High sensitivity of ultra-oligotrophic marine ecosystems to atmospheric nitrogen deposition

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[1] Using a model of plankton and organic-matter cycling we demonstrate that variable stoichiometric ratios can lead to a more than 5-fold higher sensitivity of simulated carbon export to atmospheric N deposition in the ultra-oligotrophic eastern part of the North Atlantic subtropical gyre compared to the westerly oligotrophic region near Bermuda, often used as a reference site for subtropical regions. Stronger nutrient limitation in the ultra-oligotrophic east causes higher phytoplankton C:N ratios and lower carbon assimilation efficiency of zooplankton in the model, which results in a higher export efficiency of carbon to the deep ocean compared to the less nutrient-limited western site. Our results indicate that previous estimates of oceanic carbon uptake associated with atmospheric nitrogen deposition may not be fully robust and that spatial variability in nutrient stress and ecological stoichiometry could significantly affect the biogeochemical impact of increasing atmospheric deposition of anthropogenic nitrogen. **Citation:** Mouriño-Carballido, B., M. Pahlow, and A. Oschlies (2012), High sensitivity of ultra-oligotrophic marine ecosystems to atmospheric nitrogen deposition, *Geophys. Res. Lett.*, *39*, L05601, doi:10.1029/2011GL050606.

1. Introduction

[2] Nitrogen plays a critical role in controlling primary production in both marine and terrestrial ecosystems. The supply of nitrogen to the upper layer of the open ocean occurs through upwelling and mixing of subsurface waters, atmospheric deposition and nitrogen fixation. New production (the fraction of primary production fueled by nutrients supplied from outside the euphotic zone) constrains the amount of organic carbon that can be exported to the deep ocean [*Eppley and Peterson*, 1979]. However, on long timescales and for fixed stoichiometry of organic matter, any downward flux of organic matter must be balanced by an equivalent upward flux of nutrients and carbon, unless new nutrients enter the ocean [*Broecker*, 1991]. For unchanged ocean physics and constant organic matter stoichiometry, only external nitrogen supply mechanisms, such as nitrogen fixation and atmospheric deposition, can impact the net balance of the biotically mediated flux of CO_2 between the ocean and the atmosphere [*Michaels*, 2001]. In this respect, the global export production increase that will result from the expected 21st century rise in anthropogenic atmospheric N deposition has been estimated as 5% [*Krishnamurthy et al.*, 2010, 2007] to 10% [*Duce et al.*, 2008], depending on the assumed extent of the nitrogen-limited area of the world ocean. This area comprises for the most part the subtropical oceans, characterized by strong stratification, weak mixing and low surface nutrients, where nutrient-addition bioassay experiments indicate that nitrogen is generally the limiting nutrient [*Duce et al.*, 2008].

[3] Subtropical regions have been traditionally considered relatively homogeneous with observations at single sites extrapolated to the larger region [*Emerson et al.*, 1997; *Michaels*, 1994]. However, the comparison of data from different subtropical locations reveals significant spatial heterogeneity in the biogeochemistry of this biome [*Cianca et al.*, 2007; *Mouriño-Carballido and Neuer*, 2008; *Neuer et al.*, 2002]. Current estimates of atmospheric inorganic nitrogen deposition also show large spatial heterogeneity and are more than three times higher in the oligotrophic western (NASW) than the ultra-oligotrophic eastern (NASE) [*Duce et al.*, 2008] parts of the North Atlantic Subtropical Gyre Province (NAST) [*Longhurst*, 1998]. We here set out to account for this perceived heterogeneity by running a one-dimensional ecosystem model at two different sites located at NASW (31°N–64°W) and NASE (25°N–30°W) (see Figure S1 in the auxiliary material).[1] The main goal of this study is to investigate potential implications of this heterogeneity on the sensitivity in simulated carbon export to atmospheric N deposition.

