Low-nutrient organic matter in the Sargasso Sea thermocline: A hypothesis for its role, identity, and carbon cycle implications

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Key points:

In the Sargasso Sea subsurface, oxygen is consumed without the rate of nutrient production expected from the remineralization of marine biomass

Subsurface nitrate $^{18}O/^{16}O$ points to heterotrophic bacterial assimilation of nitrate during low-nutrient organic matter remineralization

Export and remineralization of low-nutrient organic matter may explain the high rates of net community production in the subtropical ocean

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Abstract

Despite slow nutrient supply to the subtropical surface ocean, its rates of annual inorganic carbon drawdown and net oxygen production are similar to those of nutrient-rich high latitude waters. This surprisingly rapid carbon drawdown, if due to the production and export of marine biomass, cannot be explained in terms of known nutrient supply mechanisms. Moreover, carbon budgets have failed to detect the export of this organic matter. One possible explanation is the export of nutrient-poor organic matter with a composition that avoids detection as sinking particles. We describe three signs of the decomposition of such organic matter in the shallow Sargasso Sea subsurface. First, summertime oxygen consumption at 80-400 m occurs without the rate of nitrate and phosphate production expected from the remineralization of marine biomass, satisfying the observed summertime mixed layer inorganic carbon drawdown. Second, a seasonal change in the $^{18}O/^{16}O$ of subsurface nitrate suggests summertime heterotrophic bacterial nitrate assimilation down to ~400 m, as may be required for the remineralization of nutrient-poor organic matter. Third, incubation of subsurface seawater leads to nitrate drawdown and heterotrophic bacterial growth, supporting the thermocline nitrate $^{18}O/^{16}O$ evidence for heterotrophic nitrate assimilation. These three pieces of evidence suggest the export of nutrient-poor organic matter from the surface at a rate adequate to explain net community production in the Sargasso Sea. We propose that transparent exopolymer particles or related compounds, generated by a nutrient-limited upper ocean ecosystem, comprise this nutrient-poor export, and that its properties cause its flux out of the euphotic zone to be underestimated by sediment traps. Such nutrient-poor organic matter would contribute little to fisheries, deep ocean carbon dioxide storage, or organic carbon burial, so that it may change our view of the significance of net community production in the subtropical ocean.

Introduction

The net production of organic matter by upper ocean ecosystems is a central characteristic of the global ocean. It underpins the ocean's "biological pump," whereby organic matter is exported from surface waters prior to its remineralization back to carbon dioxide (CO_2). This lowers atmospheric CO_2, and portions of the organic matter sustain upper trophic levels. Moreover, a small fraction of the organic matter export is buried, thus contributing to the maintenance of diatomic oxygen (O_2) in the atmosphere.

The biological productivity of much of the open ocean is limited by the supply of the major nutrients nitrogen (N) and phosphorus (P). In particular, the sunlit upper waters of the subtropical gyres receive the major nutrients at a lower rate than the polar, subpolar, and equatorial upwelling regions (Williams and Follows, 2003). By many metrics, such as surface ocean chlorophyll concentrations and the flux of organic matter that reaches 2000 m, the productivity of the subtropical gyres appears to be appropriately depressed (Honjo et al., 2008; Lomas et al., 2013; Yoder et al., 1993). However, a different picture is suggested by upper ocean budgets of dissolved inorganic carbon (DIC) and dissolved O_2 (Emerson, 2014, and references therein).

DIC and dissolved O_2 have been used to study both the euphotic zone (the sunlit upper ocean down to the depth of the 1% light level, typically ~100 m in the subtropical North Atlantic near Bermuda) and the surface wind-mixed layer, which is typically <30 m near Bermuda during the summer but can deepen to ~200 m for brief periods in the winter (Lomas et al., 2013). For both the euphotic zone and the surface mixed layer, the warm-season (spring-summer-early fall) decline in the concentration of DIC provides a first order measure of net community production

(NCP) (Michaels et al., 1994), the net production of organic matter in the sunlit upper water column that should be equivalent to organic carbon export on time scales of months and longer. Gas exchange and other terms are also significant for seasonal changes in the upper ocean DIC concentration but can be addressed, for example, with the use of carbon isotopes (Gruber et al., 1998). For dissolved O_2, gas exchange plays a much greater role, such that the mixed layer O_2 concentration ($[O_2]$) during the summer approximately reflects a steady state between NCP (which produces O_2) and evasion of O_2 to the atmosphere (Jenkins and Goldman, 1985; Emerson, 1987; Hendricks et al., 2004). Due to the importance of gas exchange, approaches for estimating NCP from O_2 depend on whether measurements are from the surface mixed layer (Kaiser et al., 2005; Emerson et al., 2008; Stanley et al., 2010; Nicholson et al., 2015), the euphotic zone (Jenkins and Goldman, 1985; Spitzer and Jenkins, 1989; Nicholson et al., 2008, Riser and Johnson, 2008; Howard et al., 2010), or the underlying dark ocean where the exported organic matter is remineralized (Jenkins, 1982; Jenkins and Goldman, 1985; Stanley et al., 2012).

DIC and O_2-based measurement approaches suggest that annual NCP is remarkably uniform across the global ocean, being no lower in the subtropical gyres than other open ocean environments (Emerson et al., 2008; Emerson and Stump, 2010; Emerson, 2014; Hamme and Emerson, 2006; Hendricks et al., 2005; Jenkins and Doney, 2003; Munro et al., 2013; Quay et al., 2009; 2012; Reuer et al., 2007; Spitzer and Jenkins, 1989; Stanley et al., 2010, 2012). This similarity is surprising given the scarcity of major nutrients in the subtropical surface ocean and the substantial density difference between the nutrient poor surface waters and underlying nutrient-rich deep waters. Accordingly, most models do not predict it (see Emerson, 2014, for a

compilation). This unexpected result is bound up with two long-standing gaps in our understanding of productivity in the subtropical ocean, which have been brought into focus by studies at ocean time-series sites, particularly the Bermuda Atlantic Time-series Study (BATS) in the northwestern North Atlantic subtropical gyre (the Sargasso Sea). Below, we describe these problems and then propose a hypothesis to explain them as well as the overarching observation of high subtropical NCP.

The Problems:

Problem 1: Missing carbon export

Integrating over the depth range of the euphotic zone at BATS, the high NCP rates estimated from O_2 production and DIC consumption are not detected in the fluxes of organic matter from the euphotic zone by sinking as measured with sediment traps, downward mixing of dissolved and particulate organic carbon (POC) as measured by depth profiles of DOC and POC concentration, or other processes (Michaels et al., 1994; Carlson et al., 1994). On average, NCP at BATS based on the O_2 and DIC approaches described above is 2-5 mol C m^{-2} yr^{-1} (Table 1) (Spitzer and Jenkins, 1989; Cianca et al., 2013; Stanley et al., 2012; see Emerson, 2014, for a compilation). In contrast, the average annual rate of export production from 24 years of sinking POC collected in surface-moored particle interceptor sediment traps (PITS) is 0.88 ± 0.14 mol C m^{-2} yr^{-1} (Lomas et al., 2013), while the downward mixing of POC and DOC have been estimated at 0-0.05 mol C m^{-2} yr^{-1} and 0.4-1.4 mol C m^{-2} yr^{-1}, respectively (Michaels et al., 1994; Carlson et al., 1994; Hansell and Carlson, 2001; Omand et al., 2015). Measured carbon export is thus roughly 1.3-2.3 mol C m^{-2} yr^{-1}, 43-77% of the NCP estimates.

The disagreement between measured euphotic zone NCP and the organic carbon measured leaving the euphotic zone has been widely suspected to result from a tendency of sediment traps to "undercollect" sinking POC. If so, then the BATS traps would need to miss as much as ~60% of the organic matter export associated with NCP. Trap inaccuracies are thought to derive primarily from three factors: hydrodynamic biases, contamination by zooplankton "swimmers", and in-trap solubilization of material after collection (Buesseler et al., 2007). With respect to trap hydrodynamics, Buesseler et al. (2000) found no coherent difference between the export flux captured by the PITS traps at BATS and that collected by neutrally buoyant sediment traps (NBSTs) designed to minimize hydrodynamic biases (Valdes and Price, 2000; Valdez and Buesseler, 2006). With respect to "swimmers," the BATS traps are poisoned and covered with a baffle to prevent direct feeding on the collected material, and swimmers are removed prior to sample analysis. In any case, failure to remove swimmers would tend to yield an overestimate of the sinking flux rather than an apparent under-collection of POC (Karl and Knauer, 1989). The last possibility, solubilization, has proven difficult to assess, and data on this issue are scarce. Buesseler et al. (2007) conclude based on the existing data that short-term trap deployments (1-3 days) and timely processing of samples after collection, both of which are standard practice for the BATS trap program, minimize particle solubilization. However, this conclusion relies to some degree on assumptions about the particles involved.

Problem 2: Missing nutrient supply

The second problem has been best characterized for the summertime surface mixed layer, the base of which is typically <30 m deep during the summer at BATS (Lomas et al. 2013). The summertime drawdown of DIC from the mixed layer is consistent with the high NCP measured

for the euphotic zone (Gruber et al., 1998). Yet the mixed layer is isolated from dissolved nutrients, with more than 50 m of effectively nutrient-free euphotic zone water below it that separates it from the nutrient-bearing dark subsurface waters. Thus, the mixed layer DIC drawdown appears to occur without a circulation-based mechanism of major nutrient (nitrate and phosphate) supply. These observations have led to a search for (1) unseen nutrient supply mechanisms to fuel the needed export production (Hood et al., 2001; Houghton et al., 2018; Johnson et al., 2010; Katija and Dabiri, 2009; McGillicuddy et al., 1998; Villareal and Lipschultz, 1995) or alternatively (2) the production and export of organic matter with a much lower N and P content than is typical for upper ocean biomass, such that no additional nutrient supply is required (Martiny et al., 2013; Ono et al., 2001; Toggweiler, 1993).

With regard to a previously unrecognized nutrient supply mechanism, there are fewer options than frequently assumed. The nutrients in the shallow subsurface of the subtropical ocean were mostly emplaced by the regeneration of organic matter exported from the surface, such that they are paired with a DIC excess (and an O_2 deficit) determined by the stoichiometry of that organic matter (as will be discussed in detail below in the context of "preformed" nutrient changes). As a result, phytoplankton growth and carbon export driven by a greater-than-recognized supply of dissolved nutrients from below would not drive a larger net deficit in DIC within the summer mixed layer. Rather, the circulation- or mixing-based nutrient supply and resulting export production would largely offset one another in their effects on DIC (Johnson et al., 2010; Lomas et al., 2013). This is the case regardless of the specific physical mechanism, be it diapycnal diffusion, salt fingering, eddies, or frontal effects. Thus, while mesoscale features such as eddies have been shown to be an important source of nutrients to summertime Sargasso Sea surface

waters (McGillicuddy et al., 1998), they cannot explain the amplitude of the DIC drawdown in the summer mixed layer at BATS. The only mechanisms of nutrient supply that have the potential to explain the net DIC drawdown out of the summer mixed layer are biological processes: (1) N_2 fixation (for N, possibly augmented by a contribution from atmospheric N deposition) and (2) phytoplankton uptake of dissolved nutrients (N and P) from the subsurface followed by migration into the mixed layer.

An argument has been made that, while a nutrient supply problem exists for the summer mixed layer at BATS, it does not apply to the Sargasso Sea euphotic zone. The nitrate supply rate estimated with the "^{3}He flux gauge" is adequate (possibly more than adequate) to fuel the high NCP estimated for the euphotic zone from DIC and O_2 budgets (Stanley et al., 2012; 2015). However, several critical caveats must be recognized. First, as acknowledged by the originators of the ^{3}He flux gauge, an unknown fraction of the estimated nitrate supply may be consumed along the obduction region of the northern margin of the North Atlantic subtropical gyre, reducing the implied nitrate supply at BATS (Stanley et al., 2012 and references therein). Second, as already described in the context of the mixed layer, nutrient supply from below would occur with a stoichiometric burden of DIC excess and O_2 deficit, such that production immediately fueled by it would not contribute to the net drawdown of DIC or the net production of O_2. The only way around this problem is for the nutrients to be supplied during the winter when O_2 can be taken up from the atmosphere and upwelled DIC can be mixed throughout the euphotic zone, providing the baseline from which summertime DIC drawdown is calculated. Even this possibility is limited by the nutrient stocks in the euphotic zone observed in the early summer at BATS (Lomas et al., 2013), which are far too low to yield the rate of summer NCP

indicated by DIC and O_2. Thus, for the euphotic zone as for the mixed layer, circulation-driven nutrient supply (even if sporadic) is not a viable driver of summer measurements of high NCP (e.g., as observed by Luz and Barkan (2009) and Estapa et al. (2015)).

