 1110, doi:10.1029/2003GB002085.

Jenkins, W.J., and J.C. Goldman. 1985. Seasonal oxygen cycling and primary production in the Sargasso Sea. *Journal of Marine Research* 43:465–491.

Jin, X., R. Najjar, F. Louanchi, and S.C. Doney. 2007. A modeling study of the seasonal oxygen budget of the global ocean. *Journal of Geophysical Research*, 112, doi:10.1029/2006JC003731.

Karl, D.M., E.A. Laws, P. Morris, P.J.leB. Williams, and S. Emerson. 2003. Global carbon cycle (communication arising): Metabolic balance of the open sea. *Nature* 426:32.

Ledwell, J.R., A.J. Watson, and C.S. Law. 1993. Evidence for slow mixing across the pycnocline from an open-ocean tracer-release experiment. *Nature* 364:701–703.

Levitan, O., G. Rosenberg, I. Setlik, E. Setlikova, J. Grigel, J. Klepetar, O. Prasil, and I. Berman-Frank. 2007. Elevated CO$_2$ enhances nitrogen fixation and growth in the marine cyanobacterium *Trichodesmium*. *Global Biogeochemical Cycles* 13:531–538.

Longhurst, A.R. 1998. *Ecological Geography of the Sea*. Academic Press, London, 575 pp.

Marañón, E., V. Perez, E. Fernandez, R. Anadon, A. Bode, N. Gonzalez, I. Huskin, A. Isla, X.A.G. Moran, B. Mouriño, and others. 2007. Planktonic carbon budget in the eastern subtropical North Atlantic. *Aquatic Microbial Ecology* 48:261–275.

McClain, C.R., G.C. Feldman, and S.B. Hooker. 2004a. An overview of the SeaWiFS project and strategies for producing a climate research quality global ocean bio-optical time series. *Deep-Sea Research Part II* 51:4–52.

McClain, C.R., S.R. Signorini, and J.R. Christian. 2004b. Subtropical gyre variability observed by ocean-color satellites. *Deep-Sea Research Part II* 51:281–301.

McGillicuddy, D. 1999. Theory and modeling of ocean circulation, data assimilation and interdisciplinary applications: A tribute to Professor Allan R. Robinson - Introduction. *Dynamics of Atmospheres and Oceans* 29:91.

McGillicuddy, D.J., L.A. Anderson, S.C. Doney, and M.E. Maltrud. 2003. Eddy-driven sources and sinks of nutrients in the upper ocean: Results

from a 0.1° resolution model of the North Atlantic. *Global Biogeochemical Cycles* 17, 1035, doi:10.1029/2002GB001987.

McGillicuddy, D.J., Jr., L.A. Anderson, N.R. Bates, T. Bibby, K.O. Buesseler, C.A. Carlson, C.S. Davis, C. Ewart, P.G. Falkowski, S.A. Goldthwait, and others. 2007. Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms. *Science* 316:1,021–1,026.

McGillicuddy, D.J., and A.R. Robinson. 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea. *Deep-Sea Research Part I* 44:1427–1450.

McNeil, J.D., H.W. Jannasch, T. Dickey, D. McGillicuddy, M. Brzezinski, and C.M. Sakamoto. 1999. New chemical, bio-optical and physical observations of upper ocean response to the passage of a mesoscale eddy off Bermuda. *Journal of Geophysical Research* 104:15,537–15,548.

Menzel, D.W., and J.H. Ryther. 1960. The annual cycle of primary production in the Sargasso Sea off Bermuda. *Deep-Sea Research* 6:351–367.

Michaels, A.F., N.R. Bates, K.O. Buesseler, C.A. Carlson, and A.H. Knap. 1994. Carbon cycle imbalances in the Sargasso Sea. *Nature* 372:537–540.

Michaels, A.F., and A.H. Knap. 1996. Overview of the US JGOFS Bermuda Atlantic Time-series Study and the Hydrostation S program. *Deep-Sea Research Part I* 43:157–198.

Mouriño-Carballido, B., and D. McGillicuddy. 2006. Mesoscale variability in the metabolic balance of the Sargasso Sea. *Limnology and Oceanography* 51:2,675–2,689.

Mouriño, B., E. Fernandez, J. Escanez, D. de Armas, S. Giraud, B. Sinha, and R. Pingree. 2002. A Subtropical Oceanic Ring of Magnitude (STORM) in the Eastern North Atlantic: Physical, chemical and biological properties. *Deep-Sea Research Part I* 49:4,003–4,021.

Mouriño, B., E. Fernandez, H. Etienne, F. Hernandez, and S. Giraud. 2003. Significance of cyclonic SubTropical Oceanic Rings of Magnitude (STORM) eddies for the carbon budget of the euphotic layer in the subtropical northeast Atlantic. *Journal of Geophysical Research* 108, 3383, doi:10.1029/2003JC001884.

Najjar, R.G., and R.F. Keeling. 2000. Mean annual cycle of the air-sea oxygen flux: A global view. *Global Biogeochemical Cycles* 14:573–584.

Neuer, S., A. Cianca, P. Helmke, T. Freudenthal, R. Davenport, H. Megggers, M. Knoll, J.M. Santana-Casiano, M. González-Dávila, M. Rueda, and O. Llinás. 2007. Biogeochemistry and hydrography in the eastern subtropical North Atlantic gyre. Results from the European time-series station ESTOC. *Progress in Oceanography* 72:1–29.