2. Methods Summary

[4] The plankton model adapted from *Pahlow et al.* [2008] was run off-line, forced with hourly profiles of temperatures and eddy-diffusion coefficients, supplied from a 3-D circulation model [*Oschlies and Garcon*, 1999], for 31°N 64°W (NASW) and 25°N 30°W (NASE). Twelve-year (01/01/1989 to 31/12/1999 plus one initial spin-up year with the same forcing as 1989) simulations were performed in order to study the effect of atmospheric inorganic nitrogen deposition on the pelagic ecosystems. A control experiment was performed without any external nitrogen supply, and a deposition experiment (N-dep) included atmospheric nitrogen deposition as a dissolved inorganic N flux into the surface model grid box of 11 m thickness. Both experiments were initialized with January (or the closest available) climatologies calculated from observed profiles and assumed relations among unobserved quantities (see *Pahlow et al.* [2008] for details). Model simulations were analyzed for final six years of the twelve-year runs, i.e., for the time period 1994–1999.

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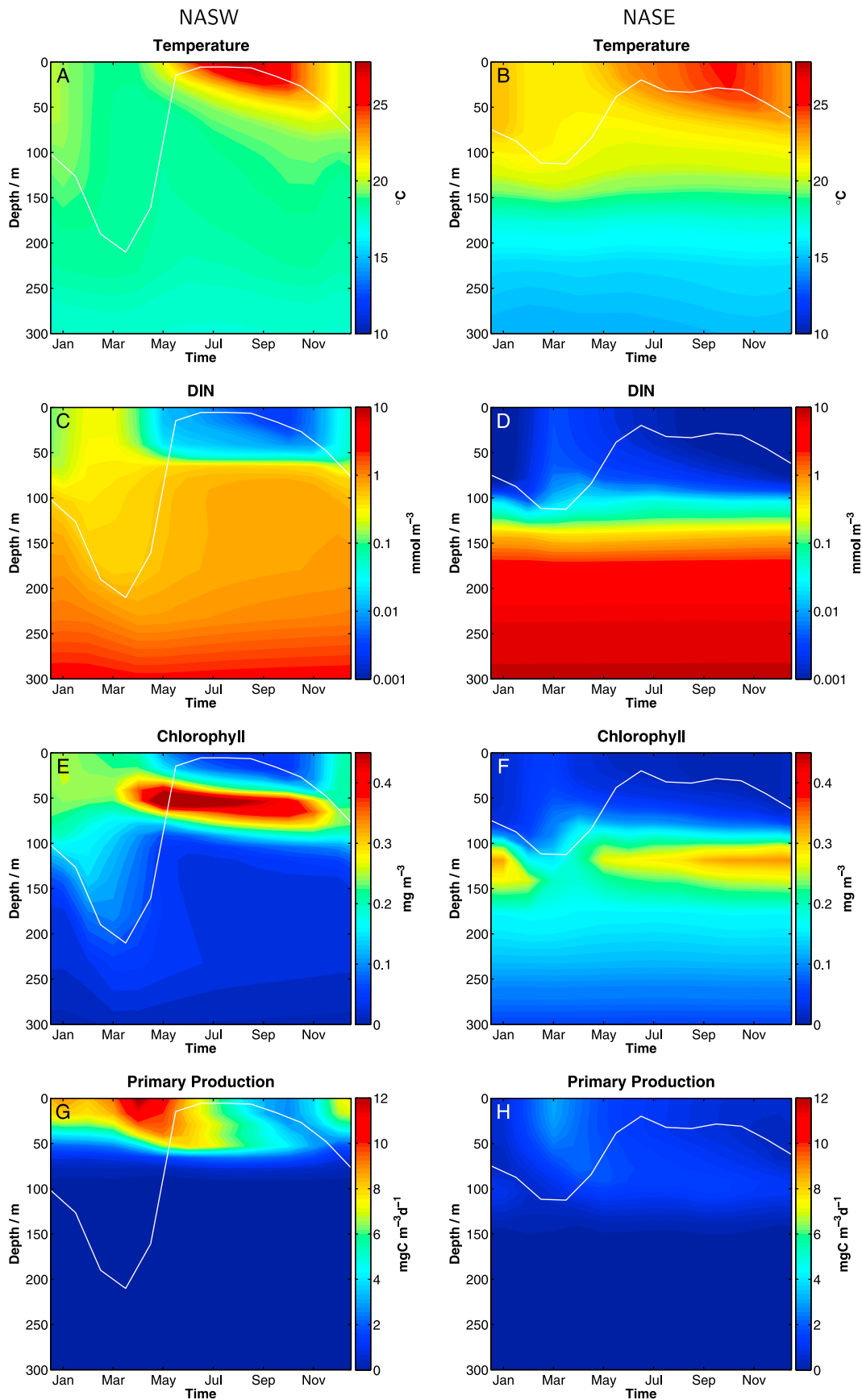[2]GEOMAR, Kiel, Germany.

