New primary production and nitrification in the western subtropical North Atlantic: A modeling study

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[1] The original definition of new primary production rests on the assumption that nitrogenous substrate taken up to fuel algal growth is coming into contact with phytoplankton for the first time that year. Therefore, should the generation of nitrate from ammonium by nitrification turn out to be significant in surface waters then nitrate uptake can no longer be simply ascribed to new production. A modeling study is presented centered on the Bermuda Atlantic Time-series Station, in the oligotrophic subtropical North Atlantic. We quantify the role of nitrification in providing nitrate to fuel primary production through a full annual cycle for the first time. The results confirm previous limited observations suggesting that a major fraction of nitrate uptake in oligotrophic regions (where nitrification will be most influential), previously ascribed to new production, may actually involve ''recycled'' nitrate.

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1. Introduction

[2] New primary production is a fundamental concept in biological oceanography. Its importance is highlighted by its strong relationship with export production and hence with the strength of the biological pump. Since the introduction of the concept by *Dugdale and Goering* [1967], however, it has increasingly been treated as a simple sum of nitrate uptake, nitrogen fixation and atmospheric deposition of nitrogenous material. The role of nitrification of ammonium has been ignored until recently, largely owing to small initial estimates of its contribution and to difficulties involved in measuring it. The neglect of nitrification is especially prevalent in modeling studies (even models which explicitly represent nitrification do not investigate the magnitude of the flux). However, the significance of ''regenerated'' nitrate was presaged ab initio by *Dugdale and Goering* [1967]: ''. . .the oxidation of ammonium to nitrate has been ignored. If nitrification rates are eventually shown to be sufficiently higher than has been assumed, the assumption that nitrate is a non-regenerated nutrient form in the euphotic zone would have to be modified.'' Recent observations have demonstrated that in oligotrophic regions nitrification can be very active in the euphotic zone [*Dore and Karl*, 1996; *Diaz and Raimbault*, 2000; *Lipschultz*, 2001; *Lipschultz et al.*, 2002; *Fernández*, 2003] and that for some periods of the year virtually all of the nitrate in the euphotic zone may be regarded as regenerated. This has significant consequences for estimates of new primary production based on nitrate concentrations and uptake and for models which do not take nitrification into account.

[3] It is worth making a brief comment at the outset on the practicalities of estimating new primary production. In particular the issues of depth and timescales are worthy of discussion. When estimating new primary production it is necessary to make a choice of what depth and over what period to integrate. There are certain assumptions that need to be acknowledged when this is done. If the surface ocean (defined as all depths shallower than the chosen integration depth) is at equilibrium over the timescale of choice, the net flux of nitrate upward across the base of the surface ocean, plus contributions from nitrogen fixers and atmospheric deposition, should match the export of particulate and dissolved organic material past this depth. To allow this estimate to be made, nitrate uptake in the surface waters is often equated with the upward flux of nitrate. This approach makes two assumptions. First, to equate nitrate uptake with the net flux of nitrate across the reference depth, there can be no source of nitrate within the surface waters. Second, material sinking out of the surface waters cannot be converted back into nitrate and brought back up into surface waters over the timescale of interest. This timescale is usually taken to be one year. There are two choices of reference depth in wide usage: the depth of the base of the euphotic zone and the maximum winter depth of the mixed layer. The former is usually defined as the depth at which the level of photosynthetically active radiation (PAR) is 1% of the value just below the surface. This depth is often used for estimates of new primary production because the euphotic depth is a (crude) measure of the depth to which photosynthesis and hence

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primary production takes place. If nitrification is significant in surface waters, however, then clearly the first assumption no longer holds with this choice of integration depth. Also, there are many mesoscale physical processes, associated with eddies and fronts, capable of bringing waters from below the euphotic zone back to the surface within a year. As a consequence, in the presence of nitrification immediately below the euphotic zone the second assumption does not hold either. For the alternative reference depth, the maximum winter mixed layer depth, by definition it is unlikely that vertical mixing will bring water up into the surface from a greater depth and the net vertical transport across the boundary due to mesoscale processes will be greatly reduced compared to the previous definition. Hence the second assumption is reasonably justified. Nitrification in surface waters will, however, once more break the first assumption. This paper is concerned with new primary production: specifically with determining the discrepancy between new primary production and nitrate uptake.

[4] Although low primary production is a defining characteristic of oligotrophic systems, the large area covered by such oceanic regions (with a dominant contribution from the subtropical gyres) means that they contribute roughly half of the total marine export production [*Jenkins and Doney*, 2003]. As a consequence they play a crucial role in the biogeochemistry of the ocean. The paucity of nutrients in the surface waters of oligotrophic regions, especially during summer months, means that the local phytoplankton are very dependent on the rapid recycling of organic matter. Sufficient ammonium can be produced by this process to make ammonium-fueled regenerated production a very significant fraction of total primary production in such settings. Ammonium is also nitrified into nitrate, however. Therefore, should nitrification be a significant flux in surface waters, its contribution relative to the total production at a site may be greatest in oligotrophic regions where recycling is so active. For this reason we focus our study on the subtropical gyre of the North Atlantic as representative of oligotrophic systems. More specifically we focus our study on the Bermuda Atlantic Time-series Study (BATS) site, located at 32N 64W in the western subtropical North Atlantic. It is a classic seasonally oligotrophic site with extremely low concentrations of nutrients in surface waters throughout the summer months. Monthly sampling at this site since 1988 provides one of the most valuable biogeochemical time series for the open ocean. Overviews of the work that it has supported are given, for example, by *Michaels and Knap* [1996], *Siegel et al.* [2001], *Lipschultz* [2001] and *Steinberg et al.* [2001]. Data can be accessed from the website http://www.bbsr.edu.

[5] BATS has been the focus of interest in recent years owing to difficulties encountered in reconciling differing estimates of new primary production at the site. Estimates from early in situ incubation measurements were greatly exceeded by those arising from integral tracer methods developed in the 1980s. It has been argued that tracer methods are more accurate; they integrate over long time and space scales and so include intermittent and localized events that may be missed by infrequent point sampling. There are a number of good reviews on the issue of new primary production in this region [*Platt et al.*, 1989; *Jenkins and Wallace*, 1992; *Lipschultz*, 2001; *Lipschultz et al.*, 2002]. Table 1 contains a list of estimates for new primary production in the region. Note that the region was in a slightly different biogeochemical regime in the 1960s [*Lipschultz et al.*, 2002] so estimates based on data from this period should be treated with a little caution [*Jenkins and Goldman*, 1985; *Musgrave et al.*, 1988]. This applies equally to early point measurements based on ^{15}N incubations. They are excluded from the table, however, because the early tracer estimates, in consistently exceeding contemporaneous total primary production estimates, gave concerns over the applicability of the ^{15}N derived estimates to annual timescales and regional lengthscales. No recent estimate of annual new production based solely on ^{15}N incubations exists to the best of our knowledge. The estimates are grouped by the technique used to calculate them. The two oxygen-based approaches and the nitrate flux technique are all integral measures, making use of the quantification of a tracer over large spatial (of order 100 km) and temporal (of order months to a year) scales. Integral tracer methods yield estimates of new primary production for the region in the range 0.33–0.84 mol N m^{-2} yr^{-1}, or 0.9–2.3 mmol N m^{-2} d^{-1}. Sediment trap data and Thorium flux measurements are both point measurements in space, though the trap estimates, at least, will have selectively ''integrated'' over quite a large area of surface water owing to the action of horizontal advection during the time it takes particles to sink through the water column. The final set of estimates come from computer simulations, many of them motivated by the need to explain the discrepancy between point and integral estimates. There is a hypothesis that mesoscale physical phenomena, such as the lifting upward of nutrient laden deeper waters by eddies [*McGillicuddy and Robinson*, 1997], can enhance primary production locally in short but very productive bursts. As a result the physics in the simulations is quite sophisticated with resolution high enough to resolve local and transient mesoscale ''events.'' Partly to minimize the already high computational costs, the biological models embedded within these physical simulations are rather simplified, being at best dissolved inorganic nitrogen-phytoplankton-zooplankton-detritus (NPZD) models and in some cases purely dissolved inorganic nitrogen. Such biological models can clearly not discriminate between new and regenerated production on the basis of the model components. Instead, they are restricted to measuring the flux of dissolved inorganic nitrogen across a chosen depth and then equating this with new primary production using the arguments and assumptions already described. In all model studies cited in Table 1 the euphotic depth was chosen as the depth for flux calculations, though the exact numerical choice of what this euphotic depth should be varied between 75 m and 126 m. The important point, however, is that these simulations equate new primary production with the net vertical flux of nitrate, as all dissolved inorganic nitrogen coming from depth is implicitly assumed to be nitrate new to the euphotic zone that year. As already discussed, significant nitrification between the euphotic depth and the maximum winter mixed layer depth on subannual timescales would mean that such estimates of new