Previous studies have shown that the rate of N_2 fixation at BATS is far too low to provide the "missing N" required to support the measured rate of NCP (Altabet 1988; Hansell and Carlson, 2001; Orcutt et al., 2001; Knapp et al., 2005). Moreover, in a biogeochemical model, if an adequately high N_2 fixation rate is imposed to simulate the observed DIC drawdown, the model also produces DON and DOC anomalies in late summer/early fall that are not observed in the environment (Hood et al., 2001). In addition, even if adequate N were supplied by N_2 fixation, it would not address the needed supply of P, which is also required for phytoplankton growth and is present at extremely low concentrations in BATS surface waters (Wu et al., 2000; Ammerman et al., 2003; Mather et al., 2008; Lomas et al., 2010). Thus, the available data indicate that N_2 fixation is not the answer.

Atmospheric N deposition represents an alternative source of N to surface waters that is not stoichiometrically linked to carbon. However, the flux of atmospheric N to the BATS site is low (Knap et al., 1986; Michaels et al., 1993; Altieri et al., 2016). More importantly, even if adequate N were supplied to BATS surface waters via atmospheric deposition, this flux would supply N but not P, which is typically present in low concentrations in atmospheric deposition (i.e., with a N/P ratio of >30; see Kanikadou et al., 2012 and references therein).

Upward nutrient transport by phytoplankton migration has been identified as a significant process in the open ocean (Villareal et al., 2014). Direct observations are limited to large diatoms and the dinoflagellate *Pyrocystis*, and this process has not yet been shown to be significant in the Sargasso Sea. Nonetheless, data from the subtropical North Pacific show that large migrating diatom mats (*Rhizosolenia* spp.) can mediate a significant upward transport of nitrate from the subsurface into the mixed layer, and high intracellular nitrate concentrations have been measured for putative migrators in both the Pacific and Atlantic (Villareal and Carpenter 1994; Villareal and Lipschultz, 1995; Villareal et al., 2014). While nitrate transport by *Pyrocystis* has not been directly shown in the Sargasso Sea, its migration has been documented in these waters (Rivkin et al., 1984), and, in a study focused on the North Pacific, this species has been estimated to transport as much as 17 µmol N m^{-2} d^{-1} into the euphotic zone (Villareal et al., 2014). However, even if this rate of nitrate supply were sustained throughout the year at ATS, it would account for a flux of only 6.2 mmol N m^{-2} yr^{-1}. Approximately half of the NCP at BATS is unaccounted for by the documented nutrient supply. This amounts to ~1.5 mol C m^{-2} yr^{-1}, or ~0.2 mol N m^{-2} yr^{-1} assuming a C/N ratio of 7. Year-round migration by *Pyrocystis* would supply only 3-4% of the N needed to fuel this outstanding portion of the NCP. In addition, *Rhizosolenia* mats are very rare at BATS (Carpenter et al., 1977), and the abundance of the large migrating diatom, *Ethmodiscus*, is also low (0.03-4.7 cells m^{-3}; Swift, 1973; Villareal and Carpenter, 1994; Villareal et al., 1999). The possibility that these migrating phytoplankton supply some quantity of subsurface nitrate to BATS surface waters in summer cannot be ruled out, but the data in hand do not make a convincing argument for the process as a central nutrient flux, especially in light of concerted efforts to find it in the Sargasso Sea.

There is evidence from culture studies that phytoplankton smaller than *Pyrocystis, Rhizosolenia,* and *Ethmodiscus* can display ascending behavior (Waite et al. 1997). However, this has not yet been shown in the open ocean. This process operating alone at BATS would require small phytoplankton to migrate 75-100 m to transport nitrate from below the euphotic zone into the upper 20-40 m meters of the water column. Nitrogen isotopic analysis indicates that nitrate assimilation by small eukaryotes occurs in the euphotic zone and on some occasions in the mixed layer of the summertime Sargasso Sea (Fawcett et al., 2011). It is possible that the mixed layer nitrate derives from migration of the small eukaryotes in question, although it would require them to migrate very large distances in just a few days. The existing eukaryotic N content and isotope data suggest that these small eukaryotes constitute ~25% of the euphotic zone biomass and rely on nitrate for ~30% of their N in the summertime mixed layer and <10% by the fall (Fawcett et al., 2011, 2014). Taking an upper bound for their growth rate of 0.5 d^{-1} (Goerike and Welschmeyer, 1998; Cuvelier et al., 2010), a growing season of 210 days (7 months), and a biomass C/N ratio of 7, this amounts to the removal of 7-11 µM DIC. Between April and October, mixed layer DIC drawdown is ~26 µM (Gruber et al., 1998). Thus, even when small eukaryotes are assumed to acquire all of their nitrate by migration into subsurface waters, biological nitrate transport could fuel less than half of the DIC drawdown.

Lacking promising mechanisms of nutrient supply that could explain the summertime mixed layer decline in DIC, the most straightforward explanation is that it results from the export of organic matter with C/N and C/P ratios far higher than Redfield's values of ~7 and ~106 (e.g., Lomas et al., 2013; Martiny et al., 2013). Indeed, when ocean models are confronted with the

existing biogeochemical data, they predict exactly this sense of deviation from Redfield stoichiometry in the subtropical regions (DeVries and Deutch, 2014; Teng et al., 2014).

However, the nature of this putative nutrient-poor organic carbon export is a mystery. Its characteristics must be such that it is neither measured by sediment traps nor apparent in calculations that consider the hydrographic transport of DOC and suspended POC from the euphotic zone to the subsurface. Suspended particulate organic matter (POM) sampled by filtration and (more importantly) sinking POM captured by sediment traps have a C/N ratio close to 7 (Martiny et al., 2013; Schneider et al., 2003), suggesting no preferential export of C relative to N. Moreover, their nutrient content aside, the magnitude of the measured downward flux of these materials cannot account for either NCP from the euphotic zone or DIC drawdown in the summer mixed layer (Michaels et al., 1994). Dissolved organic matter (DOM) produced in the subtropical euphotic zone does have an appropriately low nutrient (e.g., N) content (Hansell and Carlson, 2001). However, as with the sinking and downward mixing of POC, calculations of the downward mixing of DOC indicate that it is too slow to explain the high rates of NCP (Michaels et al., 1994; Carlson et al., 1994; Hansell and Carlson, 2001); it was included in the carbon accounting above.

The hypothesis: Export of gel-like, nutrient-poor organic matter

DOM has strong chemical similarities with carbohydrate exuded by phytoplankton (Aluwihare and Repeta, 1999), and this carbohydrate can develop a gel-like substance known as “transparent exopolymer particles” (TEP) (Alldredge et al., 1993). Phytoplankton release DOC as roughly a quarter of their organic carbon production (Teira et al., 2003), a significant fraction of which is

polysaccharide (Engel et al., 2004; Passow, 2002). This assembles to form TEP (Alldredge et al., 1993; Chin et al., 1998; Engel et al., 2004), often a significant portion of POC (Beauvais et al., 2003; Engel et al., 2004).

TEP often binds particles together, forming marine snow that may transport large quantities of biomass-derived organic matter into the ocean interior (Passow, 2002). TEP itself is positively buoyant (Azetsu-Scott and Passow, 2004; Mari, 1999; Mari et al., 2017), with a density inferred from settling experiments of 0.70-0.84 g cm^{-3} (Azetsu-Scott and Passow, 2004). Nonetheless, there is ample evidence for a role for TEP in sedimentation in the ocean (Kumar et al., 1998; Passow, 2002; Passow et al., 2001; Riebesell et al., 1995). While adding denser organic matter may or may not render TEP sufficiently negatively buoyant to sink, the addition of ballasting material such as calcium carbonate, clays, and biogenic and lithogenic silica can produce aggregates with densities that are adequate for slow sinking (1.04-1.12 g cm^{-3}; *SI 1.1*; Mari et al., 2017). Because TEP-containing aggregates likely cover a broad compositional spectrum, with TEP content varying widely, a continuum of sinking rates is to be expected, ranging from non-sinking TEP-rich particles to rapidly sinking particles with a high proportion of ballast and only a small proportion of TEP (Mari et al., 2017).

We propose that the unexpectedly high O_2 production and DIC uptake in subtropical surface waters is largely due to the production and sinking of such nutrient-poor, gel-like organic matter (Fig. 1). This gel-like organic matter (GLOM) may be TEP or a material exhibiting similar physical characteristics and having a related composition. We further propose that GLOM accumulates in the summertime mixed layer at BATS because of an increased proportion of

carbon-rich exudates from phytoplankton growing under nutrient limitation (Corzo et al., 2000; Mari et al. 2017) and/or because heterotrophic bacteria lack the N and P to metabolize it. Upon binding to an adequate number of denser particles, a fraction of it begins to sink, generating a flux of carbon-rich organic matter out of the euphotic zone. Because this material is nutrient-poor (Mari, 1999; Mari et al., 2017; Passow, 2002), it obviates the need for the as-yet-unobserved nutrient supply to the BATS euphotic zone. Because particles with large proportions of GLOM will sink very slowly and because GLOM is probably easily disaggregated and dissolved, we propose that much of the exported GLOM is hydrodynamically excluded from traps, is inadequately dense to settle into the brine-filled trap collection cups, and/or is not preserved in them.

The POM collected in sediment traps at BATS has a C/N ~7 (Schneider et al., 2003), suggesting that N-poor GLOM is not captured in the traps in significant quantities. Sediment traps have long been suspected of excluding some sinking material for hydrodynamic reasons (Gardner, 2000; Buesseler et al., 2007; see above), and low-density GLOM would be a prime candidate for such under-collection (Buesseler et al., 2006). In addition, the brine solution added to the collection cups of sediment traps prior to deployment (which typically has a density of ~1.08-1.1 g cm^{-3}) acts as a physical barrier to particles and aggregates that are less dense than the brine. These particles are then resuspended or broken up at the interface of the trap (Gardner, 2000). Indeed, laboratory experiments have shown that the addition of brine (with a density $\leq$1.08 g cm^{-3}) can decrease the flux collected in the traps by 50% (Gardner and Zhang, 1997). GLOM, which we expect to be less dense than the brine, would thus be preferentially excluded. We note that because of its shallow remineralization, GLOM export should not affect the remineralization

ratios in the mid-depth and deep ocean, explaining the consistency of 400-4000 m data with the remineralization of marine biomass with Redfield-like C-to-nutrient ratios (Anderson and Sarmiento, 1994).

GLOM may also avoid detection as suspended material in the surface ocean. Much of the GLOM that has an *in situ* size appropriate be captured on filters with the typical pore sizes (e.g., 0.7 µm pore size glass fiber filters) may be lost through disintegration on the filter. There is strong evidence that this applies to TEP. A typical average concentration of TEP in the summertime Sargasso Sea is 60-80 µg Xanthan equivalent L^{-1} (Xeq L^{-1}) (Cisternas-Novoa et al., 2015; Estapa et al., 2015), which translates to 3-4 µM C using the conversion factor of 0.63 of Engel and Passow (2001). This concentration is similar to or higher than typical measurements of total suspended POC in the region (Lomas et al., 2013). Estapa et al. (2015) sampled simultaneously for TEP and POC in the summertime Sargasso Sea, measuring average concentrations of TEP and suspended POC of ~4 µM C and 2.7 ± 0.7 µM C, respectively. Moreover, some TEP concentrations were much higher, up to 200 µg Xeq L^{-1} (or ~11 µM C), well above the POC concentration in the corresponding samples. These data raise the possibility that a large fraction of TEP is disaggregated by filtration, passes through the filter, and is binned into the much larger DOC pool. While this is not required by our hypothesis, it would be consistent with it.

In a similar vein, NCP as measured with DIC and O_2 budgets at BATS is similar to ^{14}C incubation-based measurements of net primary production (NPP) (Jenkins and Goldman, 1985), whereas ecological and biogeochemical expectations are for NCP to be a small fraction (10-25%) of NPP (Dugdale and Goering, 1967; Eppley and Peterson, 1979). GPP measurements rely

on filtration to separate ^{14}C-labeled POC from the ^{14}C-labeled DIC substrate. Thus, if the production of TEP (or GLOM) is a major fate for C fixation during the summer, disaggregation of this material upon filtration would lead to an underestimation of GPP (even disregarding the possibility that many GLOM particles may be smaller than the typically used filter size of 0.7 µm; Mari et al., 2017). This would then explain the long-troubling result of a very high NCP/NPP ratio in the subtropical North Atlantic (Jenkins and Goldman, 1985; Luz and Barkan, 2009).