Figure 1

[5] Data from the BATS (Bermuda Atlantic Time-series Study) program [*Knap et al.*, 1993] (data available at http://bats.bios.edu/) for spring and fall during the period 1993–2002, and data collected in the region from 22° to 35°N and from 15° to 34°W from the AMT program [*Robinson et al.*, 2006] for the period 1996–1999 (AMT1-AMT6 cruises, data available at http://www.bodc.ac.uk/projects/uk/amt/) were used to compute average C:N ratios of the particulate organic matter in the upper 100 m for NASW and NASE, respectively. A full methods description is included in the auxiliary material.

3. Results and Discussion

[6] Annual cycles of temperature, nitrate, chlorophyll and primary production simulated by a control model run, which assumes zero atmospheric deposition, at our two reference sites NASW and NASE are displayed in Figure 1. Both stations are subject to a relatively weak seasonal cycle where phytoplankton biomass and production increase in late winter - early spring in response to nutrient supply by a deepening winter mixed layer. Thermal stratification, depletion of surface nutrients, deepening of the deep chlorophyll maximum and declining phytoplankton biomass and production follow the late winter bloom.

[7] Differences between both sites can mainly be explained by different amplitudes of the seasonal cycle in mixed layer depth. NASW is subject to stronger seasonality than NASE, with deeper winter mixed layers extending below the nutricline and more intense thermal stratification in summer. Due to the presence of the relatively nutrient-poor North Atlantic subtropical mode water the permanent nutricline is located deeper at NASW compared to NASE. Owing to greater seasonal nutrient availability, the NASW site is characterized by a more pronounced late winter - early spring bloom and a shallower deep chlorophyll maximum thereafter.

[8] Differences in chlorophyll, primary production levels and particulate C:N ratios simulated at the two sites are generally in good agreement with observations: Modeled annual-mean depth-integrated chlorophyll for NASW and NASE (27 ± 3 and 20 ± 4 mg m^{-2}, respectively, where the standard deviation is computed from the annual means of the last 6 years of the simulation, Table S1 in the auxiliary material) agree well with observations from the BATS program for 1993–2002 (24 ± 2 mg m^{-2}) [*Mouriño-Carballido and Neuer*, 2008] and NASE from March 1992 to November 2001 (17 ± 1 mg m^{-2}) [*Marañón et al.*, 2007], respectively. Predicted annual mean net primary production (NPP) at NASW (394 ± 111 mgC m^{-2} d^{-1}) also agrees with observations (382 ± 37 mgC m^{-2} d^{-1}) [*Mouriño-Carballido and Neuer*, 2008], whereas modeled NPP is lower, although inside the range of measured variability, than observations at NASE (176 ± 102 mgC m^{-2} d^{-1} vs. 244 ± 42 mgC m^{-2} d^{-1}, calculated from monthly means reported by *Marañón et al.* [2007]). Data used to compare with the modeled NASE results were collected over a large region (22–35°N,