Table 1. Estimates for New Primary Production in the Vicinity of the Bermuda Atlantic Time-Series Study (BATS)[a]

	New Primary Production				
	Nitrogen				
	Mean	Error Range	Oxygen	Carbon	Reference
Oxygen utilization	*0.46*	*±0.08*	5.0 ± 0.9	-	*Jenkins and Goldman* [1985]
	0.42	*±0.24*	8.5 ± 0.8	-	*Sarmiento et al.* [1990]
	0.50	*±0.13*	5.5 ± 1.5	-	*Jenkins and Wallace* [1992]
Oxygen production	*0.33*	*±0.05*	3.5 ± 0.5	-	*Musgrave et al.* [1988]
	0.39	*±0.16*	4.3 ± 1.7	-	*Spitzer and Jenkins* [1989]
Sediment trap	0.19	-	-	-	*Altabet* [1989]
	0.12	-	-	0.77	*Lohrenz et al.* [1992]
	0.11	±0.07	-	-	*Siegel et al.* [1999]
^{234}Th flux	*0.14*	*0.06–0.33*	-	0.95 (0.4–2.2)	*Buesseler* [1998]
NO_3 flux	0.56	±0.16	-	-	*Jenkins* [1988]
	0.70	±0.2	-	-	*Jenkins* [1998]
	0.84[b]	±0.26	-	-	*Jenkins and Doney* [2003]
	0.47[c]	±0.15	-	-	*Siegel et al.* [1999]
Simulation	0.50	-	-	-	*McGillicuddy and Robinson* [1997]
	0.53	-	-	-	*Oschlies and Garçon* [1998]
	0.29	-	-	-	*Oschlies* [2002a]
	0.16	-	-	-	*Oschlies* [2002b]
	0.63	±0.04	-	-	*McGillicuddy et al.* [2003]

[a]Production values are in units of mol N $m^{-2}yr^{-1}$, mol O_2 $m^{-2}yr^{-1}$ and mol C $m^{-2}yr^{-1}$ for nitrate-, oxygen- and carbon-based measurements, respectively. Figures in italics represent estimates calculated by converting from oxygen or carbon units into nitrogen by using Redfield ratios of 10.9 and 6.6 respectively. Estimates have been pooled according to the method of estimate (indicated in the first column).

[b]This is also a revised version of that of *Jenkins* [1988] using a longer span of data.

[c]This is a revised version of that of *Jenkins* [1988] using the data from the entire late 1980s.

primary production may be substantially elevated by unwarranted inclusion of production fueled by upwelled regenerated nitrate.

[6] Crucial to an understanding of new primary production in this region, therefore, is the rate at which material is being recycled within surface waters and the fraction of nitrate taken up that may have come from this source. The proportion of nitrate taken up by phytoplankton that originates from shallow nitrification cannot be quantified by point measurements of nitrification, however. This is because the ratio of new to regenerated nitrate in the nitrate pool results from the combined effects of uptake and nitrification over time. By using a model constrained by observations it is possible to interpolate dynamically and therefore to clarify and to quantify the dynamics of nitrate and nitrification in surface waters in a way that cannot currently be done using observations alone.

[7] We choose to investigate the significance of nitrification in the seasonal cycle of nitrogen at BATS using a one-dimensional biogeochemical model. Specifically, we estimate the fraction of "new" primary production resulting from the uptake of nitrate that has been regenerated within surface waters. We do this using both current definitions of "surface" waters: bounded by the euphotic depth, chosen to match the classic definition of new primary production [*Dugdale and Goering*, 1967]; or bounded by the maximum winter mixed layer depth, chosen because all water above this depth can be mixed back into the euphotic zone on timescales less than year. Our results quantify how reliable nitrate uptake (plus nitrogen fixation and atmospheric deposition) is as a proxy for new primary production in the BATS region.

[8] For reference, we will use "new" to denote production arising from uptake of nitrate, nitrogen fixation and atmospheric deposition throughout. The double quotes will only be absent from the word new when it is clear that we are talking about new primary production that does not include uptake of nitrate which was generated via nitrification that year.

2. Methods

[9] The one-dimensional model used to investigate the nitrogen dynamics at BATS is one previously developed to investigate the planktonic ecosystem in this location [*Anderson and Pondaven*, 2003]. This model ably reproduces the local annual cycle in physics and plankton. More specifically, it has been successfully used to explain the pronounced drawdown of carbon in the absence of measurable nutrients [*Anderson and Pondaven*, 2003] and to investigate the efficiency of the eddy-pumping process [*Martin and Pondaven*, 2003] at this location. Rather than go into the intricacies of the model here, the reader is referred to *Anderson and Pondaven* [2003] for full details. However, a schematic of the model can be found in Figure 1 and a brief summary of the features pertinent to this study, follows. The limitations of using a one-dimensional model for this study are covered in section 4.

2.1. Model

[10] The model comprises 80 layers of 5 m thickness. Vertical mixing between these layers is parameterized using an effective diffusivity. The diffusivity is calculated using the *Gaspar et al.* [1990] algorithm. European Centre for Medium-Range Weather Forecasts (ECMWF) meteorological data including 6-hourly winds is used for forcing, with nonsolar fluxes adjusted slightly so that we match the sea surface temperature and mixed layer depths observed at BATS. The model time step is 10 min for both biology and

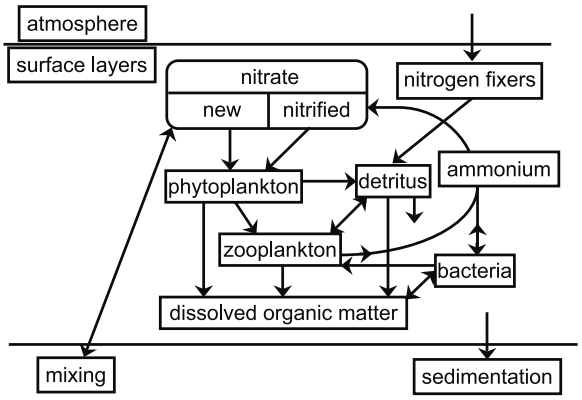

Figure 1. Schematic of the model used in the study. The split nitrate pool and nitrification are described in the text. Otherwise, model details, including equations, are given by *Anderson and Pondaven* [2003]. Note that the nitrogen taken up by nitrogen fixers only appears in the model on their demise and subsequent transition to detritus.

physics allowing it to model the full diurnal cycle in both biological and physical processes.