To summarize, given the ephemeral nature of GLOM proposed above, it could have gone undetected at BATS. Nevertheless, there should be signs of its remineralization in the subsurface. Below, we provide three forms of evidence for the remineralization of such low-nutrient organic matter at 100-400 m depth near BATS. The first involves "preformed nitrate," the quantity of nitrate in excess of that expected from the respiration of typical marine biomass, which is itself estimated from the apparent oxygen utilization. We report data from profiling floats with nitrate and O_2 sensors, corroborated by the BATS program data, that indicate a summertime decline in preformed nitrate at 80-400 m depth, consistent with the regeneration of low-N organic matter. Second, the consolidation of multiple water column profiles of nitrate oxygen isotopes ($^{18}O/^{16}O$) at BATS suggest summertime heterotrophic nitrate assimilation in subsurface waters, an expected consequence of the respiration of N-poor organic matter. Third, dark incubations of 140-200 m water samples from BATS yield heterotrophic nitrate assimilation, consistent with N limitation of heterotrophic bacteria in these subsurface waters. The first form of evidence (from the profiling floats) is the most compelling of non-Redfield export, although it has an alternative interpretation in the form of biological nutrient transport;

these data do not prove the GLOM hypothesis, but they are fully consistent with it. The latter two forms of evidence, both serendipitous, are more novel but also more speculative. While intriguing to the authors, they are included not as definitive proof but rather to point to two complementary avenues for pursuing this hypothesis and related concepts.

Materials and methods

Profiling floats – Observations were made with Teledyne/Webb Research APEX profiling floats (Johnson et al., 2010; Riser and Johnson, 2008) fabricated at the University of Washington. The floats were equipped with In Situ Ultraviolet Spectrophotometer (ISUS) optical nitrate sensors (Johnson et al., 2013) produced at MBARI and Aanderaa 3830 and 4330 (float 7663) optical O_2 sensors (Tengberg et al., 2006). Nitrate concentrations were computed from the UV spectra measured by the ISUS sensor with the TCSS algorithm (Sakamoto et al., 2009). These floats were typically set to profile from 1000 m to the surface at 5-day intervals. An array of floats (Fig. S1; Table S1) has been operating since late 2009 near BATS, giving five float years of data for analysis that cover four full annual cycles. Data analysis was restricted to profiles within a box bounded by 34°N to 28°N and 62°W to 73°W. Nitrate and O_2 data were quality controlled before analysis (*SI 1.2*; Fig. S2).

Preformed nitrate was calculated from O_2 and nitrate concentrations and computed O_2 solubility at *in situ* temperature and salinity, $(O_2)_{Sol}$, as Preformed Nitrate = $[NO_3^-]$ – 16/150 x $[(O_2)_{Sol} - (O_2)]$. For comparison with the float data, annual preformed nitrate and phosphate (PO_4^{3-}) climatologies were also computed from 20 years of BATS nitrate, phosphate, and O_2 concentration data (with Preformed Phosphate = $[PO_4^{3-}]$ – 1/150 x $[(O_2)_{Sol} - (O_2)]$). The quality

controlled profiling float data used in this study are permanently archived within the SOCCOM (Southern Ocean Carbon and Climate Observations and Modeling) float data archive at doi:10.6075/J0DR2SDD.

The oxygen isotopic composition of water column nitrate – Samples were collected onboard the R/V *Atlantic Explorer* at the BATS site (31°40'N; 64°10'W) on the following cruises: B244 in March 2009, B248 in July 2009, BV44 in October 2009, B253 in December 2009, B259 in June 2010, B260 in July 2010, B274 in October 2011, AE1203 in February 2011, B280 in April 2012, B283 in July 2012, AE1220 in August 2012, B287 in November 2012, B292 in April 2013, B295 in July 2013, and B299 in November 2013. Samples were also collected onboard the R/V *Knorr* from BATS during US GEOTRACES Intercalibration Cruise 1 in July 2008. Seawater was collected unfiltered in 60 mL HDPE Nalgene bottles that were rinsed copiously with sample water prior to filling and immediately frozen at -20°C.

Seawater nitrate+nitrite concentrations were determined by reduction to nitric oxide followed by nitric oxide chemiluminescence detection (Braman and Hendrix, 1989) in a configuration with a detection limit of ~0.01 μM. Samples from the surface to 500 m were analyzed for nitrite concentration according to the colorimetric method of Strickland and Parsons (1968), with a detection limit of ~0.005 μM. Nitrate concentration alone was calculated by difference.

The $\delta^{18}O$ and $\delta^{15}N$ of nitrate were determined by the 'denitrifier' method wherein denitrifying bacteria lacking nitrous oxide (N_2O) reductase quantitatively convert sample nitrate and nitrite to N_2O (Casciotti et al., 2002; Sigman et al., 2001). The isotopic composition of N_2O was measured

by GC-IRMS using a Thermo MAT 253 mass spectrometer and a purpose-built on-line N_2O extraction and purification system (Weigand et al., 2016). The international reference materials, IAEA-N3 and USGS-34, were used to determine the $\delta^{18}O$ of samples relative to Vienna Standard Mean Ocean Water (VSMOW): $\delta^{18}O$, in ‰ vs. VSMOW, = $\{[(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{VSMOW}] - 1\}$ x 1000), and the $\delta^{15}N$ of samples relative to N_2 in air: $\delta^{15}N$, in ‰ vs. air, = $\{[(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{air}] - 1\}$ x 1000).

Nitrate concentration and isotope data for individual BATS cruises are reported in Fawcett et al. (2015), where analytical details can also be found. A total of 220 samples from BATS were analyzed for $\delta^{18}O$ and $\delta^{15}N$, 3-7 times each. The pooled standard error for $\delta^{18}O$ and $\delta^{15}N$ was 0.12‰ and 0.04‰, respectively, for nitrate concentrations ≥0.5 µM (195 samples), and 0.22‰ and 0.14‰, respectively, for concentrations <0.5 µM (25 samples). Samples with nitrate concentrations below 0.2 µM were not analyzed.

Here, we report $\delta^{18}O$ (and $\delta^{15}N$) data for nitrate only, after removal of nitrite (Granger and Sigman, 2009). Nitrite typically declines to unquantifiable levels by ~300 m at BATS and is always undetectable by 500 m (Fawcett et al., 2015); samples collected deeper than 500 m were thus not treated with sulfamic acid to remove nitrite. This cut-off does not drive the measured upward nitrate $\delta^{18}O$ increase observed to start at roughly 500 m (see below) as verified by nitrate+nitrite $\delta^{18}O$ data from the relevant depth range (Fawcett et al., 2015). The isotopic impact of nitrite removal is addressed at length in Fawcett et al. (2015).

Nitrate $\delta^{18}O$ was adjusted for the effect of increasing salinity from deep to shallow waters (by ~1.4 psu between 800 m and 200 m; following Knapp et al., 2008; Fawcett et al., 2015) according to: $\delta^{18}O_{NO3(salinity\ corr)} = \delta^{18}O_{NO3} - (0.52 \times (sal - sal_m))$, where $\delta^{18}O_{NO3}$ is the measured $\delta^{18}O$ of sample nitrate, 'sal' is the measured salinity of that sample (http://bats.bios.edu), and 'sal_m' is the mean salinity at 1000 m. The factor of 0.52 is the approximate slope of the relationship between seawater $\delta^{18}O$ and salinity in the upper subtropical ocean (Bigg and Rohling, 2000; LeGrande and Schmidt, 2006). Hereafter, "nitrate $\delta^{18}O$" refers to the salinity-adjusted value. This adjustment tends to lower the $\delta^{18}O$ of thermocline water nitrate relative to deeper water, which yields the most conservative interpretation of the data, as described below.

The mean seasonal nitrate concentration at each depth at BATS was calculated by averaging all late winter/early spring data (4 vertical profiles) and all summer/fall data (12 vertical profiles). The mean seasonal nitrate $\delta^{18}O$ profiles were generated by concentration-weighted averaging of all late winter/early spring profiles and all summer/fall profiles. In all cases, error was calculated according to standard statistical practices. Nitrate concentration and isotope data are archived at http://www.bco-dmo.org

Seawater incubation experiments – Seawater was collected from 140 m, 160 m, and 200 m at BATS in February 2012 (AE1203) and August 2012 (AE1220). Samples were collected unfiltered in 1 L acid-washed HDPE Nalgene bottles and stored frozen until commencement of the experiments in August 2014.

Seawater was thawed at room temperature (~22°C) in the dark, after which half the volume of each 1 L sample was gently vacuum filtered, first through a combusted (450°C for 5 hours) 47 mm diameter glass fiber filter (nominal pore size of 0.7 µm), and then through a 47 mm diameter 0.2 µm pore size polycarbonate filter that had been soaked and copiously rinsed with ultra high purity deionized water (DIW). All filtration glassware was acid-washed and combusted at 500°C for 5 hours prior to use. Despite these precautions, filtration may have introduced some level of DOC contamination to the filtered aliquots (Carlson and Ducklow, 1996); however, it was the unfiltered aliquots that showed nitrate drawdown (see below), and these did not undergo any of the filtration steps.

For each month and depth, ~225 mL of filtered and unfiltered seawater were decanted in duplicate into 250 mL acid-washed HDPE Nalgene bottles. One of each of the treatments (i.e., February or August, 140 m, 160 m, or 200 m, and filtered or unfiltered) was placed in a bench-top hood that receives ambient daylight and in which the overhead light was left on ("light treatments"), and the others were placed in a drawer in the lab ("dark treatments"). On each day of the four-week experiment, all of the Nalgene bottles were uncapped briefly and then shaken vigorously to encourage exchange of CO_2 and O_2 between sample seawater and the headspace, and ensure homogeneity of subsamples (see below).

Beginning on day 1, and continuing for 28 days at intervals of 12-24 hours (early in the experiment) to ~4 days (later in the experiment), 10 mL aliquots of seawater from each 250 mL bottle were subsampled into acid-washed 15 mL centrifuge tubes and immediately frozen for later nitrate concentration and isotope analysis. In addition, 1 mL aliquots of each treatment were

pipetted into acid-washed 1.5 mL cryovials to which 25 µL of glutaraldehyde (Grade I, Sigma-Aldrich) was added (1% v/v). Cryovials were gently agitated and incubated at 4°C for 1-2 hours to allow the fixative to bind to cellular components, then frozen at -80°C for later flow cytometric analysis.

Seawater nitrate concentration and $\delta^{18}O$ (and $\delta^{15}N$) for each time-point of the experiment were analyzed as described above. We note that volume restrictions precluded the removal of nitrite from samples, such that the reported nitrate concentration and isotope data are more accurately a measure of the nitrate+nitrite pool.

Microbial community composition and cell abundance at each time-point was determined by flow cytometric analysis of 250 µL of glutaraldehyde-preserved seawater. Heterotrophic bacteria were identified by nucleic acid staining with SYBR Green I (1:7500) according to Marie et al. (1997) and Gasol and Del Giorgio (2000). In brief, a blue laser (488 nm) was used for excitation of SYBR Green I-stained and autofluorescent cells. Heterotrophic bacteria were discriminated from the picoautotrophic cyanobacteria, *Prochlorococcus*, by gating the cell populations using side scatter, green fluorescence (emission detection at 533 nm; indicative of relative nucleic acid content), and red fluorescence (emission detection >670 nm; indicative of chlorophyll content). Samples were analyzed using a BD Accuri C6 flow cytometer at a flow rate of 35 µL min^{-1} and with a core diameter of 16 µm. Polystyrene-based latex beads (0.91 µm) were used to assess instrument performance and standardize scatter and fluorescence measurements.

Results

Float data – O_2 and nitrate concentrations for the upper 300 m of the water column measured in 2010-2013 by the profiling float array are shown in Fig. 2a-b. Deep, wind-driven mixing is evident in the homogenization of the upper water column O_2 concentration and brief increase in the surface nitrate concentration in late winter/early spring of 2010 and 2011. In 2012 and 2013, the gradient in O_2 concentration and lack of an increase in surface nitrate suggest that spring mixing did not penetrate as deeply as in the previous two years. Billheimer and Talley (2013) note a near cessation of Eighteen Degree Water formation in 2012, which is reflected in these float data. In the summer, thermal stratification of the upper water column sets in, the available nitrate is rapidly consumed by phytoplankton, and O_2 is produced in the euphotic zone. The decrease in O_2 below the euphotic zone is due to its consumption by heterotrophic bacteria during the decomposition of organic matter sinking out of surface waters.

From the float-derived O_2 and nitrate concentration data, the concentration of preformed nitrate was calculated (Fig. 2c). The preformed nitrate parameter was originally defined in order to quantify the nitrate entering the deep ocean dissolved in the ventilating water, as opposed to "regenerated" nitrate that is added to the subsurface by organic matter decomposition. However, the partitioning of nitrate into these two origins is calculated based on the assumption of decomposition of organic matter with the elemental stoichiometry of Redfieldian marine biomass (i.e., $C/N/P/-O_2$ = 106/16/1/-150) (Anderson, 1995; Anderson and Sarmiento, 1994). Thus, changes in preformed nitrate, despite its name, can result from decomposition that deviates from Redfield stoichiometry. One could equivalently use the tracer "NO" as an indicator of non-Redfieldian stoichiometric changes (Fig. S4; where "NO" (μM) = $(150/16)*[NO_3^-]_{measured}$ +

$[O_2]_{measured}$); Broecker 1974). However, the absolute value of this property in the surface mixed layer interferes with the clarity of the seasonal thermocline changes.