15–34°W) and include a total of 47 stations visited from March 1992 to November 2001 (11 in winter, 23 in spring, 4 in summer and 9 in autumn). Although these observations cover all seasons of the year, they are not sufficient to resolve the seasonal trends in all variables in a region that is under the influence of episodic pulses of productivity associated with different types of mesoscale dynamics [*Mouriño et al.*, 2005]. For BATS, observations include biogeochemical data collected at 31.2°N 64.5°W for the 1993–2002 period, sampled monthly except during the bloom season (February to April) when sampling is twice per month. This could explain, at least partially, the larger discrepancy between modeled and observed NPP at NASE compared to NASW. As a result of more intense nutrient limitation, the modeled molar C:N ratio of particulate organic matter (POM) is higher at NASE (8.5) compared to NASW (7.5) (Figure 2). This is in excellent agreement with observed C:N ratios of suspended POM collected in the upper 100 m in the NASE region (9.0 ± 2.3) and at BATS (7.6 ± 2.1), respectively (see methods).

[9] Estimates of atmospheric inorganic nitrogen deposition in NASW (0.043 mmolN m^{-2} d^{-1}) are more than three times higher than in the NASE region (0.012 mmolN m^{-2} d^{-1}) [*Duce et al.*, 2008]. Because deeper winter mixing reaches layers with much higher DIN concentration at NASW (Figures 1c and 1d), nitrogen supply via vertical mixing into the upper 150 m is also much higher (about four times, Table S1) at NASW than at NASE. Hence, the NASW site also displays higher primary production and export production already in the control run without deposition. While absolute changes in simulated gross and net primary production, phytoplankton respiration and heterotrophic respiration induced by atmospheric N deposition are somewhat larger at NASW than at NASE, absolute changes in net community production and export production turn out to be considerably larger at the ultra-oligotrophic NASE than at the oligotrophic NASW (see Figure 2 and Table S1). The relative increase in modeled surface chlorophyll, zooplankton biomass, and detrital carbon in response to atmospheric nitrogen deposition is about 2 times higher at NASE compared to NASW. Changes in simulated dissolved organic carbon and nitrogen are less than 3% for both sites (data not shown). Relative increments in net primary production and heterotrophic respiration for NASE are both larger than 50%, i.e., almost twice those for NASW. As a result, the relative increment in net community production (NCP) at NASE amounts to about 50%, which is more than four times the value for NASW.

[10] Simulated PON export increases roughly in proportion to the N deposited from the atmosphere, and consequently the absolute increase is larger at NASW than at NASE (Table S1). However, the increase in simulated export of POC is much smaller at NASW, where it increases by only 2.3 mgC m^{-2} d^{-1} (10%), than at NASE, where the increase amounts to 3.2 mgC m^{-2} d^{-1} (28%). A somewhat

