Global estimates of net carbon production in the nitrate-depleted tropical and subtropical oceans

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[1] Nitrate availability is generally considered to be the limiting factor for oceanic new production and this concept is central in our observational and modeling efforts. However, recent time-series observations off Bermuda and Hawaii indicate a significant removal of total dissolved inorganic carbon (CT) in the absence of measurable nitrate. Here we estimate net carbon production in nitrate-depleted tropical and subtropical waters with temperatures higher than 20°C from the decrease in the salinity normalized CT inventory within the surface mixed layer. This method yields a global value of 0.8 ± 0.3 petagrams of carbon per year (Pg C yr⁻¹, Pg = 10¹⁵ grams), which equates to a significant fraction (20 – 40%) of the recent estimates (2.0 – 4.2 Pg C yr⁻¹) of total new production in the tropical and subtropical oceans [Emerson et al., 1997; Lee, 2001]. The remainder is presumably supported by upward flux of nutrients into the euphotic zone via eddy diffusion and turbulent mixing processes or lateral exchange. Our calculation provides the first global-scale estimate of net carbon production in the absence of measurable nitrate. We hypothesize that it is attributable to dinitrogen (N₂) fixing microorganisms, which can utilize the inexhaustible dissolved N₂ pool and thereby bypass nitrate limitation.

INDEX TERMS: 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4806 Carbon cycling; 4825 Geochemistry; 4835 Inorganic marine chemistry; 0330 Atmospheric Composition and Structure: Geochemical cycles.


1. Introduction

[2] Net carbon production manifests itself though changes in salinity (S) normalized CT (NCₜ = Cₜ × 35/S) in oligotrophic oceans. The resulting vertical export of particulate inorganic carbon as CaCO₃ (EPIC) and organic carbon in both particulate and dissolved forms (EPOC and EDOC), respectively is related to ΔNCₜ as follows:

$$\Delta NC_t = EPIC + EPOC + EDOC + APOC + ADOC$$  

The ΔNCₜ (mol C m⁻² yr⁻¹) also includes the particulate (APOC) and dissolved (ADOC) organic carbon accumulating in the mixed layer. Lateral and vertical mixing of waters with different levels of NCₜ and net air-sea CO₂ exchange influence NCₜ as well [Lee et al., 2000]. Biological production of particulate and dissolved organic carbon either exported from the surface ocean or accumulating in the surface ocean generally dominates the other processes during the seasonal warming period. This net production of organic carbon in both particulate and dissolved forms occurs in tandem with sea surface temperature (SST) increase and can be quantified by time-integration of the NCₜ concentration decrease within the surface mixed layer during the summer season.

[3] Multi-year measurements at the Bermuda Atlantic Time-series Study (BATS, 31°50’S, 64°10’W) and the Hawaii Ocean Time-series (HOT, 22°45’N, 158°W) sites suggest that much of the net carbon production may occur in the absence of measurable nutrients [Michaels et al., 1996; Emerson et al., 1997]. Because of lack of observations this phenomenon has been neither confirmed nor quantified in other nitrate-depleted tropical and subtropical oceans. Analysis of recently collected NCₜ data throughout the nitrate-depleted tropical and subtropical oceans, however, shows that decrease in surface NCₜ concentration is correlated with SST increase (Figures 1a and 1b) [Lee et al., 2000] and can be quantified using empirical NCₜ-SST algorithms along with seasonal changes in SST and in mixed layer depth. Here we quantify the mixed layer NCₜ decrease in nitrate-depleted tropical and subtropical oceans with SST >20°C. Furthermore we hypothesize that this net carbon production is a previously undocumented form of new production, one supported by N₂ fixing microorganisms. The new production values determined from the mixed layer NCₜ drawdown in the nitrate-depleted waters are compared with literature estimates on N₂ fixation.

2. Computation Methods

[4] We estimate an annual rate of global new production in the nitrate-depleted oligotrophic waters, E₉ₐₐₜ, for each 4° latitude × 5° longitude grid cell, from changes in the NCₜ inventory within the surface mixed layer corrected for...
Figure 1. Plots of NC\textsubscript{T} versus sea surface temperature in areas between 40°N and 40°S. (a) NC\textsubscript{T} data in (sub)tropics excluding the western (sub)tropical Atlantic Ocean. (b) NC\textsubscript{T} data in the western (sub)tropical Atlantic Ocean. Data collected for waters with temperatures higher than 20°C and with no measurable amount of nitrate (<0.1 μmol kg\textsuperscript{-1}) are used to generate the fits. The solid lines are the regression results for data collected from the HOT and BATS sites. Insets are residual plots of results for data collected from the HOT and BATS sites.