The float-derived preformed nitrate concentrations are high in the spring and summer euphotic zone (Fig. 2c). Since surface nitrate concentrations are below detection at this time (Fig. 2b), the preformed nitrate maxima can be attributed to the production of O_2 above saturation by phytoplankton (i.e., $[(O_2)] > [(O_2)_{Sol}]$). Below the euphotic zone, a spring-to-fall decrease in preformed nitrate is apparent, reaching values as low as -2 μM. This feature is biogeochemically and physically separated from the surface layer, and at times penetrates deeper than 300 m. Realistic variations in apparent oxygen utilization (i.e., $[(O_2)_{Sol} - (O_2)]$) or the N/-O_2 remineralization ratio for typical marine biomass are insufficient to explain a negative preformed nitrate anomaly as low as -2 μM (Emerson and Hayward, 1995; Abell et al., 2005).

The Aanderaa optode O_2 sensor used in this work is characterized by a relatively slow response (Bittig et al., 2012) that will result in a bias in O_2 concentration in steep gradients. In some conditions, this bias could contribute to the minimum in preformed nitrate. However, the preformed nitrate minimum occurs in Eighteen Degree Water where O_2 gradients are low. For this reason, we argue that biases resulting from slow sensor response time are not important (*SI 1.2*; Fig. S3).

The O_2 and nitrate concentration at 130 m and on the 26.4 isopycnal surface (which lies near 200 m) are shown in Fig. 3a-d. The mean rate of O_2 decline at 130 m after deep mixing is 35 ± 12 μM y^{-1} (Fig. 3a). Assuming the decomposition of typical marine biomass, such a decrease calls

for ~3.8 µM of nitrate production. The observed rate of nitrate increase is <10% of this (mean nitrate production rate of 0.3 ± 1.1 µM y^{-1}; Fig. 3b; Table S2). At ~200 m, the mean rate of O_2 decline is 24 ± 16 µM y^{-1} (Fig. 3c), and three quarters of the expected nitrate production is observed (2.2 ± 1.1 µM y^{-1}, instead of the ~2.8 µM y^{-1} predicted by Redfield stoichiometry; Fig. 3d; Table S2).

Oxygen isotopes of nitrate – For both the winter/spring and summer/fall, the average $\delta^{18}O$ of nitrate varies little between 1000 m and 600 m, and we observe no difference in absolute value between the two seasonal profiles (Fig. 4a). In both seasons, nitrate $\delta^{18}O$ rises by more than 7‰ from ~150 m into the euphotic zone, due to isotopic fractionation during nitrate assimilation by phytoplankton (Knapp et al., 2008; Fawcett et al., 2015). A weak upward nitrate $\delta^{18}O$ rise is also observed in the subsurface, from 1.4‰ at 500 m to 1.7‰ at 200 m in the winter/spring, and 1.6‰ at 500 m to 2.1‰ at 200 m in the summer/fall. Most importantly for our study, student's t-tests indicate that nitrate $\delta^{18}O$ at 200 m in the summer/fall is significantly higher than in the winter/spring by an average of 0.4‰ ($p < 0.01$), 250 m ($p < 0.001$), 300 m ($p < 0.001$), and 400 m ($p < 0.001$).

Like its $\delta^{18}O$, the $\delta^{15}N$ of nitrate also rises into the euphotic zone due to nitrate assimilation (Fawcett et al., 2015; Fig. 4b). However, nitrate $\delta^{18}O$ and $\delta^{15}N$ have different depth gradients in the subsurface. While nitrate $\delta^{18}O$ rises upward from ~500 m, nitrate $\delta^{15}N$ declines upward from ~700 m to 200-150 m. The upward decline is due to the remineralization of newly fixed N, which is low in $\delta^{15}N$ (Knapp et al., 2008; Fawcett et al., 2015). Also in contrast to nitrate $\delta^{18}O$, neither nitrate $\delta^{15}N$ nor nitrate concentration show a seasonal change below the euphotic zone

(Fig. 4b,c).

Seawater incubations – In all but one treatment (February 200 m light), unfiltered sample nitrate concentrations decreased in both the dark and the light during the experiments (Fig. 5a; Fig. S5a-b), and the $\delta^{18}O$ of the remaining nitrate rose (Fig. 5b; Fig. S5c-d; the $\delta^{15}N$ of the remaining nitrate also rose (not shown)). In contrast, no change was observed in the filtered samples. Plotting the nitrate concentration and $\delta^{18}O$ data in "Rayleigh" space (i.e., nitrate $\delta^{18}O$ vs. $\ln([NO_3^-]_{measured}/ [NO_3^-]_{initial})$) for the dark experiments, which we take to be more representative of the BATS subsurface than the light experiments, provides an estimate of the average oxygen isotope effect for nitrate assimilation ($^{18}\varepsilon$) of 3.5‰ ± 0.3‰ (p-value < 0.001; 95% confidence interval of 2.9‰ to 4.1‰; Fig. 5b; $^{18}\varepsilon = (^{16}k/^{18}k - 1) \times 1000$, where ^{16}k and ^{18}k are the rate coefficients of the reaction for ^{16}O- and ^{18}O-containing nitrate, respectively).

Flow cytometric analysis showed that heterotrophic bacterial abundance initially ranged from 3.5 x 10^4 to 8.1 x 10^4 cells mL^{-1}, and was lowest in the deepest samples (Fig. 5c). After a ~4-day lag period during which cell abundances decreased slightly, heterotrophic bacteria grew in all the unfiltered incubation bottles along with the decline in nitrate concentration, increasing 3- to 5-fold in abundance by day 20 to 28. *Prochlorococcus* initially comprised 5-8%, 2-7%, and 0.3-2% of the total cell abundance in the unfiltered 140 m, 160 m, and 200 m seawater samples, respectively, but declined to undetectable levels by day 5 in all cases. No other autotrophic (i.e., chlorophyll-containing) cells were detected in any of the experiments. For the filtered samples, particle concentrations were below the quantification limit of the flow cytometric method, and no increase in cell abundance was observed at any time during the experiments.

Discussion

Evidence for subsurface remineralization of nutrient-poor organic matter

A decrease in the concentration of O_2 without an increase in nitrate concentration has been observed previously in the thermocline of the Sargasso Sea (Ono et al., 2001) as well as the subtropical North Pacific (Abell et al., 2005). The high-resolution data from the profiling floats deployed near BATS and the BATS hydrographic data from the upper 400 m indicates an even greater spring-to-fall mismatch between O_2 consumption and nitrate (and phosphate) production than observed by Ono et al. (Fig. 6a-c; Table S2).

This discrepancy causes a decrease in preformed nitrate (and phosphate) concentration in the subsurface, indicating less than the expected amount of nitrate (and phosphate) production for the amount of O_2 consumed. The decrease in preformed nitrate from early spring to fall spans the water column from ~80 m to 300-400 m (Fig. 6a). This trend is mirrored in the BATS hydrographic data for both nitrate and phosphate when many years of observations are combined (Fig. 6b, c). Integrated from 80 and 300 m, preformed nitrate decreases by 0.88 mmol m^{-2} d^{-1} during the summer and early fall (Fig. S6). These data are consistent with the remineralization of organic matter below the BATS euphotic zone that is rich in carbon and poor in N and P relative to typical marine biomass; quantification is pursued below.

The DOC that accumulates in the summertime mixed layer at BATS is transported downward upon wintertime mixed layer deepening (Carlson et al. 1994; Hansell and Carlson, 2001; Goldberg et al., 2009). Its subsequent remineralization is expected to contribute to the O_2

consumption observed in the subsurface (Jenkins, 1982; Jenkins and Goldman, 1985; Stanley et al., 2012) and possibly also to the negative preformed nitrate signal. However, seasonal data from BATS show that elevated subsurface DOC concentrations resulting from wintertime mixed layer deepening decline rapidly thereafter (typically within a month; Carlson et al. 1994; Hansell and Carlson, 2001; Goldberg et al., 2009). The DOC decline does not overlap in time with the summertime decline in O_2 or the accumulation of negative preformed nitrate (and phosphate) in the subsurface (Fig. 3, Fig. 6), such that DOC remineralization cannot explain the O_2 or preformed nutrient changes. Moreover, the rapidity of the subsurface DOC concentrations decrease upon cessation of winter mixing begs the question of whether much of the DOC concentration decline may be due to dilution by lateral and vertical exchange in the thermocline and with underlying water as opposed to *in situ* remineralization. Finally, the existing data from BATS suggest that the rate of surface DOC production is too low to explain the summertime mixed layer DIC drawdown. Even if all of the summertime mixed layer DOC production (net accumulation of 10-12 µM; Carlson et al., 1994; Hansell and Carlson, 2001) derived from excess DIC fixation in the absence of nutrients, it could account for <50% of the observed DIC removal (26 µM over the spring-summer-early fall; Gruber et al. 2008).

Letscher et al. (2016) made the observation that lateral transport of nutrients and carbon at non-Redfieldian proportions helps to fuel NCP in the downwelling subtropical gyre regions, including the Sargasso Sea surrounding BATS. The seasonal signals in nitrate, O_2 and preformed nitrate that we report here should help to evaluate lateral transport on smaller scales than addressed by the global ocean model used by Letscher et al. (2016). Preliminarily, we note that our new nitrate data are consistent with prior data in indicating that nitrate is exceedingly scarce

in the surface mixed layer not only at BATS but in surrounding waters, including the waters to the west and the north (Hansell and Follows, 2008; Moore et al., 2013; Jenkins et al., 2015). This suggests that the calculations of Letscher et al. (2016) for the upper ~110-130 m, in isolation, may not help to explain NCP and DIC drawdown in the ~30 m deep summer mixed layer. Alternatively, high lateral N input to the BATS site may be occurring not as nitrate but rather as DON. While we cannot attest to viability of this possibility, we are not familiar with data arguing for substantial DON convergence in the surface mixed layer or euphotic zone of subtropical regions such as the BATS site (Knapp et al., 2005; Hansell and Follows, 2008; Letscher et al., 2013). Finally, consistent with our interpretation, Letscher et al. (2016) require non-Redfiedian organic matter export to approach the observed NCP at BATS. Accordingly, while lateral transport is likely critical to the resupply of nutrients to the upper waters of the subtropical gyres on the large scale, we expect that the non-Redfieldian composition of exported organic matter reconstructed here is fundamental to the high summertime NCP observed in the Sargasso Sea and similar environments (Martiny et al., 2013; Ono et al., 2001).

Evidence for nitrate assimilation by heterotrophic bacteria

The $\delta^{18}O$ of water column nitrate – Laboratory and field data indicate that nitrification produces nitrate with a $\delta^{18}O$ that is ~0-1‰ lower than that of the nitrate in the inflowing Antarctic Intermediate Water and Subantarctic Mode Water (at 600-1200 m) (Buchwald et al., 2012; Sigman et al., 2009). *In situ* nitrification accounts for a greater fraction of the nitrate at shallow depths in the Sargasso Sea (Palter et al., 2005), where it would work to lower the $\delta^{18}O$ of the nitrate pool (Rafter et al., 2013; Sigman et al., 2009), which should lead to an upward decrease in nitrate $\delta^{18}O$ into the shallow subsurface as more regenerated, low-$\delta^{18}O$ nitrate is added. Instead,

nitrate $\delta^{18}O$ is observed to increase upward beginning at 400-500 m (Fig. 4a), to values ~0.5‰ higher than global deep nitrate, which is inconsistent with *in situ* nitrification acting alone.

A nitrate-consuming process such as nitrate assimilation is required to explain this $\delta^{18}O$ rise. Nitrate assimilation by phytoplankton at the base of the euphotic zone at BATS is one possibility. However, nitrate assimilation is likely limited to the upper ~120 m of the BATS water column, and late winter deep mixing at BATS is not well-suited to propagate the signal to depths greater than ~200-250 m, as any assimilation signal is held in a very low concentration of nitrate near the base of the euphotic zone (Fig. 2b; Fig. 4c). As a related alternative, it is possible that the subsurface $\delta^{18}O$ rise is a remnant geochemical signal of nitrate assimilation by phytoplankton in higher-latitude surface waters that has been subducted into the BATS thermocline. There are shallow subsurface waters in the subpolar North Atlantic with a significantly elevated nitrate $\delta^{18}O$ (Marconi, 2017); however, it is not yet clear if this high latitude signature can propagate and persist into the thermocline of the subtropical gyre.

While the year-round subsurface $\delta^{18}O$ elevation is potentially due to phytoplankton nitrate assimilation, near BATS or further afield, the summertime increase in nitrate $\delta^{18}O$ observed at 200-400 m does not fit with the same explanation. Within the 200-400 m depth interval, nitrate $\delta^{18}O$ increases from an average of 1.6‰ in the late spring to 2.0‰ in the summer and fall (Fig. 4a). The seasonal rise in $\delta^{18}O$ has the wrong sense to be explained by downward mixing or wintertime subduction at higher latitudes of the signal of phytoplankton nitrate assimilation, as this would drive a higher subsurface nitrate $\delta^{18}O$ in the winter and spring. Moreover, ventilation of the thermocline from higher latitudes occurs over multiple years (Jenkins, 1998), masking

seasonal ventilation changes. Similarly, mode water formation and thermocline ventilation peak in the winter (Kelly and Dong, 2013), such that any injection of nitrate with a high $\delta^{18}O$ occurs in the wrong season to explain the observed seasonality.