[11] The invaluable resource of the BATS data set (see http://www.bbsrc.edu) provides the data used to initialize the model for the chosen location. The model was calibrated using a repeating annual loop of BATS data from 1991 only, lasting 5 years. The model is then run for the years 1992–1995.

[12] The biological model includes variables for nitrate, ammonium (actually a joint pool of nitrite and ammonium as discussed below), phytoplankton, zooplankton, bacteria, detritus and both labile and semilabile dissolved organic matter (DOM). Detritus sinks at a rate of 10 m d^{-1} with the exception of nitrogen-fixer detritus which sinks at a rate of 5 m d^{-1}. The half saturation constants for uptake of nitrate and ammonium are 0.15 mmol N m^{-3} and 0.05 mmol N m^{-3}, respectively. To simulate the observed adaptation of phytoplankton to low light levels, the initial slope of the photosynthesis-irradiance curve (α) is taken to be 0.105 mgC mgChl a^{-1} h^{-1} (μEinst m^{-2} s^{-1})$^{-1}$ in the mixed layer and 0.164 mgC mgChl a^{-1} h^{-1} (μEinst m^{-2} s^{-1})$^{-1}$ deeper down. Both values are in the range of observed values [*Tagushi*, 1976]. The model further incorporates a variable carbon to chlorophyll ratio, the air-sea flux of carbon dioxide, uncoupled carbon and nitrogen dynamics (to allow for non-Redfield dynamics) and nitrogen fixation. Atmospheric deposition is not simulated in this model as it is not a significant source of new nitrogen to the euphotic zone at BATS [*Hastings et al.*, 2003]. All tracers are restored at the base of the model (400 m) to observed averages, from BATS where available.

[13] It is worth discussing the recycling of matter in the model in a little more detail since it is crucial to this study. The explicit modeling of the microbial loop makes the model well-suited to studying nitrogen dynamics. Nitrate and ammonium taken up by phytoplankton, to form particulate organic nitrogen (PON), are eventually either exported from the system to depth, excreted as ammonium by zooplankton or find their way into the detritus or dissolved organic nitrogen (DON) pools. The remineralization of detritus takes place at a rate of 0.045 d^{-1} and 0.055 d^{-1} for detrital carbon and nitrogen respectively. As a result, C:N increases with depth. These remineralization rates were chosen, within the range of observations, to match the model Particulate Organic Matter (POM) output to sediment trap data [*Anderson and Pondaven*, 2003]. DON is taken up by bacteria whose low gross growth efficiency (17%) makes them the dominant source of ammonium in the model. Ammonium in turn is nitrified to nitrate. In the standard model used here this occurs at a maximum rate of 0.15d^{-1}. The actual rate is often lower in accordance with observations which have suggested that light can inhibit nitrification [*Olson*, 1981; *Ward*, 1987]. To simulate this we use the following profile:

$$\text{nitrification rate} = R_{\max}^{NH4}[1 - PAR(z)/PAR(0)], \qquad (1)$$

where $PAR(z)$ is the amount of photosynthetically active radiation (PAR) measured at depth z. The only parameter needed is the maximum nitrification rate $R_{\max}^{NH4}$.

[14] In order to keep track of the source of nitrate, the model is modified slightly with respect to the work by *Anderson and Pondaven* [2003]. The nitrate variable is now split into new and regenerated nitrate where new denotes a source deeper than the maximum winter mixed layer depth. At the start of each year all nitrate in the model is assigned to the new nitrate variable. Over the course of the year, any nitrate generated by nitrification passes into the regenerated nitrate compartment. There is no flux between the two nitrate compartments. As a result of this splitting we can determine both the amount of nitrate regenerated each year throughout the water column and the fraction of annual "new" production that is fueled by nitrate that has actually been generated through nitrification that year. Nitrate uptake by phytoplankton does not distinguish between new and regenerated nitrate pools but uses only their sum. The uptake of new and regenerated nitrate at a given depth is in the same proportion as the size of their respective pools at that depth and time.

[15] It should be noted that the variable termed "ammonium" in our model is technically a joint pool of nitrite and ammonium. Under nitrification ammonium is first converted to nitrite which is in turn converted into nitrate. For computational reasons it is preferable not to model nitrate, nitrite and ammonium independently. The uptake of either nitrite or ammonium by phytoplankton constitutes regenerated production in the standard sense. Consequently it is sensible to group nitrite and ammonium into one variable: our "ammonium." We implicitly assume that the half saturation constants for uptake of nitrite and ammonium are equal. BATS has good nitrite data but there are insufficient data for ammonium for the periods we simulate. With a little care though the nitrite observations can still be compared to the model "ammonium" field (see section 3.1). From now on we drop the inverted commas from model "ammonium" for simplicity.

[16] The choice of the maximum nitrification rate $R_{\max}^{NH4}$ is clearly a crucial one. Unfortunately, we could find no depth-

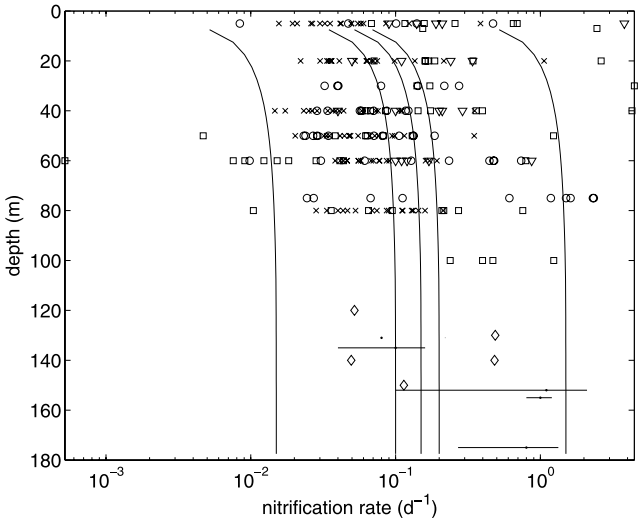

Figure 2. Nitrification rate profiles (solid lines) used in the model runs together with observations. The model profiles correspond to maximum nitrification rates of 0.015 d^{-1}, 0.1 d^{-1}, 0.15 d^{-1}, 0.2 d^{-1} and 1.5 d^{-1}. These profiles assume light inhibition and show nitrification rate in mid-June when PAR is maximum. Observations are from: (triangles) the Gulf of Lyons in the NW Mediterranean [*Diaz and Raimbault*, 2000]; (dots) Station ALOHA in the Pacific [*Dore and Karl*, 1996] (error bars are also shown); (diamonds) 16°S 150°W in the oligotrophic Pacific [*Raimbault et al.*, 1999]; and the subtropical North Atlantic [*Fernández*, 2003]. For the latter, there are three periods of data: (circles) September–October 2000; (squares) September–October 2001; (crosses) February–March 2001. Note the logarithmic ordinate axis.