Figure 1. Vertical distribution of (a, b) temperature, (c, d) dissolved inorganic nitrogen (DIN), (e, f) chlorophyll and (g, h) primary production simulated by the control model run for the 1994–1999 period at the two references stations located in the (left) Western (NASW) and (right) Eastern (NASE) sides of the subtropical North Atlantic. Note the logarithm scale for DIN. Solid lines indicate mean monthly mixed-layer depths calculated from modeled temperature profiles. Gradients apparent in the monthly climatologies within the mixed layer are a result of averaging over a period of one month and across six years, and mixed-layer depth varying strongly on a time scale of days to weeks.
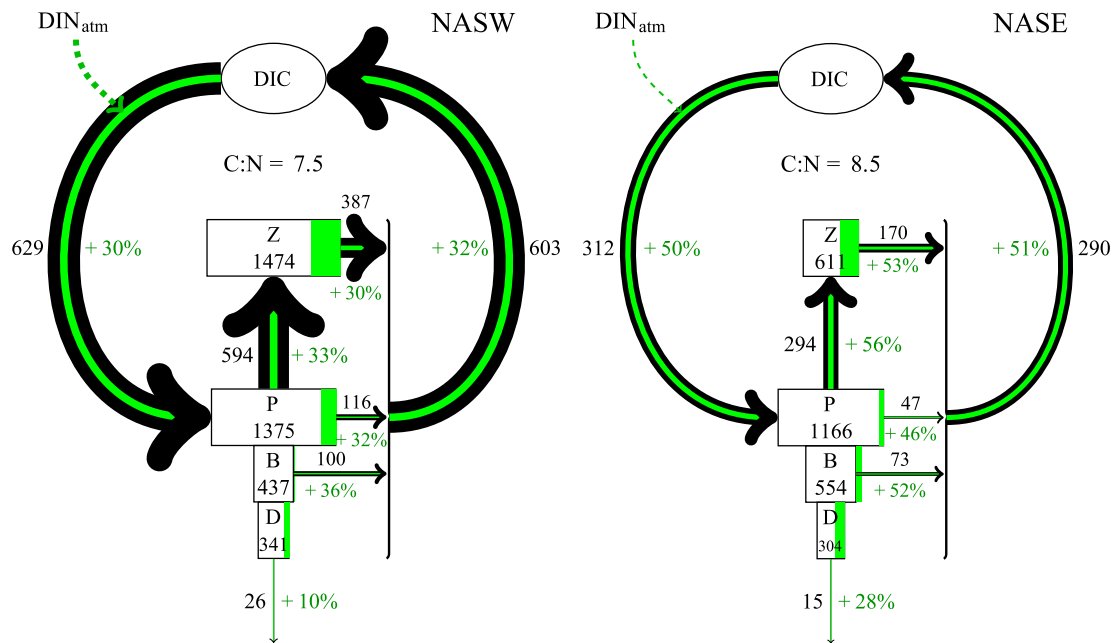
Figure 2. Schematic of main state variable and fluxes computed for the upper 150 m at the two reference stations NASW and NASE. DIC is dissolved inorganic carbon. P, Z, B and D are particulate organic carbon in phytoplankton, zooplankton, bacteria and detritus, respectively. C:N is the modeled molar carbon to nitrogen ratio of the particulate organic matter. Numbers in black refer to total standing stocks in $mgC\ m^{-2}$ and fluxes in $mgC\ m^{-2}\ d^{-1}$ for the atmospheric deposition simulations. The black area of the arrows represents the control run and the total arrow width is proportional to the carbon fluxes given by the numbers in black. Arrows and boxes size in green color are proportional to the absolute changes in simulated carbon stock and fluxes in response to atmospheric deposition of inorganic nitrogen. Numbers in green indicate the percentage of change (respect to the control run) that result from the simulated atmospheric deposition.

larger *relative* increase in POC export at NASE could have been expected because of the smaller background POC export fuelled by the very low nitrogen supply by vertical mixing. However, the larger *absolute* increase in simulated POC export at the NASE site, where atmospheric nitrogen deposition is about three times smaller than at NASW, came as an unexpected result. Previous estimates of the impact of atmospheric N deposition on the marine carbon pump have assumed constant C:N stoichiometry and therefore predicted the increase in POC export to be smaller in areas with less N deposition [*Duce et al.*, 2008; *Krishnamurthy et al.*, 2010, 2007]. The increase in POC export relative to atmospheric nitrogen deposition in our simulations varies from well below (4.5 ± 4.4 at NASW) to far above (22 ± 17 at NASE) Redfield proportions (Table S1). Examination of the model behaviour to the north (30°N, 30°W) and south (20°N, 30°W) of our NASE simulation demonstrates that our comparison between NASW and NASE is part of a general relationship between oligotrophy and sensitivity to atmospheric N deposition (Figure 3). Our results are obtained from a numerical model that, although it had been calibrated by data from different time series sites, will require further testing against in situ observations, preferentially at different sites displaying different degrees of oligotrophy.