As with phytoplankton, heterotrophic bacteria are known to fractionate the O (and N) isotopes of nitrate during nitrate assimilation (Granger et al., 2010). Indeed, our dark seawater incubations show this effect (Fig. 5b; Fig. S5c-d). Nitrate assimilation by heterotrophic bacteria degrading N-poor organic matter, occurring *in situ*, may thus explain the spring-to-summer increase in nitrate $\delta^{18}O$ between 400 m and 200 m depth at BATS. If the spring-to-fall decrease in preformed nitrate and phosphate observed at BATS signals the remineralization of nutrient-poor organic matter, it is within this time window that sporadic events of heterotrophic bacterial nitrate assimilation should occur, and these events would work to raise the $\delta^{18}O$ of the nitrate, as we observe in the BATS subsurface.

Importantly, the $\delta^{18}O$ elevation in nitrate can occur without net nitrate drawdown. This can happen if the events of assimilation are alternated with the subsequent remineralization of the heterotrophic biomass and the occurrence of nitrification through the summer, whenever organic matter flux to the subsurface has an adequately low C/N to lead to net metabolic ammonium production. In this context, the lack of a summertime rise in nitrate $\delta^{15}N$ at 200-400 m (Fig. 4b) is consistent with *in situ* nitrate assimilation, as the re-nitrification of the assimilated nitrate would yield no net $\delta^{15}N$ change. Moreover, the N isotope effect of heterotrophic nitrate assimilation may be lower than its O isotope effect (Granger et al., 2010), such that the N isotopic imprint of this process may be more difficult to detect. Finally, it is possible that any

weak δ^{15}N rise due to heterotrophic nitrate assimilation is overprinted by the export and remineralization of particularly low-δ^{15}N N from N recycling (as well as N fixation and possibly atmospheric N deposition) in the euphotic zone during the summer and fall (Fawcett et al., 2014; Gobel et al., 2013; Knapp et al., 2010; Orcutt et al., 2001).

The float data suggest that approximately a quarter of the expected nitrate production is "missing" at 200 m (~0.6 µM; Table S2; Fig. 3c-d). Using the mean isotope effect for bacterial nitrate assimilation estimated from the dark incubation experiments ($^{18}\varepsilon$ = 3.5‰ ± 0.3‰; Fig. 5b), we calculate that the 0.4‰ spring-to-fall nitrate δ^{18}O rise at 200 m requires the consumption of 10 ± 2% of the ambient nitrate pool, or 0.26 ± 0.05 µM (*SI 1.3*). This amounts to ~40% of the "missing" nitrate, the remainder presumably being explained by the O_2 consumption associated with the respiration of N-poor organic matter. One implication is that the net C/N supply ratio to the heterotrophic bacterial community, calculated by averaging the float data from 130 m and 200 m, could be as high as 39 ± 17 (*SI 1.3*). While highly uncertain, a C/N ratio of this order is consistent with N-limitation of the bacteria remineralizing carbon-rich organic matter (Kirchman, 1994; Fagerbakke et al., 1996; Del Giorgio and Cole, 1998, and references therein; Church, 2008), which then mechanistically justifies their assimilation of nitrate.

Shallower than 175 m, the sense of the seasonal δ^{18}O change appears to reverse, although the seasonal distinction is statistically much weaker than between 200 and 400 m depth. We explain these observations as the result of phytoplankton nitrate assimilation within the euphotic zone, which yields substantial δ^{18}O elevation (>5‰ above ~120 m; Fig. 4a), and the downward transport of this nitrate δ^{18}O elevation by mixing, which occurs dominantly in the wintertime

when the mixed layer deepens. We reason that without this large wintertime signal from vertical mixing, a spring-to-fall $\delta^{18}O$ rise would also develop in the 100-200 m depth interval, coincident with the decrease in preformed nitrate.

Incubation of subsurface seawater – The incubation experiments were not originally designed to detect subsurface remineralization of low-N organic matter. Nevertheless, they provide an unexpected complement to the nitrate $\delta^{18}O$ evidence for *in situ* heterotrophic bacterial nitrate assimilation in the BATS thermocline. It is well-known that some marine heterotrophic bacteria can assimilate nitrate (Allen et al., 2001). Given the observed nitrate drawdown and nitrate $\delta^{18}O$ rise during the experiments (Fig. 5a, b), the low background of particulate organic N in the Sargasso Sea subsurface seawater, the recalcitrant nature of dissolved organic N in the subsurface at BATS (Hansell and Carlson, 2001; Knapp et al., 2005), and the extremely low ambient ammonium concentrations at the depths from which incubation seawater was collected (Fawcett et al., 2014; Lipschultz, 2001; Treibergs et al., 2014), the evidence for nitrate consumption and the increase in heterotrophic bacteria in the incubations is remarkably consistent with an innate capacity for heterotrophic nitrate assimilation in the shallow subsurface at BATS. Initial bacterial abundances were slightly lower than is typically observed in the BATS subsurface (4-8 x 10^4 cells mL^{-1} vs. 1-4 x 10^5 cells mL^{-1}; Fig. 5c; Carlson and Ducklow, 1996), likely due to the seawater samples having been frozen for ~2 years. We are nonetheless confident that the heterotrophic bacteria that grew in the unfiltered seawater were present at the time of its collection and are not the result of experimental contamination. The simplest pieces of support for this assertion are that (1) no bacterial growth was observed in the filtered samples and (2) growth was observed in every unfiltered sample, not only a subset of them. In addition, the flow

cytometry cytograms show the growth of bacterial populations in the unfiltered samples that resemble native populations from the Sargasso Sea and other oligotrophic regions (Cavender-Bares et al., 2001; Zubkov et al., 2004; 2007).

The heterotrophic nitrate assimilation rates observed in the incubations (averaging 0.04 µM d^{-1}) are too rapid to apply within the BATS thermocline; the entire 3.5 µM of "missing" nitrate between 100-200 m (Fig. 3) could be accounted for by nitrate assimilation alone in a matter of months, without even considering the effect of O_2 consumption without nitrate production (i.e., the subsurface decrease in preformed nitrate; Fig. 2c; Fig. 6a,b). Seawater incubations are vulnerable to "bottle effects" that can lead to unrepresentative rates, but such incubations are nevertheless useful for identifying and characterizing processes (e.g., Kirchman et al., 1991; Carlson and Ducklow, 1996; Quay et al., 2010). In this vein, the key lessons from heterotrophic nitrate assimilation in the incubations are (1) that the N content of the organic matter available for remineralization in these subsurface waters is so low that heterotrophic bacteria are limited by N, a situation that would not arise if the remineralization were dominantly of Redfieldian marine biomass or its degradation products, and (2) that the resident bacteria readily turn to nitrate assimilation to grow on this N-poor organic matter.

POM cannot have been the main C source to the heterotrophic bacteria in the incubations given that its concentration in the Sargasso Sea thermocline is <1 µM C and its C/N ratio is typically <8 (Martiny et al., 2013). Rather, the concentration, C/N, and apparent bioavailability of DOM at 140-200 m depth at BATS are appropriate to explain the heterotrophic bacterial growth and nitrate assimilation in the incubations, contingent on the bacterial growth efficiency (BGE; *SI*

1.4).

Assuming a mean bacterial C/N ratio of 5 (Gundersen et al., 2002) and a BGE of 14-49% (Carlson and Ducklow, 1996; Pedler et al., 2014), we calculate that the observed bacterial nitrate drawdown requires an average of 11-38 µM DOC. If we disregard the August 200 m dark treatment in which the quantity of nitrate drawdown was more than double that of any other treatment, this demand decreases to an average of 9-30 µM DOC. In the 100-250 m depth interval at BATS, the DOC concentration varies seasonally between 50 µM (during summer and autumn) and 65 µM (during late winter deep mixing) (Carlson et al., 1994). Of this, approximately 10-20 µM is considered biologically available on the time-scale of hours to months (Hansell, 2013; Zweifel et al., 1993). This range is roughly sufficient but on the low end to explain the bulk of the nitrate consumption in our incubations unless BGE was consistently high. It is possible that the mean bacterial C/N requirement over the course of our experiments may have been less than 5. In a series of batch culture experiments, Vrede et al. (2002) found that under conditions of C limitation and inorganic N availability, bacterial C/N declined (to as low as 3.6). As with a higher BGE, a lower C/N would decrease the DOC requirement suggested by the extent of bacterial nitrate consumption. We cannot rule out, however, that the bacterial C/N requirement could have been >5, as under conditions of N limitation, bacteria have been shown to alter their C/N ratios (4.9 – 11; Vrede et al., 2002); if this were the case in our incubations, it would imply a higher DOC requirement. Another possibility is that the labile fraction of the DOC pool in the subsurface at BATS may be greater than 10-20 µM; below we describe several arguments for why this may be the case.

First, work on the role of DOC in the BATS carbon budget has focused on the ability of deep mixing and thermocline ventilation to carry DOC produced in the euphotic zone into the shallow subsurface, followed by net consumption of this pool. If this is the only process at work, however, the stability of the deep DOC concentration through summer and fall (Carlson et al. 1994; Hansell and Carlson 2001) implies that there is little net respiration over this period, with all net respiration occurring in the spring months immediately after deep mixing. Yet the incubations suggest that the DOC pool is reactive, and no less reactive in August than in February immediately following a deep mixing event. The implication is that DOC is being respired continuously in the shallow subsurface, such that DOC must also be continuously supplied. There is not an adequately vigorous circulation to carry N-poor DOC to these depths from the euphotic zone in summer (Carlson et al., 1994). Rather, the solubilization of sinking carbon-rich organic matter in the summertime subsurface could both fuel the observed O_2 drawdown and explain the greater inferred lability of the DOC in our incubations than is suggested by the decrease in DOC concentration over the seasons at BATS or with increasing ventilation age.

Second, in the presence of adequate nitrate and given sufficient time, heterotrophic bacteria may consume some of the "semi-refractory" DOC pool once the labile DOC has been exhausted. A number of studies suggest that surplus inorganic nutrients stimulate bacterial DOC consumption (e.g., Kroer, 1993; Zweifel et al., 1993; Letscher et al. 2015), although others conclude that inorganic nutrients do not enhance DOC utilization (e.g., Carlson and Ducklow, 1996; Kirchman, 1990). Such experiments are typically conducted on the time-scale of days, whereas our incubations lasted for four weeks, which perhaps allowed the consumption of less labile

DOC to begin while nitrate concentrations were still high (Del Giorgio and Cole, 1998). This is supported by the findings of the year-long study by Pedler et al. (2014), who observed a diverse bacterial assemblage continue to use semi-refractory DOC in seawater for the entirety of the experiment once the more labile pool had been consumed. In addition, Letscher et al. (2015) recently showed that surface ocean DOC is significantly more recalcitrant to remineralization by the surface layer microbial community than it is to degradation by heterotrophic bacteria occupying the upper mesopelagic (i.e., the depth range from which our samples were collected). They also observed the concomitant consumption of nitrate by the subsurface microbial community during its remineralization of surface DOC (Letscher et al. 2015).

Above, we have argued that the bioavailability of the *in situ* subsurface DOM pool at BATS could explain the results of our incubations. However, we cannot completely rule out the possibility that some DOC leached out of the HDPE bottles into the incubation seawater, that there was some bacterial degradation of the HDPE bottles that resulted in DOC production (Restrepo-Florez et al. 2014), or that freezing and thawing of sample seawater rendered the *in situ* DOC pool more available to the bacteria. Samples for bulk DOC concentration analysis are typically collected in glass bottles to ensure that potential contamination is avoided (Sharp et al., 1995). However, it has been shown that polyethylene bottles do not introduce significant DOC contamination to seawater left at room temperature for three months, provided the bottles are soaked in 10% HCl and rinsed with sample prior to filling (Kepkay and Wells, 1992), as our sample bottles were (see Materials and Methods). Moreover, to explain our observations, not only would a significant quantity of DOC need to leach out of the HDPE bottles, but it would need to be labile DOC, which is highly unlikely if sourced from the HDPE itself. Bacterial

degradation of the HDPE bottles themselves is also highly unlikely. The only available data show losses of 0-1.6% of HDPE exposed to marine bacteria for months (Lobelle and Cunliffe, 2011; Artham et al., 2009). Moreover, it appears that very few strains of bacteria can actually degrade HDPE, and there is no evidence that those bacteria that do degrade HDPE can actually use it as a carbon source (Restrepo-Florez et al., 2014). Finally, there is no consensus as to the effect of freezing on the lability of DOC, with studies reporting both an increase and a decrease in DOM aromaticity after freezing (Chen et al., 2016; Peacock et al., 2015). Thus, while we cannot rule out alteration of some fraction of the DOC pool due to sample freezing, this could just as easily have decreased its lability as increased it. We conclude that our interpretation of the data is far more plausible than that of marine bacteria consuming DOC sourced from contamination, HDPE degradation or cryo-alteration, especially on the time scale of days and weeks and at the level of the growth response observed in the bottles.