specific data for BATS and so we were forced to look for data from other oligotrophic sites. Only four suitable data sets could be found: from Station ALOHA in the Pacific [*Dore and Karl*, 1996]; from the Gulf of Lyons in the NW Mediterranean [*Diaz and Raimbault*, 2000]; from the Pacific at 16S 150W [*Raimbault et al.*, 1999]; from the mid-subtropical North Atlantic [*Fernández*, 2003] which should be most representative of the situation at BATS. For the last three data sets we estimated specific nitrification rates by dividing the estimated nitrification flux into nitrate from ammonium and nitrite by the simultaneous sum of nitrite and ammonium concentrations. We do this to be consistent with our model which uses a joint ammonium-nitrite pool. For the first data set, ammonium data are not available and so the rate is calculated using just the nitrite concentration. Specific nitrification rates calculated from the above data sources are clearly very variable (Figure 2) spanning three orders of magnitude. This may partly reflect current difficulties in measuring nitrification. For the 242 observations shown in Figure 2 the arithmetic and geometric means are 0.25 d^{-1} and 0.09 d^{-1}, respectively. We choose $R_{\max}^{NH4} = 0.15\ d^{-1}$ as the value for our base run to give nitrification rates between the two means (Figure 2). We also carry out sensitivity analyses (described in the next section) on the magnitude of $R_{\max}^{NH4}$ and on the vertical extent of nitrification to ensure, as far as possible, that our results are robust.

2.2. Model Runs

[17] A suite of model variations are used to explore the sensitivity of the model to various parameterizations and changes in key parameters. For clarity, each of the runs is briefly described here. Table 2 contains a summary of all runs.

[18] The base run (Run 1) uses the nitrification profile described above (equation (1)) with a maximum nitrification rate of $R_{\max}^{NH4}$ equal to 0.15d^{-1}. Runs 2 and 3 are as Run 1 but using a maximum value of nitrification rate which is 33% below and above the value in the base run (Run 1), respectively. Two further sensitivity runs are conducted at more extreme values to take into account the huge variability seen in the observations (Figure 2). Run 4 uses $R_{\max}^{NH4} = 0.015\ d^{-1}$ and Run 5 uses $R_{\max}^{NH4} = 1.5\ d^{-1}$. There are only 9 observations (4%) lower and higher respectively than these two values, and both extreme values differ from the arithmetic and geometric means of observations by an order of magnitude. Run 6 removes the control of light on nitrification using instead a uniform, constant profile of rate equal to the maximum in Run 1. This is motivated by the observations collated in Figure 2 which show little effect of light inhibition near the surface. Run 7 also tests the influence of light on nitrification rates but at the other extreme. In this run nitrification is set to zero throughout the euphotic zone with the standard profile being used at greater depths. Run 8 is identical to Run 1 except that the parameter responsible for limiting the uptake of nitrate in the presence of ammonium (ψ) is halved. This is done because, as mentioned previously, the modeled ammonium is actually a joint pool of ammonium and nitrite. Since there is currently no observational evidence for limitation of nitrate uptake in the presence of nitrite, Run 8 investigates how sensitive the results of the base run are to this form of uptake limitation. Finally, it may be noted that the maximum winter mixed layer depth typically occurs in late January or early February. Therefore, in Run 9 the regenerated nitrate in the model is reset to zero on the day of the deepest winter mixed layer each year rather than on 1st January as in all of the other runs. It is unwise to compare annual values for Run 9 to other runs owing to the different periods of integration.

Table 2. Summary of Runs Described in This Paper[a]

Label	Effect of Light on Nitrification	$RNH4_{max}$, d^{-1}	ψ, mmol N m^{-3}	Comments
1	Y	0.15	1.50	base run
2	Y	0.10	1.50	
3	Y	0.20	1.50	
4	Y	0.015	1.50	
5	Y	1.5	1.50	
6	N	0.15	1.50	
7	Y	0.15	1.50	nitrification zero in euphotic zone
8	Y	0.15	0.75	
9	Y	0.15	1.50	nitrate reset when deepest mixed layer

[a]Here ψ is the parameter controlling the inhibition of nitrate uptake in the presence of ammonium.

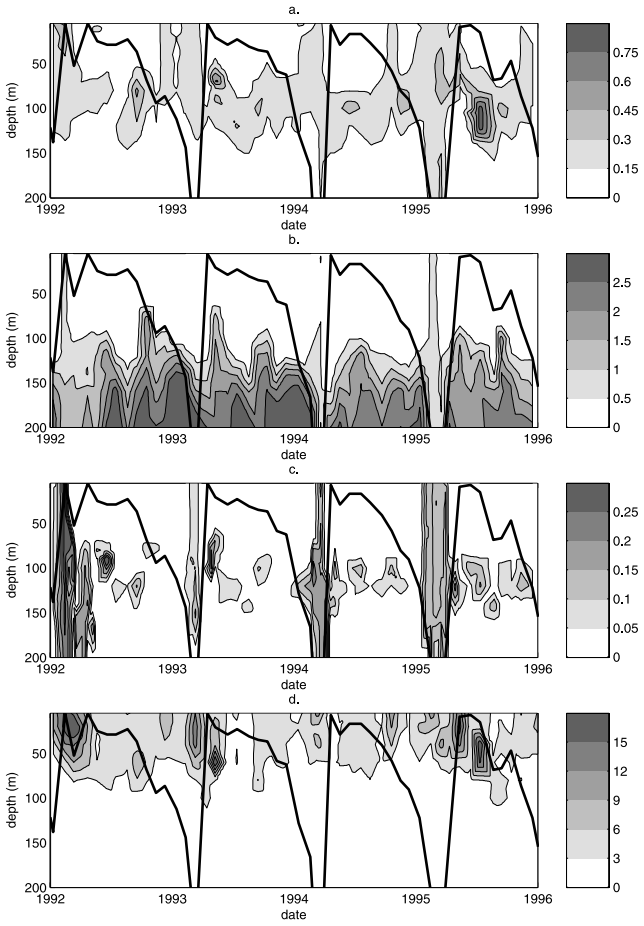

Figure 3. Observations from Bermuda Atlantic Time-series Study station. (a) Chlorophyll a (μg Chl a m^{-3}), (b) nitrate (mmol N m^{-3}), (c) nitrite (mmol N m^{-3}) and (d) primary production (mmol C m^{-3} d^{-1}). The thick solid line is the depth of the mixed layer in all plots. These data can be downloaded from http://www.bbsr.edu. Euphotic depth data were not available.

However, it is possible to compare summer estimates. This allows us to gauge the effect of the timing of the nitrate reset on our results.

3. Results

3.1. Reproduction of Seasonal Cycle at BATS

[19] Before quantifying nitrification in various scenarios we describe the annual cycle in the plankton ecosystem at BATS and how well our model reproduces it. Figure 3 shows observations for the period 1992–1995 for chlorophyll, nitrate, nitrite and primary production. On an annual basis there is a small spring bloom, fueled by nitrate brought up during winter mixing, followed by the development of a deep chlorophyll maximum around 100 m (Figure 3a). The nitrate field (Figure 3b) displays a well-defined nutricline, at ~100 m, with surface values typically very low bar the odd excursion due to deep winter mixing. Furthermore, the spring bloom often depletes nitrate considerably deeper than the mean nutricline depth though concentrations soon recover. Although the nitrite data (Figure 3c) are a little more variable they, like chlorophyll, show a deep maximum developing at 100 m during the summer with significant values only extending to the surface during the deep winter mixing/spring bloom period. Primary production (Figure 3d) displays the small spring bloom with low values, extending down to roughly 80 m, characterizing the summer.