[11] An explanation for the larger absolute enhancement of simulated carbon export at NASE despite the lower atmospheric N deposition can be found in the ecological stoichiometry simulated by the model. The stronger nutrient limitation at NASE causes particulate C:N ratios to be higher at NASE than at NASW, in close agreement with observations (see above). A consequence of the higher C:N ratios is

a lower food quality. Ingestion rates and carbon assimilation efficiencies are low for poor-quality (i.e., nitrogen poor) prey for both micro and mesozooplankton [*Flynn and Davidson*, 1993; *Jones and Flynn*, 2005]. This effect is treated in our
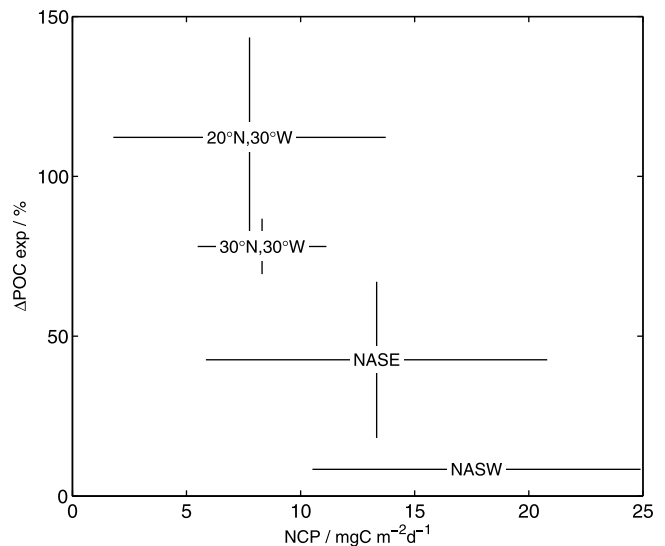

Figure 3. Increase (%) for year 2000 atmospheric N deposition with respect to the control model run in vertical flux of particulate organic carbon (POC) versus net community production (NCP) for NASW (31°N 64°W), NASE (25°N 30°W), 20°N 30°W and 30°N 30°W. Bars represent standard deviations of annual means.

model [*Pahlow et al.*, 2008] by letting carbon assimilation efficiency decrease with increasing food C:N ratios, so as to maintain constant zooplankton C:N [*Kiorboe*, 1989]. The NASE site is thus characterized by a lower zooplankton carbon assimilation efficiency (about 0.6) compared to NASW (about 0.9). Most of this difference can be ascribed to the much greater relative contribution of (nitrogen-poor) phytoplankton to total ingestion at NASE (86%) compared to NASW (50%), owing to reduced availability of zooplankton as a more nitrogen-rich food source (Table S1). Food quality in terms of C:N ratio is determined mainly by the C:N ratio of phytoplankton, which is the dominant food source at both sites. Detritus constitutes only a small fraction (<10%) of total ingestion and, despite its high C:N ratio, has only a small effect on total food quality.

[12] Grazing on non-autotrophic food items (detritus and bacteria) can yield total gross ingestion rates higher than NPP (Table S1). The unassimilated carbon is channelled into sinking detritus, which in reality might happen either in the form of fecal pellets or via dissolved organic carbon and subsequent formation of transparent exopolymer particles (TEP), eventually contributing to the particulate export. Had we neglected the dependence of carbon assimilation efficiency on prey C:N ratios, as is common in most zooplankton formulations [*Mitra*, 2006], this would have little effect on simulated primary production but would profoundly underestimate carbon export associated with N-impoverished food [*Mitra et al.*, 2007]. Zooplankton carbon assimilation efficiency could thus exert a strong control on the modeled C:N ratios of the export of organic matter (Table S1). Decoupled C- and N-based export ratios may, in turn, give rise to strong regional variations in the efficiency of the biological carbon pump and, as shown here, in its sensitivity to environmental change.