Regardless of the source of the DOC supporting nitrate drawdown in the incubations, sustained heterotrophic nitrate assimilation at depth in the BATS water column is unlikely because heterotrophic organisms respire most of the carbon in their diet, leaving N in excess of requirements for growth even when the diet has a higher C/N ratio than their own biomass. However, at times of low sinking particle flux and minimal zooplankton migration (e.g., during the mid-summer), heterotrophic bacteria in the water column relying largely on an extremely nutrient-poor carbon source may turn to nitrate assimilation for brief periods and/or at low levels, as suggested by our data.

Implications for the upper ocean carbon budget at BATS – Above, we present three lines of

evidence for the remineralization of nutrient-poor (carbon-rich) organic matter in the BATS subsurface. Below, we show that the rate of remineralization derived from the float data is adequately high that, if this organic matter originates in the mixed layer, it can account for the high NCP at BATS.

The profiling float data indicate that nitrate is regenerated at <10% of the expected rate at 130 m and ~75% of the expected rate at 200 m (Fig. 3a-d). We interpret these changes with depth to derive from a changing ratio of remineralization of GLOM and "normal" (Redfieldian) sinking organic matter, with the lower rate of nitrate regeneration at 130 m indicating the greater importance of GLOM in the shallower remineralization depths. Making an end-member assumption that the organic matter being remineralized in the BATS subsurface (i.e., nutrient-free GLOM) is essentially pure carbohydrate (as is true of TEP) with a remineralization ratio of C to O_2 of 1 to 1 ($CH_2O + O_2 \leftrightarrow CO_2 + H_2O$), the decline in preformed nitrate integrated from 80 m to 300 m equates to a subsurface remineralization rate of 3.0 mol C m^{-2} yr^{-1} (i.e., -0.88 × -150/16 × 1/1 × 365 × 1/1000). If, instead, the remineralization ratio of C to O_2 of Redfieldian marine biomass is used, the decline in preformed nitrate equates to a subsurface remineralization rate of 2.1 mol C m^{-2} yr^{-1} (i.e., -0.88 × -150/16 × 106/150 × 365 × 1/1000). Either case could account for essentially all of the NCP at BATS inferred from euphotic zone O_2 production and of the carbon export required to explain the DIC drawdown from the surface mixed layer (Table 1). A smaller amount of subsurface GLOM remineralization would be implied by the data if it were associated with heterotrophic nitrate assimilation (which our nitrate $\delta^{18}O$ data suggest may explain 0.26 μM (~40%) of the seasonal preformed nitrate decline). However, even if the rate of N-poor GLOM export is 60% of that calculated above (1.3-1.8 mol C m^{-2} yr^{-1}, depending on the

stoichiometry used), when added to previously measured POC and DOC export fluxes, it would approximately match O_2 measurements of NCP and explain most of the summer mixed layer DIC drawdown in the Sargasso Sea.

Implications for subtropical ocean NCP – GLOM export out of the euphotic zone of the subtropical gyres would account for the high rates of NCP measured in these regions. If GLOM is proportionally more important to export production in these regions than in high latitude and upwelling systems, its export weakens the NCP gradients measured across the global ocean, helping to explain the observed uniformity of NCP (Emerson, 2014 and references therein). However, the shallow remineralization of GLOM has an important consequence with regard to its role in the biological pump (Koeve, 2005). A large fraction of the excess CO_2 resulting from subsurface remineralization of GLOM would have the opportunity to escape back to the atmosphere upon wintertime deep mixing (to ~250-300 m depth near BATS; Lomas et al., 2013), making it less important in ocean CO_2 storage (Fig. 1). In addition, because nutrient-poor GLOM is likely metabolized dominantly by bacteria, its production and sinking is poorly suited to fuel the growth of zooplankton or the upper trophic levels that rely on them, helping to explain the infertility of the subtropical gyres with regard to fisheries. Our hypothesis of a form of carbon export ill-suited to reach the deep ocean and its sediments can also explain why deep sediment trap and sediment respiration-based reconstructions suggest much stronger spatial gradients (e.g., between the subtropical gyres and upwelling regions) than are suggested by surface ocean NCP measurements (Honjo et al., 2008). At the same time, the hypothesis requires that shallow sediment traps are obfuscating our large-scale view of the ocean by failing to capture significant fluxes of ephemeral, less physically robust forms of organic matter.

Conclusions – After decades of study, the export of organic carbon from the upper subtropical North Atlantic near Bermuda remains enigmatic, with regard to the nutrients that fuel it, its biological and geochemical identity, and its detection in the interior. Having summarized these unknowns, we propose here that there is an as-yet underappreciated contribution to export by a form of low-nutrient, sinking organic carbon. In our proposal, gel-like organic matter (GLOM) rich in carbon but poor in N and P, akin to TEP, is produced by phytoplankton under nutrient limitation, and a portion sinks into the shallow subsurface, where it is respired by heterotrophic bacteria (Fig. 1). As a source of preliminary support, we have presented evidence for the subsurface remineralization of carbon-rich organic matter exported from the euphotic zone at BATS, and have shown that the calculated rate of this carbon-rich export is adequate to explain the observed drawdown of DIC in the summertime mixed layer.

Our proposal helps to explain a range of otherwise challenging observations from the Sargasso Sea near Bermuda. In particular, the production of GLOM in surface waters, which requires a minimal supply of nutrients, can explain the drawdown of mixed layer DIC and production of euphotic zone O_2 at BATS that have long been recognized to be unsupported by an observed source of nutrients. Moreover, because of the proposed physical characteristics of GLOM, its export can explain the longstanding failure to account for the measured NCP of the mixed layer and euphotic zone with sediment trap-based measurements of carbon export.

There is much to be done to test the GLOM hypothesis and, if it is correct, understand its implications. As one important avenue, our incubation experiments should be repeated to include

measurements of DOC, POC, their chemical compositions and other properties. Another approach could be the measurement of ^{14}C-labeled DOC excreted over the course of ^{14}C incubation-based measurements of NPP, although we note that adequately interrogating the GLOM hypothesis requires that such data be collected from many experiments conducted over different seasons. It is likely (and implied by our incubations) that the remineralization of GLOM in the subsurface at least partly involves its breakdown to DOC prior to oxidation to CO_2. If so, higher DOC remineralization rates are required than if the only source of DOC to the subsurface is by circulation transport as dissolved (not sinking) material (Carlson et al., 1994). Accordingly, studies of subsurface DOM remineralization will help in assessing the importance of GLOM. Furthermore, if GLOM (such as TEP) is important in NCP, investigations will be required to understand the mechanisms and sensitivities of production, survival, and export of this material into the ocean interior. Such studies would have the benefit of the tools and findings of prior work on TEP and similar materials (e.g., Azetsu-Scott and Passow, 2004; Beauvais et al., 2003; Chin et al., 1998; Cisternas-Novoa et al., 2015; Corzo et al., 2000; Engel and Passow, 2001; Engel et al., 2004; Kumar et al., 1998; Mari et al., 2017; Passow, 2002, Passow et al., 2001), but additional methods for detecting and quantifying these materials may be needed.

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Author contributions: Float preparation, deployment, and data transmission were carried out by SCR's laboratory, and the initial float data analysis was performed by KSJ. SEF collected samples at sea, carried out the incubation experiments, and analyzed nitrate concentration and isotope data in DMS's laboratory. NVO performed the flow cytometry analyses. All authors

contributed to the completion of the manuscript.

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Table and figure captions

Table 1. Compilation of geochemical estimates of NCP at BATS.

Fig. 1. The production and fate of typical marine organic matter compared to that proposed for nutrient-poor GLOM. a) In the sunlit upper ocean (the euphotic zone), phytoplankton growth ("phyto") is fueled by the upward supply of subsurface nitrate (NO_3^-). This growth fixes atmospheric CO_2 dissolved in surface waters into biomass with a C:N ratio of 106:16. This organic matter is transported into the subsurface through its consumption and repacking as fecal pellets by zooplankton and the higher trophic levels that rely on them (e.g., fish), and by aggregation and passive sinking. Here, the shaded grey area represents the idealized remineralization-driven decline in the flux of sinking organic matter with depth in the water column (i.e., the "Martin curve"). The decrease in organic matter flux below the euphotic zone is due largely to its remineralization by heterotrophic bacteria (shown as dark grey cylinders), which consumes oxygen (O_2) and produces CO_2 and nitrate in approximate ratios of O_2:C:N of -150:106:16. Much of the CO_2 produced above the base of the winter mixed layer will escape back to the atmosphere during deep winter mixing, whereas excess CO_2 deriving from remineralization below the winter mixed layer will be retained in the deep ocean on 100-1000 year timescales. A small fraction of the organic matter produced in the surface escapes remineralization in the water column and is buried in deep ocean sediments, resulting in the geologic sequestration of carbon, contributing to the atmospheric reservoir of O_2 and providing an indicator in the sedimentary record. b) Under conditions of nutrient limitation that are characteristic of the summer and fall at BATS, phytoplankton produce carbohydrates ("CH_2O") in surface waters that assemble to form nutrient-poor GLOM (i.e., with a C:N >> 106:16 and C:P

>> 106:1). A portion of this GLOM sinks slowly into the shallow subsurface where it is respired by heterotrophic bacteria, resulting in the consumption of O_2 without the production of the quantity of nitrate expected from the decomposition of typical marine biomass. During times when GLOM export dominates the flux of sinking organic matter, heterotrophic bacteria degrading GLOM may consume nitrate to satisfy their N requirements. Because GLOM is remineralized in the shallow subsurface, much of the excess CO_2 produced during its decomposition will have the opportunity to escape back to the atmosphere upon wintertime deep mixing rather than being stored in the deep ocean. Similarly, GLOM will not contribute to the flux of organic carbon to the seabed. Finally, we expect GLOM to be dominantly metabolized by heterotrophic bacteria such that it will contribute little to fueling higher trophic levels. Panels a and b should be taken as end-members, with biomass-derived sinking organic matter and GLOM often associated with one another in the sinking flux.

Fig. 2. Profiling float-derived concentrations (0-300 m) from 2010-2013 of a) oxygen; b) nitrate; and c) preformed nitrate, where preformed nitrate = $[NO_3^-] - 16/150 \times [(O_2)_{Sol} - (O_2)]$.

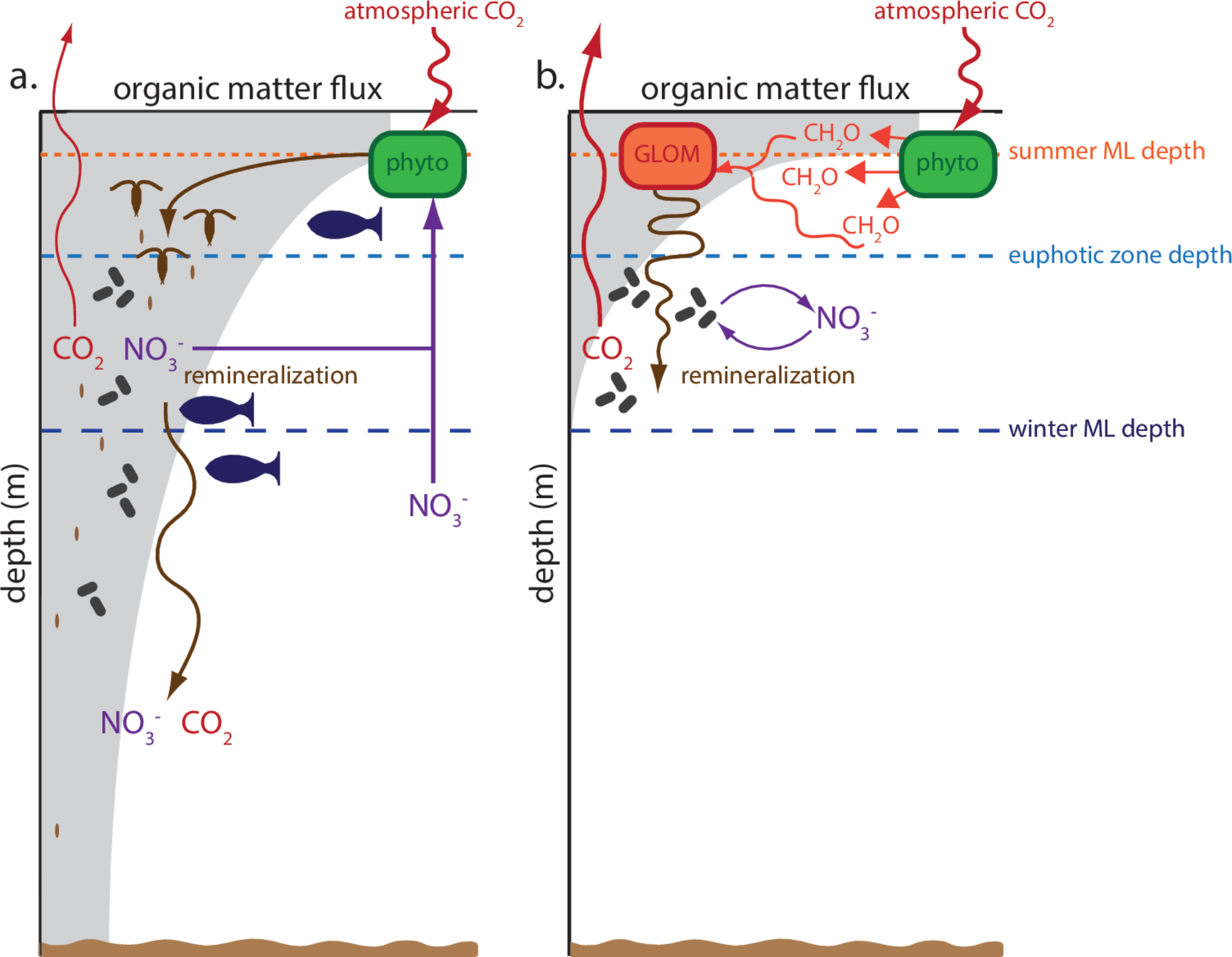
Fig. 3. Profiling float-derived concentrations of a) oxygen at 130 m; b) nitrate at 130 m; c) oxygen at 200 m; and d) nitrate at 200 m.