[20] Figure 4 shows the same fields but for model output. The model does a reasonable job of reproducing the annual cycle in chlorophyll (Figure 4a), particularly the development of the deep chlorophyll maximum around 100 m, although concentrations are generally a little too high and extend too deep during the spring bloom (a consequence of

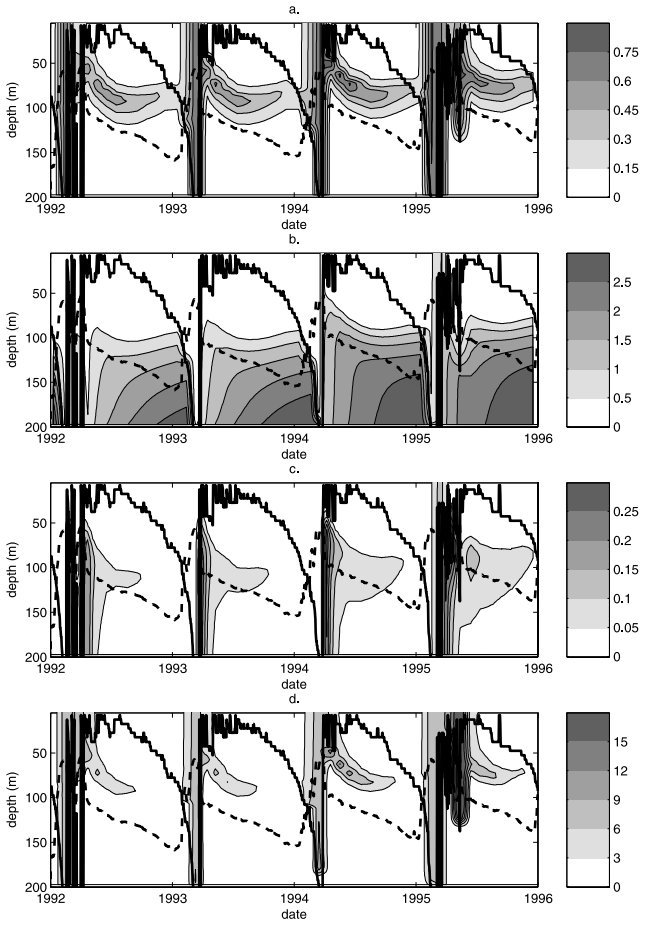

Figure 4. Model output corresponding to observations in Figure 3. (a) Chlorophyll a (μg Chl a m^{-3}), (b) nitrate (mmol N m^{-3}), (c) nitrite plus ammonium (mmol N m^{-3}) and (d) primary production (mmol C m^{-3} d^{-1}). Although the model generates output for every day, only output on days corresponding to observations in Figure 3 are used to generate these plots for consistency. Note that a constant elemental ratio is used to calculate primary production in carbon units from the nitrogen unit value produced by the model. The thick solid line is the mixed layer depth, and the thick dashed line is the depth of the euphotic zone in all plots.

using a fully mixed layer in the model). The model also does a good job of simulating nitrate concentrations (Figure 4b). The nutricline at 100 m is well reproduced together with the brief deeper depletions and upward mixing events seen in the spring. The model displays less short period variability than observations. Such variability can be caused by mesoscale physical features, such as eddies, which our one-dimensional model cannot simulate. Only a full three-dimensional model could attempt to reproduce such variability and there are significant problems associated with producing such a model (see section 4). Furthermore, there remain questions over whether such events actually contribute much to nitrate uptake at a fixed location [*Martin and Pondaven*, 2003]. Consequently we feel that our model reproduces the nitrate field as well as can be expected for a one-dimensional model and well enough for the topic addressed here. Because our model combines ammonium and nitrite into one pool a little care needs to be exercised when comparing the evolution of the model "ammonium" to observations for nitrite. Little data exist for ammonium in the BATS region and what data there are do not fully cover our period of interest. *Brzezinski* [1988] suggests that concentrations are typically one fifth to one quarter those of nitrite at depths of 60 m or deeper, occasionally being of equal magnitude. At shallower depths ammonium concentrations are typically greater than those of nitrite but with concentrations that are typically below 50 μmol m^{-3}, the lowest value contoured in our plots. *Lipschultz* [2001] gives observations of nitrite and ammonium at BATS for the period mid-June 1992 to mid-June 1994. Ammonium concentrations are generally below 50 μmol m^{-3}, only peaking just over 80 μmol m^{-3} and are very variable with little seasonal or depth pattern. As shown in Figure 3c, nitrite concentrations are regularly in excess of 50 μmol m^{-3} in the deep maximum, often exceeding 100 μmol m^{-3}. Hence nitrite observations are probably within a factor of two of the total nitrite and ammonium concentration. With this caution, the model does a reasonable job of reproducing the observed development of the deep maximum at 100 m and the vertical mixing in spring (Figure 4c).

[21] At first sight, the model does a poor job of reproducing primary production observations (compare Figures 3d and 4d). Although the timing of the spring bloom is correct (Figure 4d) there are a number of detracting features. First, the spring bloom extends too deep. This is a consequence of having a fully mixed layer. In reality material will not be constantly homogenized over winter mixed layer depths. To capture this in a model would require a considerably more sophisticated vertical mixing scheme which in turn would require better physical data to calibrate it. For this reason it is not implemented here. Second is the fact that modeled primary production appears confined to a maximum between 80 m and 100 m during the summer months whilst observations (Figure 4d) show primary production roughly uniform up to the surface. The discrepancy is not as significant as it would appear. The underestimate of primary production in surface waters in the important summer period is not as bad as it appears from Figure 4d. This is partly because the contouring in Figure 4d accentuates the difference between model output and observation values. Second, the model displays a considerable variability in daily profiles (see auxiliary material Figure S1[1]). Hence caution should be exercised when comparing the model profiles with a set of observations taken just once each month annually for four years. Furthermore, it should be noted that primary production observations are made in carbon units while the model calculates it in nitrogen units. A constant elemental C:N ratio for cells is used to convert model values into carbon units for comparison. Recent surface observations near Bermuda, however, show that the elemental C:N ratio of phytoplankton cells can considerably exceed "standard" values when nutrient-stressed. *Mongin et al.* [2003] have recently shown that using our model with identical nitrogen dynamics but with a variable C:N ratio considerably reduces the observed discrepancy in modeled and observed primary production. As we are interested in the nitrogen cycle our findings are not affected by the use of the fixed C:N ratio. In general, therefore, the model does a reasonable job of reproducing primary production. Incidentally, it is uncertain whether the curious staggered bloom at the start of 1995 is a genuine in situ feature of the local ecosystem or the effect of advection through the site of a water mass with different properties and history.

3.2. Nitrification and Nitrate Uptake

[22] We now turn our attention to nitrification. The stocks and uptake fluxes of total and regenerated nitrate are integrated using both reference depths previously described. They are also integrated over two periods: the whole year and the summer. The annual integrated values can be found in Table 3 with those for the summer in Table 4. The summer is defined here as 1 June to 31 August. The summer is the period for which the system is oligotrophic, when the influence of nitrification on "new" primary production will be most significant. For both annual and summer values an average over the four years 1992–1995 is given.