[13] Export C:N ratios computed by our model reach values of about 20 at NASE, higher than the majority of the observations and considerably larger than the export C:N ratios of about 9 simulated at NASW. The average C:N ratio determined with drifting particle traps deployed at the European Station for Time-Series in the Ocean, Canary Islands (ESTOC, 29.2°N 15.5°O) at 200 m was 9.1 [*Neuer et al.*, 2007], whereas POC/PON fluxes computed from sediment traps at BATS gave a C:N ratio of ∼6 [*Schnetzer and Steinberg*, 2002]. Higher simulated C:N ratios at NASE are consistent with indications of carbon overconsumption in the mixed layer available just to the north of NASE [*Koeve*, 2006], excess carbon export at ESTOC [*Neuer et al.*, 2007], and C:N ratios of particulate export fluxes close to Redfield ratios measured at BATS [*Schnetzer and Steinberg*, 2002]. A recent study reporting the comparison of net production and shallow remineralisation rates at BATS and ESTOC estimated from a 1D tracer budget approach for oxygen, DIC and nitrate suggests a C:N ratio for shallow remineralisation of 40 ± 162 at ESTOC and 10.2 ± 3.6 at BATS [*Fernández-Castro et al.*, 2011]. The only time-series of vertical export fluxes available at NASE derives from the sediment traps deployed at ESTOC, which is close to the high end of productivity inside the NASE region [*Mouriño-Carballido and Neuer*, 2008]. In fact, BATS and ESTOC exhibit similar phytoplankton biomass and primary production, although vertical POC export based on sediment traps indicates a much higher annually averaged export ratio at BATS (0.07–0.08) than at ESTOC (0.02)

[*Neuer et al.*, 2002]. This difference could, at least partially, be explained by slower sinking rates of the particulate organic matter at NASE, due to a higher contribution of smaller size classes of slowly sinking or suspended POC [*Alonso-González et al.*, 2009]. These processes may not be represented realistically by our current model.

4. Conclusions

[14] According to our model, current atmospheric nitrogen deposition causes a carbon export about 4 times larger than the Redfield equivalent of the added nitrogen at NASE, whereas the carbon export associated with atmospheric nitrogen deposition at NASW is lower than expected from Redfield stoichiometry (Table S1). This suggests that the carbon cycle of ultra-oligotrophic systems is more sensitive to perturbations in the external nutrient supply than oligotrophic systems such as represented by BATS. The reason for this unexpected behaviour is that homeostatic regulation of the zooplankton tends to deflect a greater fraction of carbon primary production to export in ultra-oligotrophic regions and that, at the same time, zooplankton grazing constitutes a major control on phytoplankton there [*Legendre and Lefèvre*, 1995].

[15] Among the expected effects of global change is an expansion of the oligotrophic subtropical gyres and their ultra-oligotrophic areas [*Polovina et al.*, 2008], where N_2-fixation and atmospheric deposition could have a major impact on the carbon cycle. N_2 fixation is considered the dominant external source of nitrogen into the surface ocean in preindustrial times. However, atmospheric deposition is rapidly approaching current estimates of oceanic N_2 fixation [*Duce et al.*, 2008], and is predicted to increase in the next decades as a result of fossil-fuel burning, land-use changes and intensification of agricultural activities [*Gruber and Galloway*, 2008]. According to our model results, for each N atom supplied through atmospheric deposition at NASE there will be about 5 times more C atoms exported to the deep ocean compared to NASW. The same argument will hold to other sources of allochthonous nitrogen, e.g., nitrogen fixation. Spatial and temporal variability in carbon-to-nutrient ratios should be taken into account when assessing biogeochemical impacts of potential future changes in atmospheric nitrogen supply to the ocean.

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