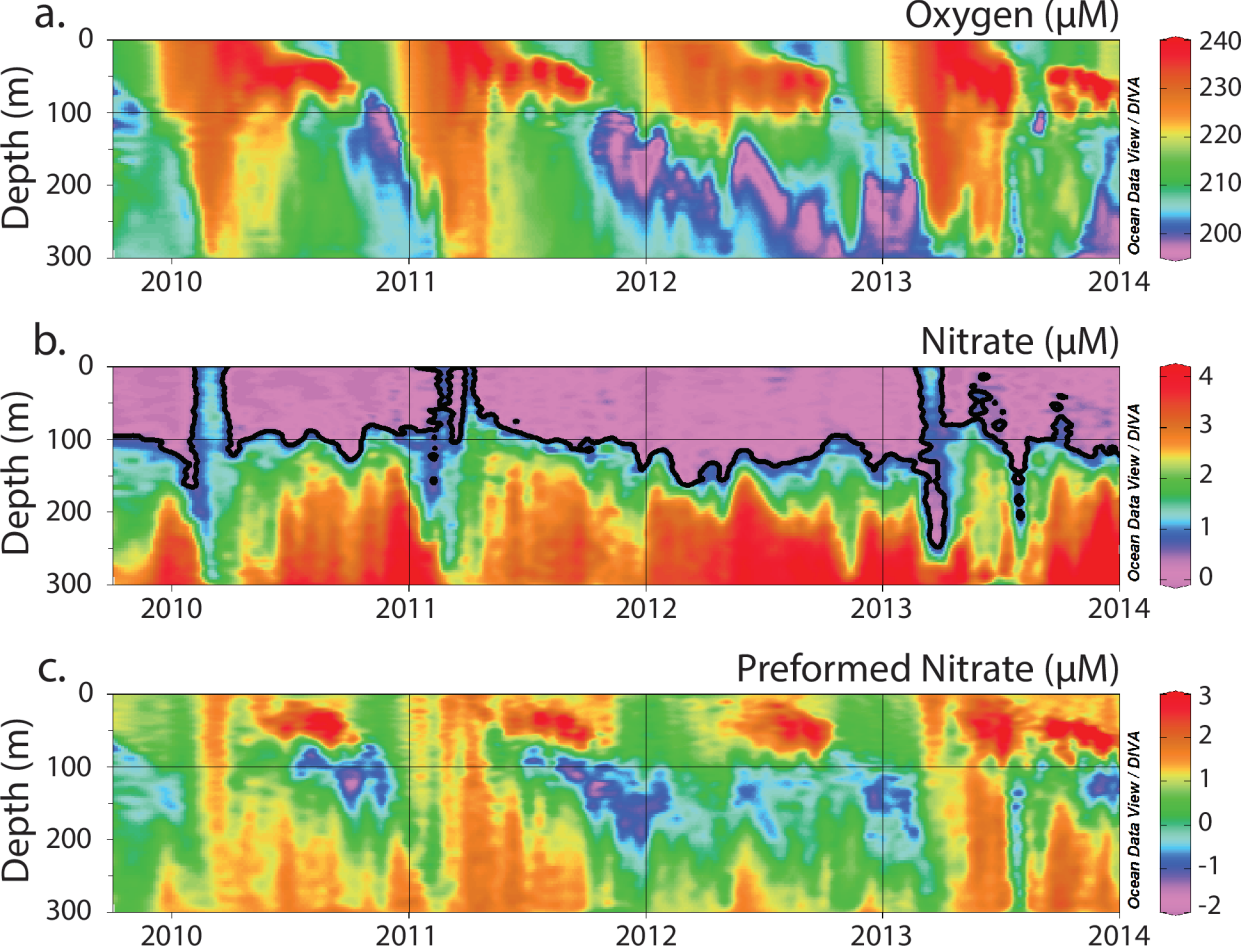
Fig. 4. Depth profiles of a) nitrate $\delta^{18}O$ and b) nitrate concentration at BATS, averaged for the late winter/early spring (February to April, 4 profiles) and summer/fall (June to December, 12 profiles). Note that in panel a, the 1‰ to 6‰ range of the x-axis has been expanded (left of the vertical dashed line). Error bars indicate ± 1 S.D. about the mean at each depth. Nitrate concentration and isotope data for individual BATS cruises averaged here are reported in

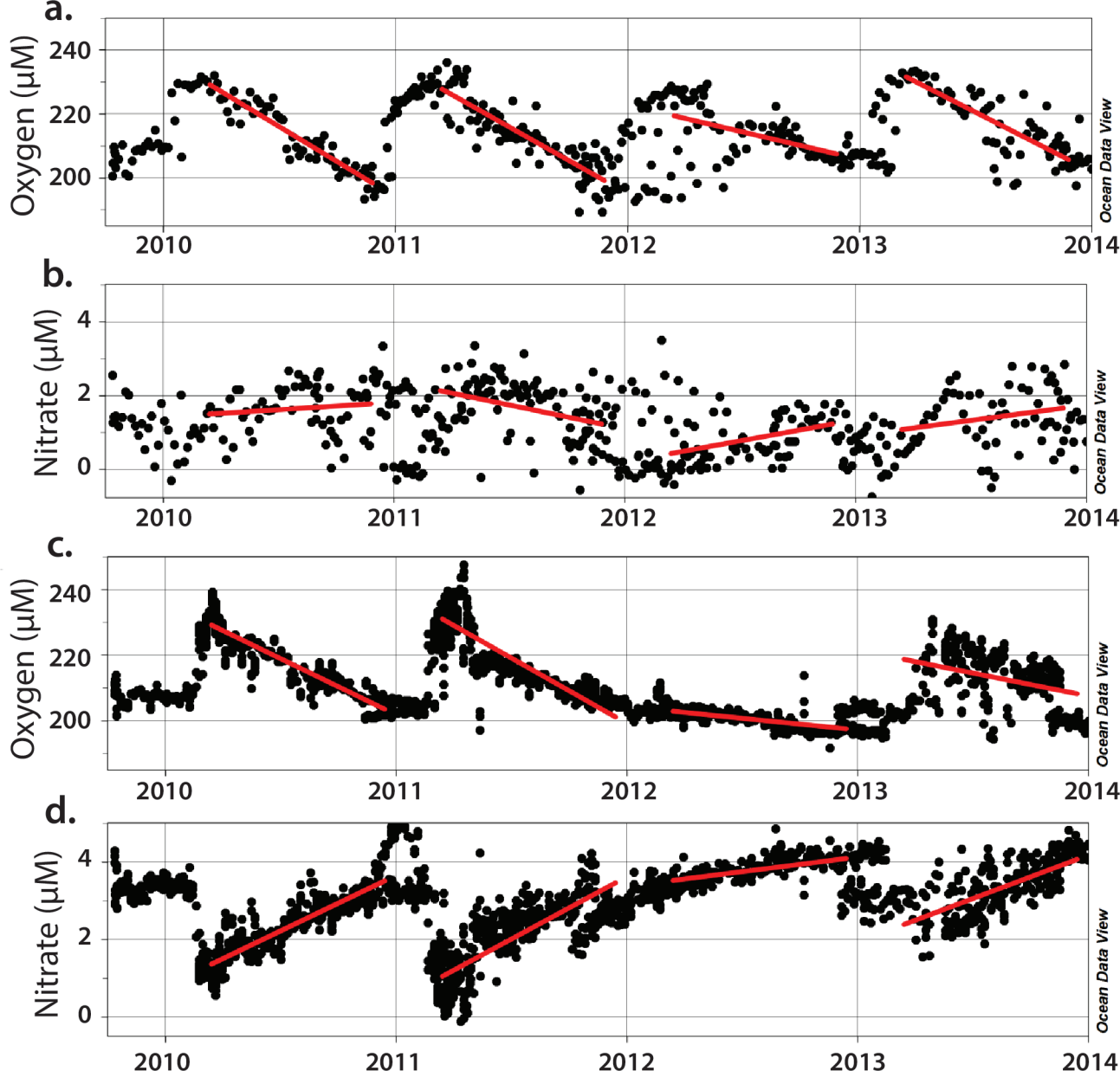
Fawcett et al. (2015).

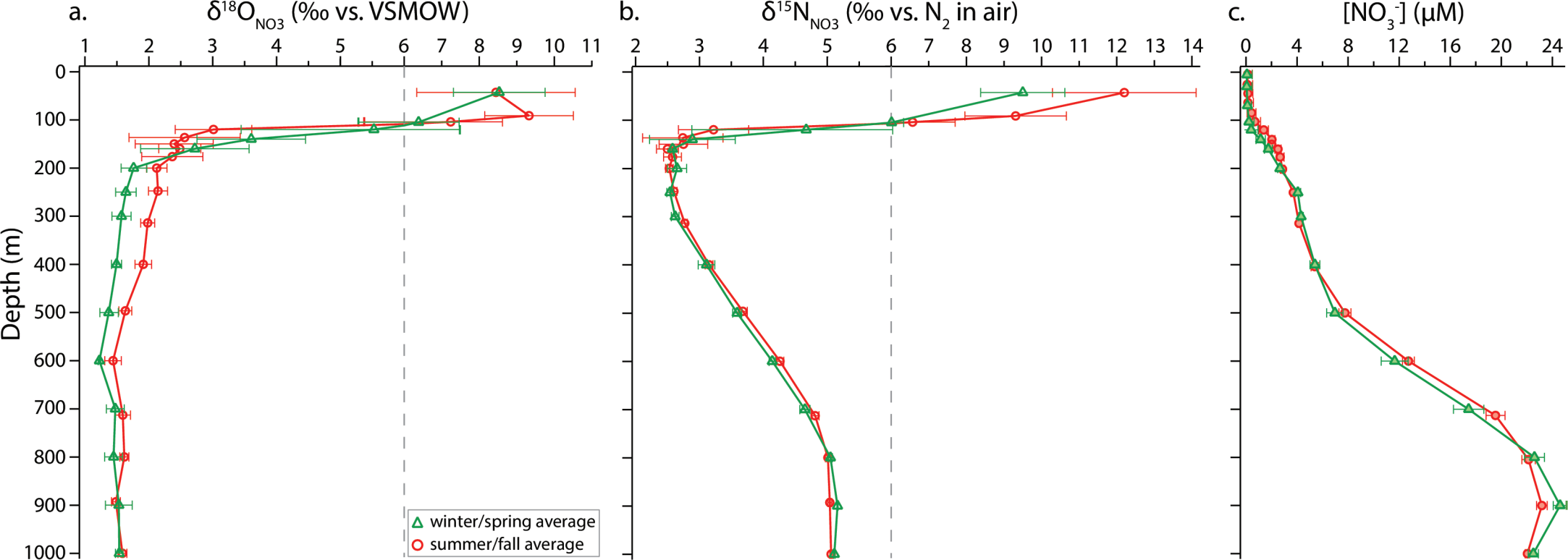
Fig. 5. Results of incubations of shallow subsurface water from the Sargasso Sea. a) Nitrate concentration over the four-week dark incubation experiments in the unfiltered treatments (filled symbols), with the corresponding filtered treatments indicated by the crosses and dashed lines. b) Nitrate $\delta^{18}O$ in the dark experiments plotted in Rayleigh space, with the slope of the linear regression providing an estimate of the average oxygen isotope effect ($^{18}\varepsilon$) of heterotrophic bacterial nitrate assimilation. Error bars indicate ± 1 S.D. of replicate (n = 2-3) measurements. c) Flow cytometry counts showing the abundance of heterotrophic bacteria in the unfiltered incubation bottles during the experiment. No growth was detected in the filtered samples. For nitrate concentration and oxygen isotope data from the light experiments, see Fig. S5.