[23] Consider first the nitrate budget for the base run (Run 1). Integrating over the euphotic zone (as in the original *Dugdale and Goering* [1967] definition of new production) the annual average nitrate uptake is 1.17 mmol N $m^{-2}d^{-1}$ (Table 3). This is within the range of estimates (0.9–2.3 mmol N m^{-2} d^{-1}) coming from integral tracer techniques described earlier. Over half (55%) of this uptake is of nitrate that has been regenerated within the euphotic zone (0.64 mmol N $m^{-2}d^{-1}$) and hence is not new in the sense defined by *Dugdale and Goering* [1967]. Related to this, the annual mean ratio of stocks of regenerated to total nitrate is 0.67. Much of the shift toward regenerated nitrate takes place during the summer months. Table 4 shows that although the mean daily uptake of nitrate is lower during the summer than the annual average (reflecting the typically lower productivity during this period) a greater fraction of that taken up is of regenerated nitrate (82%). Carrying out the integrals for Run 1 over the maximum winter mixed layer depth the ratio between regenerated and total nitrate take up decreases slightly compared to the euphotic depth calculation when calculated over the full year (Table 3), but

[1]Auxiliary materials are available in the HTML. doi:10.1029/2005GB002608.

Table 3. Mean Daily Uptake and Standing Stocks of Regenerated and Total Nitrate Calculated for the Years 1992–1995 by the Model[a]

	Using d_{WML}^{max}						Using d_{Euph}					
	Uptake			Stocks			Uptake			Stocks		
Run	NO_3^{nit}	NO_3^{tot}	Ratio	NO_3^{nit}	NO_3^{tot}	Ratio	NO_3^{nit}	NO_3^{tot}	Ratio	NO_3^{nit}	NO_3^{tot}	Ratio
1	0.80	2.08	*0.39*	184	433	*0.43*	0.64	1.17	*0.55*	25.8	38.6	*0.67*
2	0.69	1.96	*0.35*	179	427	*0.42*	0.56	1.08	*0.52*	23.9	36.2	*0.66*
3	0.89	2.17	*0.41*	187	438	*0.43*	0.71	1.24	*0.57*	27.3	40.6	*0.67*
4	0.31	1.38	*0.22*	172	418	*0.41*	0.30	1.37	*0.22*	21.0	33.0	*0.64*
5	1.49	2.64	*0.56*	276	559	*0.49*	1.48	2.63	*0.56*	44.8	68.8	*0.65*
6	0.81	2.07	*0.39*	183	430	*0.42*	0.65	1.17	*0.55*	25.6	38.4	*0.67*
7	0.48	1.71	*0.28*	175	421	*0.42*	0.33	0.83	*0.40*	18.3	29.4	*0.62*
8	0.82	2.11	*0.39*	186	430	*0.43*	0.65	1.17	*0.56*	25.0	37.3	*0.67*

[a]Uptake values are in units of mmol N $m^{-2}d^{-1}$. Standing stock values are in units of mmol N m^{-2}. NO_3^{nit} and NO_3^{tot} are used to denote nitrate produced by nitrification and total nitrate respectively. The ratio is that for the preceding two columns, i.e., regenerated nitrate to total nitrate. For comparison, new primary production estimates from integral tracer methods (Table 1) are in the range 0.9–2.3 (−0.4/+0.7) mmol N m^{-2} d^{-1}.

not if done over the summer (Table 4). However, regenerated nitrate still constitutes 39% and 89% of the total nitrate uptake for the year and summer months respectively.

[24] Runs 2 and 3 demonstrate that the results of Run 1 are not very sensitive to changes in the maximum rate of nitrification, either on an annual (Table 3) or a summer (Table 4) timescale. The fraction of regenerated to total nitrate, whether in uptake or stocks, only changes by a few percent with respect to Run 1 despite a 33% change in parameter value. This is regardless of whether the euphotic depth or the maximum winter mixed layer depth are used for the integration. The reason for this is that if the nitrification rate is decreased (increased) then ammonium accumulates (declines) such that the product of nitrification rate and ammonium concentration changes little. As this product must equal uptake of regenerated nitrate over the course of the year this is why the uptake of regenerated nitrate varies little between the runs.

[25] A more extreme test of sensitivity is provided by Runs 4 and 5. Reducing the maximum rate of nitrification by a factor of 10 (Run 4) results in a significant drop in the uptake of both regenerated and total nitrate. Although the ratio of their uptake drops by nearly a factor of two to 22% for the whole year (Table 3) it is still 69% (Table 4) for the key summer period. Increasing the maximum nitrification rate by a factor of 10 (Run 5) increases both uptakes and their ratio. Regenerated nitrate now accounts for 89% of the total nitrate taken up during the summer and 56% of that taken up over the whole year.

[26] It has already been mentioned that our parameterization of the vertical nitrification profile (equation (1)) includes light-inhibition. We carry out two extreme tests of the sensitivity of our results to this phenomenon. In Run 6 light inhibition is removed. The nitrification rate is held constant with depth at 0.15 d^{-1}. The change with respect to Run 1 (Tables 3 and 4) is very small with stocks and fluxes very similar and ratios of regenerated to total nitrate nearly identical. At the other extreme of light sensitivity, in Run 7 the nitrification rate is set to zero throughout the euphotic zone. Total nitrate uptake is, unsurprisingly, significantly reduced as a major source of nitrate has been curtailed. The decrease in uptake of regenerated nitrate is greater than that for total, however. Hence the fraction of nitrate uptake comprising regenerated nitrate also falls considerably. Despite this reduction, regenerated nitrate still constitutes 28% of the total amount of nitrate taken up annually when integrated over the maximum winter mixed layer depth, or 40% when integrated over the euphotic depth. In the summer, 80% of nitrate taken up still comes from a recycled source. This fraction remains high because despite nitrification being suppressed in the euphotic zone it still takes place between the base of the euphotic zone and the

Table 4. Mean Daily Uptake and Standing Stocks of Regenerated and Total Nitrate Calculated for the Summer Periods of the Years 1992–1995 by the Model[a]

	Using d_{WML}^{max}						Using d_{Euph}					
	Uptake			Stocks			Uptake			Stocks		
Run	NO_3^{nit}	NO_3^{tot}	Ratio	NO_3^{nit}	NO_3^{tot}	Ratio	NO_3^{nit}	NO_3^{tot}	Ratio	NO_3^{nit}	NO_3^{tot}	Ratio
1	0.85	1.03	*0.83*	240	422	*0.57*	0.84	1.02	*0.82*	23.9	28.2	*0.85*
2	0.76	0.94	*0.81*	236	416	*0.57*	0.75	0.93	*0.81*	21.4	26.3	*0.81*
3	0.92	1.11	*0.83*	242	427	*0.57*	0.91	1.09	*0.83*	31.7	41.8	*0.76*
4	0.34	0.49	*0.69*	161	407	*0.40*	0.33	0.48	*0.69*	16.6	22.0	*0.76*
5	1.50	1.69	*0.89*	320	526	*0.61*	1.49	1.68	*0.89*	34.9	53.7	*0.65*
6	0.86	1.05	*0.82*	236	419	*0.56*	0.85	1.03	*0.83*	23.0	26.9	*0.86*
7	0.37	0.45	*0.82*	224	410	*0.55*	0.35	0.44	*0.80*	16.9	21.0	*0.80*
8	0.76	0.84	*0.90*	236	419	*0.56*	0.74	0.82	*0.90*	23.0	26.9	*0.86*
9	0.82	1.03	*0.80*	215	422	*0.51*	0.83	1.02	*0.81*	22.9	28.2	*0.81*

[a]The summer is defined as 1 June (year day 152) to 31 August (year day 243). Uptake values are in units of mmol N $m^{-2}d^{-1}$. Standing stock values are in units of mmol N m^{-2}. NO_3^{nit} and NO_3^{tot} are used to denote nitrate produced by nitrification and total nitrate, respectively. The ratio is that for the preceding two columns, i.e., regenerated nitrate to total nitrate.