3. Results and Error Analysis

An important assumption in our approach and conclusions is that temporal NC\textsubscript{T} decrease in the mixed layer can be quantified by using NC\textsubscript{T}-SST relationships derived from large-scale spatial NC\textsubscript{T} and SST data along with observed temporal SST and mixed layer depth fields. The results of this method are compared favorably with multi-year records of monthly NC\textsubscript{T} and SST observations from the BATS and the HOT sites [Lee et al., 2000]. Surface NC\textsubscript{T} values observed during the late spring-early summer period at these time-series sites, when nitrate concentrations are less than 0.1 μmol kg\textsuperscript{-1} and SST higher than 20°C, are inversely correlated with mixed layer temperature [Bates et al., 1996; Winn et al., 1998] and resulting relationships are in quantitative agreement with the regional algorithms.

Table 1. Estimated Rates of Total and N\textsubscript{2}-Supported New Production (Pg C yr\textsuperscript{-1}) in Nitrate-Depleted Waters (SST > 20°C and nitrate < 0.1 μmol kg\textsuperscript{-1}) During the Warming Period

<table>
<thead>
<tr>
<th>Ocean</th>
<th>Region</th>
<th>Area (×10\textsuperscript{12} m\textsuperscript{2})</th>
<th>Net air-sea CO\textsubscript{2} flux\textsuperscript{a} (Pg C yr\textsuperscript{-1})</th>
<th>N\textsubscript{2}-supported new production\textsuperscript{b} (Pg C yr\textsuperscript{-1})</th>
<th>Annual new production\textsuperscript{b} (Pg C yr\textsuperscript{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic</td>
<td>40°N–40°S</td>
<td>49.1</td>
<td>0.03</td>
<td>0.2</td>
<td>1.09</td>
</tr>
<tr>
<td>Indian</td>
<td>North of 40°S</td>
<td>43.3</td>
<td>0.01</td>
<td>0.1</td>
<td>0.79</td>
</tr>
<tr>
<td>Pacific</td>
<td>40°N–40°S</td>
<td>119</td>
<td>–0.02</td>
<td>0.5</td>
<td>2.29</td>
</tr>
<tr>
<td>Global</td>
<td>40°N–40°S</td>
<td>211.4</td>
<td>0.02</td>
<td>0.8</td>
<td>4.17</td>
</tr>
</tbody>
</table>

\textsuperscript{a}The gas-exchange formulation proposed by Wanninkhof [1992] for long-term winds is combined with the global climatology of ΔpCO\textsubscript{2} [Takahashi et al., 1997] to estimate the net air-sea CO\textsubscript{2} flux for each grid cell in which the mixed layer NC\textsubscript{T} concentration decreases as season progresses.

\textsuperscript{b}N\textsubscript{2}-supported new production is estimated from integrating decrease of the mixed layer total NC\textsubscript{T} during the warming period and values are corrected for changes in net air-sea CO\textsubscript{2} fluxes.

\textsuperscript{c}An annual rate of new production is obtained from Lee [2001].
depth fields derived from vertical density gradients are on average 10% lower than the value using those from vertical temperature gradients, although the magnitude of the error may vary geographically. (3) Net air-sea CO₂ fluxes; the estimated global rate is subject to an error of ±0.03 Pg C yr⁻¹ depending on the choice of relationships between gas exchange and wind speed. The probable error of the estimated global rate due to these three sources of error is dominated by (1) and thus is about ±0.3 Pg C yr⁻¹.

4. Discussion

Our estimates of new production in nitrate-depleted waters do not prove that N₂ fixation is the cause. But it is a distinct possibility. Therefore we compare our results with estimates and known regional patterns of N₂ fixation. In the comparison we assume that N₂ fixing microorganisms are exclusively responsible for the mixed layer NC₅ drawdown in nitrate-depleted warm waters, and we also assume an elemental C:N ratio of 7 to convert marine N₂ fixation rates to new production.