Neuer, S., R. Davenport, T. Freudenthal, G. Wefer, O. Llinás, M. Rueda, D.K. Steinberg, and D. Karl. 2002. Differences in the biological carbon pump at three subtropical ocean sites. *Geophysical Research Letters* 29, 1885, doi:10.1029/2002GL015393.

Oschlies, A. 2001. Model-derived estimates of new production: New results point towards lower values. *Deep-Sea Research Part I* 48:2,173–2,197.

Palter, J.B., M.S. Lozier, and R.T. Barber. 2005. The effect of advection on the nutrient reservoir in the North Atlantic subtropical gyre. *Nature* 437:687–692.

Platter, G.K., N. Gruber, H. Frenzel, and J.C. McWilliams. 2005. Decoupling marine export production from new production. *Geophysical Research Letters* 32, doi:10.1029/2005GL022660.

Polovina, J.J., E.A. Howell, and M. Abecassis. 2008. Ocean's least productive waters are expanding. *Geophysical Research Letters* 35, doi:10.1029/2007GL031745.

Quiñones, R.A., and T. Platt. 1991. The relationship between the F-ratio and the P-R ratio in the pelagic ecosystem. *Limnology and Oceanography* 36:211–213.

Riser, S.C., and K.S. Johnson. 2008. Net production of oxygen in the subtropical ocean. *Nature* 451:323–325.

Robinson, C., P. Serret, G. Tilstone, E. Teira, M.V. Zubkov, A.P. Rees, and E.M.S. Woodward. 2002. Plankton respiration in the Eastern Atlantic Ocean. *Deep-Sea Research Part I* 49:787–813.

Santana-Casiano, J.M., M. González-Dávila, M. Rueda, O. Llinás, and E.F. González-Dávila. 2007. The interannual variability of oceanic CO_2 parameters in the northeast Atlantic subtropical gyre at the ESTOC site. *Global Biogeochemical Cycles*, doi:10.10292006GB002788.

Sarmiento, J., T.M.C. Hughes, R.J. Stouffer, and S. Manabe. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* 393:245–249.

Sathyendranath, S., A. Longhurst, and C. Caverhill. 1995. Regionally and seasonally differentiated primary production in the North Atlantic. *Deep-Sea Research Part I* 42:1,773–1,802.

Siegel, D.A., D.J. McGillicuddy, and E.A. Fields. 1999. Mesoscale eddies, satellite altimetry, and new production in the Sargasso Sea. *Journal of Geophysical Research* 104:13,359–13,379.

Smith, R.D., M.E. Maltrud, F.O. Bryan, and M.W. Hecht. 2000. Numerical simulation of the North Atlantic Ocean at 1/10°. *Journal of Physical Oceanography* 30:1,532–1,561.

Steinberg, D.K., C.A. Carlson, N.R. Bates, R.J. Johnson, A.F. Michaels, and A.H. Knap. 2001. Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): A decade-scale look at ocean biology and biogeochemistry. *Deep-Sea Research Part II* 48:1,405–1,447.

Sweeney, E.N., D.J. McGillicuddy, and K.O. Buesseler. 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 Part II* 50:3,017–3,039.

Teira, E., B. Mourino, E. Marañón, V. Perez , M.J. Pazo, P. Serret , D. de Armas, J. Escanez, E.M.S. Woodward, and E. Fernandez. 2005. Variability of

chlorophyll and primary production in the Eastern North Atlantic Subtropical Gyre: Potential factors affecting phytoplankton activity. *Deep-Sea Research Part I* 52: 569–588.

Varela, M.M., A. Bode, E. Fernandez, N. Gonzalez, V. Kitidis, M. Varela, E.M.S. Woodward. 2005. Nitrogen uptake and dissolved organic nitrogen release in planktonic communities characterized by phytoplankton size-structure in the Central Atlantic Ocean. *Deep-Sea Research Part I* 52:1,637–1,661.

Tyrrell, T., E. Marañón, A.J. Poulton, A.R. Bowie, D.S. Harbour, E.M.S. Woodward. 2003. Large-scale latitudinal distribution of *Trichodesmium* spp. in the Atlantic Ocean. *Journal of Plankton Research* 25:405–416.

Ueyama, R., and B.S. Monger. 2005. Wind-induced modulation of seasonal phytoplankton blooms in the North Atlantic derived from satellite observations. *Limnology and Oceanography* 50:1,820–1,829.

Wang, X.J., R. Murtugudde, A.J. Busalacchi, and R. Le Borgne. 2005. De-coupling of net community production and new production in the euphotic zone of the equatorial Pacific: A model study. *Geophysical Research Letters*, 32, L21601, doi:10.1029/2005GL024100.

Williams, P.J.leB., and P.A. Del Giorgio. 2005. Respiration in aquatic ecosystems: History and background. Pp. 1–17 in *Respiration in Aquatic Ecosystems*, P.A. Del Giorgio, and P.J. leB. Williams, eds, Oxford University Press, New York.

Williams, P.J.leB., and N.W. Jenkinson. 1982. A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. *Limnology and Oceanography* 27:576–584.

Williams, P.J.leB., P.J. Morris, and D.M. Karl. 2004. Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. *Deep-Sea Research Part I* 51:1,563–1,578.