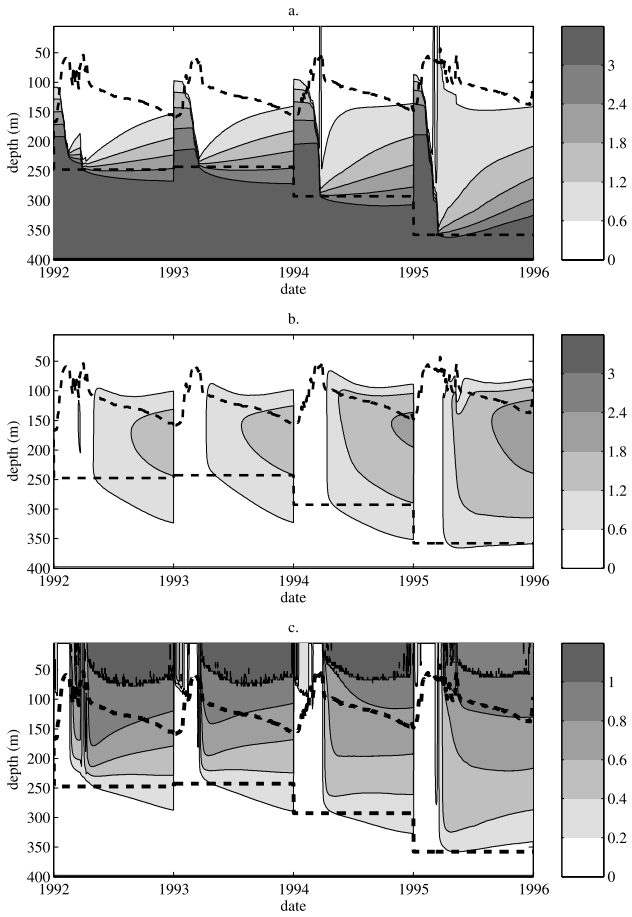

Figure 5. Concentrations of (a) new and (b) regenerated nitrate (both in units of mmol N m^{-3}) as a function of depth and time. (c) The ratio between regenerated and total nitrate concentrations. In all three plots the upper dashed line is the euphotic depth while the lower one is the maximum depth of the winter mixed layer for that year.

maximum winter mixed layer depth. Despite vertical mixing augmenting concentrations of new nitrate just below the euphotic zone as the year progresses, these concentrations never match those due to regenerated nitrate. Hence any nitrate being mixed upward into the euphotic zone is still much more likely to come from regenerated nitrate than from below the maximum depth of the winter mixed layer.

[27] In accordance with observations the model parameterizes the suppression of nitrate uptake in the presence of ammonium, here following the model of *Fasham et al.* [1990]. It is contentious whether the parameter controlling inhibition of nitrate uptake in the presence of ammonium (ψ) should be as large as it is in the model given that some of the "ammonium" is nitrite. There is currently no evidence that nitrite inhibits nitrate uptake. Run 8 demonstrates that reducing the relevant inhibition parameter by a factor of 2 makes virtually no difference to the results (Tables 3 and 4). Hence inhibition of nitrate uptake by ammonium is not a first order controlling process.

[28] The final run (Run 9) examines how sensitive our results are to the choice of the day on which regenerated nitrate is reset to zero. This reset should logically take place at the time each year at which the mixed layer is deepest. However, as this date changes each year, computing and comparing yearly averages would be very difficult given this choice. Hence a compromise of 1 January is used in all runs except Run 9. In Run 9 the reset does take place on the day of the deepest winter mixed layer. Table 4 demonstrates that using 1 January as the reset date results in an increase in the fraction of total nitrate taken up from regenerated nitrate over the summer by just a few percent. Hence we are justified in studying the values based on a 1 January to 31 December year.

4. Discussion

[29] From observations at BATS, *Lipschultz* [2001] concluded that during the oligotrophic period of the year "much of the nitrate is simply recycled nitrate produced in situ via nitrification." Our results go some way toward quantifying this source of nitrate by tracking the relevant biogeochemistry through the year for the first time. The advantage of our approach is that we can determine when the contribution of nitrification to nitrate uptake is greatest and also how it varies with depth. Like *Lohrenz et al.* [1992] we find that within the euphotic zone during the summer by far the majority of nitrate is actually coming from nitrate recycled via nitrification. Furthermore, our results suggest that over an annual timescale, much of the nitrate between the base of the euphotic zone and the maximum depth of the winter mixed layer may also be regenerated. This is apparent in Figure 5 which demonstrates that for the majority of the year in waters shallower than 200 m more than half of the nitrate comes from nitrified ammonium.

[30] The latter point has implications for estimates of new primary production related to mesoscale physical phenomena. Such processes are currently a favored option for providing the "missing" nitrate flux needed to close the BATS nitrogen budget [*McGillicuddy et al.*, 1998; *Oschlies and Garçon*, 1998; *Williams and Follows*, 1998a; *Siegel et al.*, 1999; *Oschlies*, 2002a, 2002b; *McGillicuddy et al.*, 2003; *Williams and Follows*, 2003; *Martin and Pondaven*, 2003]. The ageostrophic circulation associated with features such as eddies and fronts can result in strong localized upwelling which brings nutrient-rich waters to the surface. The majority of these upwelled waters, however, will originate from depths shallower than the top of the thermocline. As a consequence, our results demonstrate that a significant fraction of the nitrate upwelled by mesoscale processes may actually have been regenerated that year. Hence, although our model does not simulate such phenomena, much of the associated extra uptake will be of regenerated nitrate.

[31] Our results also have implications for point measurements. Nitrification in surface waters will introduce significant errors into estimates of nitrate uptake from ^{15}N incubation experiments in two ways. First, the ratio of ^{15}N nitrate to total nitrate is crucial to these estimates but the creation of nitrate via nitrification during the incubation will cause this ratio to change during the experiment leading to underestimation of uptake. Second, if some of the nitrate in the incubated sample has recently originated

from nitrification, the ratio of ^{15}N nitrate to total nitrate will give an overestimate of new nitrate uptake. The correct ratio to use is that of ^{15}N nitrate to the total nitrate that has not come from nitrification. Which of the two sources of error described above dominates will be a function of the timescale of the incubation. As a crude indication, using the value taken in our study, the second effect will dominate for all incubations shorter than the inverse of the specific nitrification rate, 7d. To continue using ^{15}N incubations to calculate new production it is necessary to find a way of accurately quantifying the contribution of nitrification. Such work has been pioneered by Fernández and coworkers [*Fernández*, 2003; *Fernández et al.*, 2005]. Technical issues remain, however, regarding the extent to which the amount of regenerated nitrate already present in the sample prior to the experiment may contribute to measured nitrate uptake.

[32] It is worth sounding a note of caution. This work is intended as a preliminary study. It is a first attempt to put current knowledge concerning nitrification into a dynamical model to quantify the process of nitrification throughout the year. Accordingly we have been very careful to use nitrification rates well within the range of observations. However, the current paucity of observations means that more data are needed, especially in the BATS region, to consolidate our results, though the subtropical North Atlantic data of *Fernández* [2003] should be representative of BATS.