Several methods to determine N₂ fixation rates at the HOT site show broad agreement. New production rates derived from direct measurements of nitrogenase activity of isolated Trichodesmium colonies are in accord with the rate obtained from an indirect method using mass balance of the N:P ratio in upper thermocline waters. However, they are smaller than the rate estimated from the ¹⁵N isotopic composition of exported particulate matter [Karl et al., 1997] and our estimate for the grid point including the HOT site (Figure 3a). Rates derived from multi-year direct measurements of N₂ fixation rate with Trichodesmium biomass at the BATS site [Orcutt et al., 2001] are significantly smaller than our estimate for the grid point including the BATS site (Figure 3b). Directly measured rates are possibly underestimates because they do not include the potential contributions from other N₂ fixers that are found at these time-series sites [Zehr et al., 2001]. In addition to the well-recognized contributions from Trichodesmium, other less well-described N₂ fixation pathways are also possible, including endosymbiotic association of unicellular cyanobacteria and eucaryotic algae (especially diatoms) and free-living autotrophic and heterotrophic prokaryotes. Moreover, the N₂ fixation process is well known to be variable in both time and space, which makes large-scale direct estimation of stochastic bloom phenomena inaccurate if not biased.

Our estimated global new production rate supported by N₂ fixation of 0.8 ± 0.3 Pg C yr⁻¹ is approximately 4 times higher than the values derived from extrapolation of the limited direct shipboard measurements of N₂ fixation rates to the global scale using a historical dataset for Trichodesmium abundance [Capone and Carpenter, 1982; Carpenter and Capone, 1992]. When a more recent comprehensive representation of global Trichodesmium abundance is used, an average N₂ fixation rate that is derived from numerous direct measurements at various sites in the tropical oceans yields a global rate [Capone and Carpenter, 1999] which agrees well with our value (Figure 3c). Our global estimate is also similar in magnitude to the values derived from anomalies in the ratio of N:P in the upper thermocline waters of the North Atlantic and North Pacific [Gruber and Sarmiento, 1997; Deutsch et al., 2001]. This geochemical method does not quantify gross N₂ fixation but rather net N₂ fixation. Thus, it would not capture N₂ fixation if a certain marine environment simultaneously supports temporally coupled and comparable rates of N₂ fixation and denitrification [Karl et al., 1997]. If nitrogenase activity occurs during the seasonal cooling period and/or a fraction of new production is supported by high abundance of N₂ fixers in coastal regions and in marginal seas [Capone and Carpenter, 1999], our inferred new production supported by N₂ fixation would be low.
There are other sources of nitrogen that can support new production in nitrate-depleted waters but they appear to be less likely candidates. Inputs of fixed nitrogen from the atmosphere into the global oceans are estimated to be about 18 teragrams of nitrogen (Tg N yr\(^{-1}\), Tg = 10\(^{12}\) grams) \cite{Galloway et al., 1995}, which could sequester a maximum of 0.14 Pg C yr\(^{-1}\) if all of the atmospheric nitrogen was bioavailable and was deposited in the oligotrophic waters. Another possibility is that dissolved organic nitrogen (DON) utilization rather than N\(_2\) fixation fuels the NC\(_T\) drawdown in nitrate-depleted waters. There is no appreciable DON drawdown during the spring-summer warming period at the HOT site \cite{Church et al., 2002}. However, this remains a possibility due to a lack of DON measurements in the world ocean except for the HOT site.

Comparison of our new production estimate with those inferred for N\(_2\) fixation provided by other studies critically depends on knowledge of the C:N ratio in dissolved and particulate organic matter produced by marine N\(_2\) fixers. However, we do not know enough about all of the complex processes leading to this C:N stoichiometry. The elemental C:N ratio of 7 used in this study for conversion of N\(_2\) fixation rates to new production is much lower than the measured ratios of 20–30 in semi-labile dissolved organic matter produced by phytoplankton \cite{Church et al., 2002}. A large range of the elemental C:N ratio results in a similar magnitude of uncertainty in values of N\(_2\)-supported new production derived from direct measurements and indirect geochemical methods.

The distribution of N\(_2\)-supported new production shows distinct regional patterns in the global oceans (Figure 3). Significantly higher values are estimated for the tropical North Atlantic Ocean compared to the values for other basins. This is qualitatively consistent with results from other geochemical studies \cite{Michaels et al., 1996, Gruber and Sarmento, 1997}. It has been postulated that the atmospheric iron supply, which is essential for N\(_2\) fixation, plays a role in governing the spatial distribution of N\(_2\) fixation \cite{Falkowski, 1997}. Evidence for Fe-limitation is largely circumstantial; direct field assessments are not yet available.

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