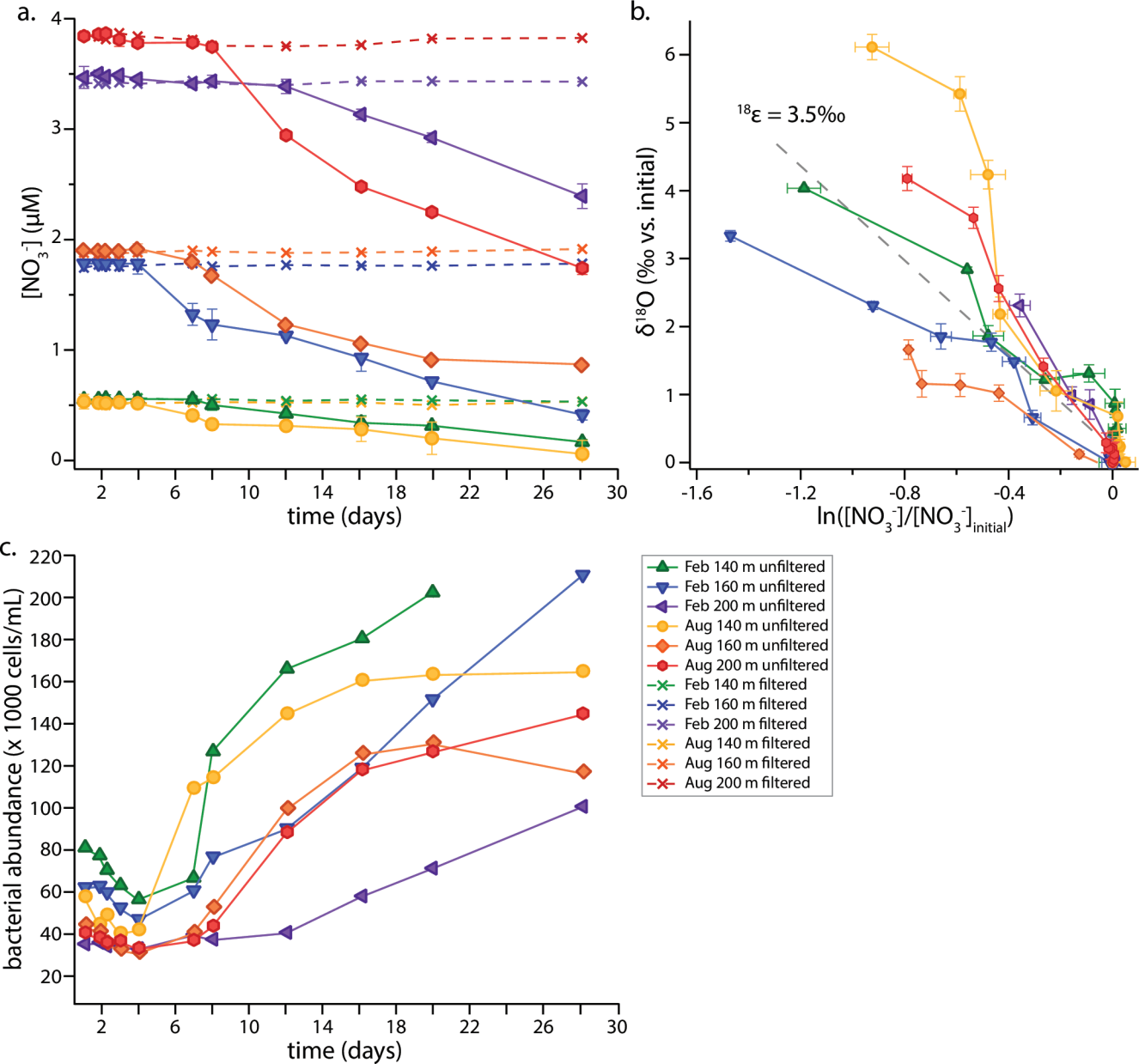
Fig. 6. a) Average preformed nitrate concentration in the upper 400 m measured by the profiling float array from 2010-2013; annual average preformed b) nitrate and c) phosphate concentrations in the upper 400 m derived from measurements at BATS from 1988-2008 (http://bats.bios.edu). Contours are included to emphasize the similarity between the float data and BATS data.


a.
organic matter flux
atmospheric CO_2
phyto
CO_2
NO_3^-
remineralization
NO_3^-
NO_3^-
CO_2
depth (m)
b.
organic matter flux
atmospheric CO_2
GLOM
CH_2O
CH_2O
CH_2O
phyto
summer ML depth
euphotic zone depth
NO_3^-
CO_2
remineralization
winter ML depth
depth (m)


a.
Oxygen (µM)
Depth (m)
0
100
200
300
2010
2011
2012
2013
2014
240
230
220
210
200
Ocean Data View / DIVA
b.
Nitrate (µM)
Depth (m)
0
100
200
300
2010
2011
2012
2013
2014
4
3
2
1
0
Ocean Data View / DIVA
c.
Preformed Nitrate (µM)
Depth (m)
0
100
200
300
2010
2011
2012
2013
2014
3
2
1
0
-1
-2
Ocean Data View / DIVA


a.
Oxygen (µM)
240
220
200
2010
2011
2012
2013
2014
Ocean Data View
b.
Nitrate (µM)
4
2
0
2010
2011
2012
2013
2014
Ocean Data View
c.
Oxygen (µM)
240
220
200
2010
2011
2012
2013
2014
Ocean Data View
d.
Nitrate (µM)
4
2
0
2010
2011
2012
2013
2014
Ocean Data View


a.
δ18O_NO3 (‰ vs. VSMOW)
b.
δ15N_NO3 (‰ vs. N2 in air)
c.
[NO3-] (μM)
Depth (m)
winter/spring average
summer/fall average


a.
[NO3-] (μM)
time (days)
b.
18ε = 3.5‰
δ18O (‰ vs. initial)
ln([NO3-]/[NO3-]initial)
c.
bacterial abundance (x 1000 cells/mL)
time (days)
Feb 140 m unfiltered
Feb 160 m unfiltered
Feb 200 m unfiltered
Aug 140 m unfiltered
Aug 160 m unfiltered
Aug 200 m unfiltered
Feb 140 m filtered
Feb 160 m filtered
Feb 200 m filtered
Aug 140 m filtered
Aug 160 m filtered
Aug 200 m filtered

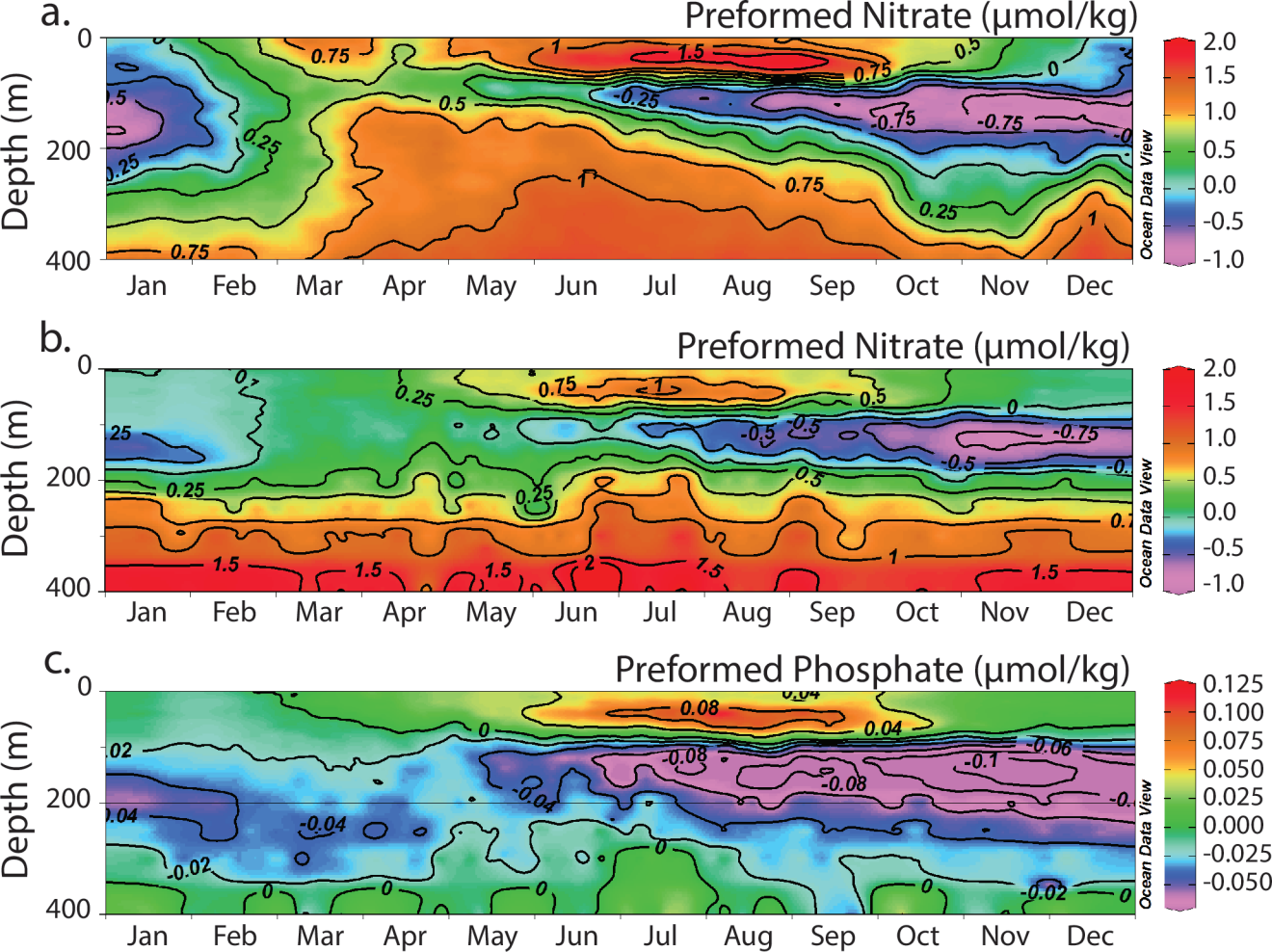

a.
Preformed Nitrate (µmol/kg)
b.
Preformed Nitrate (µmol/kg)
c.
Preformed Phosphate (µmol/kg)
Depth (m)
0
200
400
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Ocean Data View
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
0.125
0.100
0.075
0.050
0.025
0.000
-0.025
-0.050

Table 1: Geochemical estimates of NCP from BATS

NCP (mol C m^{-2} yr^{-1})	Geochemical technique	Reference
3.6 ± 0.7	Oxygen utilization rate (OUR) using ^{3}He ventilation	Jenkins, 1980
3.4	O_2 mass balance	Jenkins, 1982
3.3-4.8	Oxygen utilization rate (OUR) using seasonal drawdown in O_2 stock	Jenkins and Goldman, 1985
3.6 ± 0.6	Euphotic zone O_2 production	Spitzer and Jenkins, 1989
3.2[a]	Seasonal (April to December) drawdown of DIC and DOC (integrated from 0-150 m)	Michaels et al, 1994
2.3 ± 0.9[b]	Carbon isotope mass balance (mixed layer DIC)	Gruber et al., 1998
2.5 ± 0.5	Oxygen utilization rate (OUR) using ^{3}He ventilation	Jenkins, 1998
2.1-2.5[c]	Oxygen utilization rate (OUR) using seasonal drawdown in O_2 stock (100-250 m)	Hansell and Carlson, 2001
2.6-3.5	Summertime mixed layer DIC drawdown estimated from global DIC, pCO_2, and alkalinity	Lee, 2001
1.5 ± 0.4	Modeled remineralization rate (100-250 m) using mean annual DIC cycle	Ono et al., 2001
5.0 ± 1.0[d]	Oxygen utilization rate (OUR) using drawdown in O_2 stock (100-2800 m)	Jenkins and Doney, 2003
1.1-2.8	Mixed layer net O_2 production (O_2/Ar)	Luz and Barkan, 2009
2.1 ± 0.5	Oxygen utilization rate (OUR) using ^{3}He ventilation	Stanley et al., 2012
2.8	Euphotic zone O_2 production	Cianca et al., 2013
4.3 ± 0.9[e]	Upward physical nitrate flux computed from ^{3}He flux	Stanley et al., 2015
3.0 ± 1.0	Average of estimates compiled in Table 1	
3.8 ± 1.2	*Average of available geochemical measurements*	*Emerson, 2014*

[a]Decreases to 2.6 mol C m^{-2} yr^{-1} if only DIC is considered

[b]Mixed layer estimate. Increases to 3.8 mol C m^{-2} yr^{-1} if extrapolated to the euphotic zone assuming 40% of NCP occurs below the mixed layer

[c]Increases to 3.3-3.9 mol C m^{-2} yr^{-1} if the 100-400 m depth interval is considered

[d]Based on numerical integration of aphotic zone oxygen consumption rates between 100 m and 2800 m

[e]Assumes C:NO_3^- of 106:16