[33] The model we have used does have drawbacks. Large scale advection through the BATS site is not taken into account in our one dimensional model. *Rintoul and Wunsch* [1991] estimate the net organic matter influx between 24N and 36N as 0.46 mol N m^{-2} yr^{-1}. The timescales and depths over which nitrate is generated from this material will clearly influence what can and cannot be truly regarded as new nitrate. Despite the low residual velocities of the area's currents (few cm s^{-1} from the northeast), the local biogeochemistry may be very sensitive to spatial gradients in biological and chemical fields as well as to the horizontal convergence or divergence of the flow. Other three-dimensional transport processes such as Ekman flux [*Williams and Follows*, 1998b] and isopycnal transport are similarly not taken into account. As previously stated though, there is very little data for spatial variability of nitrite and ammonium in the vicinity of BATS; indeed, there are precious few observations of ammonium at all. Without further focused observations a three-dimensional model would be forced to make assumptions concerning these critical processes that cannot be verified, with the necessary sensitivity analyses too numerically costly.

[34] Rather than being a specific simulation of BATS biogeochemistry, our model should be seen instead as a process study investigating the role played by nitrification in a general location within the subtropical gyre or a mean over some fraction of the gyre. Furthermore, as BATS is at the very NW edge of the gyre, and consequently substantially less oligotrophic than the interior, the results reported here are likely to be underestimates.

[35] Before ending, it is worth raising the broader question of what we mean by new production and export. For example, a little care is warranted when defining export. As *Jenkins and Doney* [2003] point out, there are effectively at least two production "loops", each involving different definitions of new and export production. The first is the one associated with the annual cycle, escape from the "loop" involving penetration into the permanent thermocline. The second loop is slower and returns some of the nutrients that accumulate in the permanent thermocline to the surface, typically after a decade [*Jenkins and Doney*, 2003; *Williams and Follows*, 2003]. In this second case, export involves material sinking sufficiently far past the base of the permanent thermocline to avoid the spiraling resupply line. A third loop might involve the much slower return of deep nutrients by the thermohaline circulation. Ultimately, true export involves only material that accumulates in the sediment and does not leach back out into the overlying water. All subsequent loops are dependent on the first for their input "raw materials," though. A major source of confusion is that people are often not clear about which "definition" of export they are using. We consider only the first loop here and define export accordingly.

[36] It may be recalled that it is only the pool of regenerated nitrate in the model which is reset to zero on 1 January each year. Consequently, the stocks of all other variables, including ammonium, are carried over into the next year. It may be argued therefore that the first nitrate that is generated by nitrification of ammonium each year should still count as new nitrogen since it is being generated from biological material created the previous year. Continuing this argument, if nitrogen taken up as nitrate to create new phytoplankton takes of order one year or more to pass through the system and reappear as nitrate via nitrification, then does nitrification actually matter since the nitrate generated is still predominantly new to the surface layer that year? The point each year at which the cumulative depth-integrated nitrification equals the maximum winter total stock of particulate nitrogen, dissolved organic nitrogen and ammonium gives a first-order estimate of how long it takes nitrogen to pass around the recycling loop (see auxiliary material Figure S2). For the years 1992, 1993, 1994 and 1995 the periods are 189, 294, 253 and 147 days, respectively. Although there is considerable variability, the mean is 220 days, corresponding to mid-August. At face value this would reduce our estimates of regenerated nitrate uptake by of order one half. Should we really be worried about nitrification "contaminating" our estimates of new production via nitrate uptake? The short answer is yes.

[37] The delay in the recycling of material highlights the broader issue of which timescale to use for estimating export. Most people assume that timescale and depth horizon for export can be defined independently. We ourselves do this by arbitrarily choosing one year as the integration time. However, the two scales are fundamentally related if a consistent definition is to be adopted. This leads us to argue that the approach we have adopted, to quantify the fraction of nitrate uptake using regenerated nitrate, may actually be an underestimate. Consider the hypothetical situation in which the mixed layer penetrates to the same depth every year (i.e., the top of the permanent thermocline remains constant), where there are no advection (lateral or vertical), vertical mixing though the permanent thermocline, atmospheric deposition or nitrogen fixation and where no

material sinks past the top of the permanent thermocline. The system above the permanent thermocline is then closed. The recycling of nitrate via nitrification means that there will always be nitrate uptake by phytoplankton in the system following deep winter mixing or storm events. However, there is no export into the permanent thermocline by definition. If we wish to equate new production with export for this system (a seemingly pointless exercise) then we must adopt *Dugdale and Goering* [1967] in spirit rather than word and preclude all nitrate uptake, since for any year after the first (which should be ignored if we are considering an indefinitely repeating system) all nitrate will have been recycled. The exact time it takes for the nitrate to be recycled is immaterial.

[38] Now let the system be a little open such that a fraction of material does sink out each year and such that a little annual replacement of the system's waters with fresh external ones also takes place. Imposing equilibrium over an annual cycle, clearly the nitrogen content of the sinking material and removed waters equals that of the freshly imported material. This is very familiar as the initial motivation for the definition of new production. However, note that if the fraction of material exported from the system, into the permanent thermocline, is much less than the standing stock of nitrate above the thermocline at the height of winter then the nitrate mixed up to the surface by winter convection in subsequent years should not all be ascribed to new production when taken up by phytoplankton as the majority of it has been recycled within a year. Without knowing the flux into the system of new material it is impossible to know the relationship between total nitrate uptake and export production even if nitrification is measured all year. This is not because most of the nitrate has been recycled via nitrification that year but because it has been in previous years.

[39] Two conclusions can be drawn. First, if you wish to equate new production to export production (as defined by the first export loop) then it doesn't matter if nitrate is regenerated using organic matter created above the permanent thermocline the previous year, or even longer ago. It is still regenerated and should not be equated with new production. Second, the only way to estimate the true amount of new primary production (defined here as equaling export production over one year into the permanent thermocline) is to quantify the rate of delivery of fresh dissolved inorganic nitrogen into the system above the permanent thermocline (plus nitrogen fixation). Simple nitrate uptake measurements may be misleading as they may ''double-count'' the contribution of nitrogen that has resided above the permanent thermocline for a number of years, being recycled several times in the meantime. A key and tricky issue here is the residence time of water above the permanent thermocline in the subtropical gyre. For example, the background flow at BATS is sufficiently large and directed such that much of the water seen there will have spent the previous year in the western boundary current. Waters further south and east are likely to have resided above the thermocline within the gyre for more than a year making the issue of what nitrate is truly ''new'' a significant one. For this reason, this ''consistent'' definition of export cannot be investigated with a one-dimensional model. The variability in residence times over the region will also complicate attempts to extrapolate findings from a single location such as BATS to the rest of the gyre. Lateral advection, subduction, mixing, atmospheric deposition and nitrogen fixation will all influence the net input to a given location or region. The former three processes will most likely dominate [*Jenkins and Doney*, 2003; *Williams and Follows*, 2003]. Furthermore, these three fluxes can be directly estimated by integral tracer methods such as helium flux gauge measurements [*Jenkins*, 1988, 1998; *Siegel et al.*, 1999; *Jenkins and Doney*, 2003]. Tracer methods, therefore, currently provide the best means of quantifying new primary production in the sense of *Dugdale and Goering* [1967] in the field provided that they are performed over suitable periods, lengthscales and depth ranges [*Lipschultz*, 2001].

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