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Biogeosciences Discussions

Interactive comment on "The fate of new production from N_2 fixation" *by* M. R. Mulholland

Anonymous Referee #2

Received and published: 24 August 2006

Referee's report, MS-NR: bgd-2006-0025, "The fate of new production from N2 fixation"
Author(s): M. Mulholland

General Comments The author addresses a timely, important question relevant to the field of Biogeosciences; that is, does the carbon (C) and nitrogen (N) fixed by diazotrophs contribute to "new" or "regenerated" production? The distinction between new and regenerated production has implications for carbon sequestration to the deep ocean, and thus away from the atmosphere, on thousand-year time scales. This manuscript serves as a review of much of the current literature, including observations of diazotrophic 1) N2 fixation and N release rate estimates 2) C fixation and C release rate estimates and 3) trophic interactions/dynamics. The most significant concern this reviewer has with this manuscript is largely semantic; while the stated purpose of the paper is to examine the evidence for diazotroph's contribution to new and/or regenerated production, it seems the terms "new" and "regenerated" production are not de-

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fined early on in the text. While the author understands the terms, defining these terms would greatly improve the clarity of the manuscript by giving a common definition and thus understanding of this critical terminology to both the author and reader. It seems a fundamental question raised by this manuscript is, "can gross N2 fixation still contribute to new production?" - on one hand it would seem that it could, since any N introduced by N2 fixation is "new" to the euphotic zone, although if gross N2 fixation includes fluxes from diazotrophs in the form of NH4+/DON, these forms of N are traditionally considered "regenerated" forms of N. This question is further motivation for the author to not just define the terms above, but to also explain their definition/categorization (for consistency w/ previous literature? to be consistent w/ a steady state model? etc.). The other major comment/question this reviewer has is does the author have any suggestions for experimental design and/or how to better address what appears to be an unresolved question based on the data presented here - does C and N "fixed" by diazotrophs contribute to new or regenerated production? How else can this question be tested to yield meaningful answers? What should the community work on? Method development? Culture studies? Field studies? In particular since this manuscript is largely a review of previous work, it seems that the perspective the author has gained from compiling this comprehensive set of data would lend itself to making suggestions for how best for the oceanographic community to proceed to make tractable progress on this difficult issue.

Specific Comments

Relevant scientific questions/within the scope of Biogeosciences: Yes, resolving the fate of N and C fixed by diazotrophs, as well as determining how it is cycled, and how much of it contributes to "new" vs. "regenerated" production, and by what means/pathways, is a critical question for the field to resolve, and is very relevant to Biogeosciences.

Novel concepts, ideas, tools or data: Whether or not the author is presenting any new data is unclear; much of the data, especially in the form of the tables, seems to be

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largely taken from a 2006 Limnology and Oceanography paper by the author. Since this issue of Biogeosciences is dedicated to the proceedings from a conference, it does not seem necessary that this manuscript strictly present new concepts, ideas, tools or data; however, if this manuscript is largely a review of previous work, it would be useful to the reader if the author explicitly stated that - it would help the reader understand the intent of this manuscript. Of course, if new information is presented here, this reviewer also encourages the author to emphasize that to draw the reader's attention to this important information.

Substantial conclusions: Again, since this is essentially a review of the material regarding a very complicated question, it may be unrealistic to expect substantial conclusions to be drawn, or result in arbitrary conclusions, especially considering the state of the data. However, this reviewer would again encourage the author to pose potential experiments or means of helping to resolve the vexing state of the data; are there experiments that could be performed to discern between the diazotrophic contribution to new vs. regenerated production that have not been tested? How does the author recommend the community proceed to make progress to resolve these issues?

Clarity of methods and assumptions: Again, since this is a review, less detail for methods is perhaps reasonable. However, since the methods for these measurements often contribute to the high variability of the data, it is important to at least describe the differences in techniques and their attendant assumptions; this is done.

Results sufficient to support conclusions: Again, this is a review of the poor state of our understanding of C and N cycling as mediated by diazotrophs. Since much of the data is contradictory, few conclusions are drawn, which is appropriate given the lack of other constraints.

Experimental and calculation descriptions: See methods and assumptions section.

Credit to related work/identification of new contributions: The author acknowledges the other work that is cited, although some other references and data could also be in-

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cluded to round out the study (see below). Additionally, it would be useful to the reader if the author explicitly identified the original contributions presented in this manuscript.

Title: This reviewer thinks that the title of this manuscript could be revised to more clearly express the questions at hand. As currently stated, "The fate of new production from N2 fixation", does not pose a question as to what kind of production is supported by new N from N2 fixation; instead it implies that N2 fixation supports "new" (and thus "export") production. Since "new production" must be balanced by export production (Eppley & Peterson, 1979, etc), this title suggests the manuscript will be a study of the mechanisms by which new N (and thus new production) is exported from the surface ocean. Instead, the question is, as stated in the last sentence of the abstract, "... the fate of production from N2 fixation will be examined..."; this reviewer suggests a title such as, "the evidence for new vs. regenerated production supported by N2 fixation". This would alert the reader to the primary goal of the author, which is to highlight the discrepancy in data for new vs. regenerated production supported by (new) N from N2 fixation. To be clear, this reviewer would suggest that the N introduced to the surface ocean from N2 fixation is by definition "new N", and so that flux of "new N" to surface waters, in steady state, must be balanced by an export flux of N. It would seem the simplest way to do so would be by that N supporting new (and thus export) production, although as the author describes, the traditional mechanisms for the trophic transfer of N do not seem to apply to N2 fixation... thus the relevance of the stated goal of the manuscript.

Abstract: One sentence describing the function of this manuscript, i.e., that it reviews the state of the literature regarding the fate of C and N from N2 fixation and its potential contribution to new and/or regenerated production, could help the reader appreciate/anticipate the content and structure of the paper.

Overall presentation structure: Language fluency: Not a problem

Units: Not a problem

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Suggested clarifications/reductions/eliminations: perhaps eliminating Figure 1; see comments below. Also, this reviewer strongly suggests that the author defines "new N", "regenerated N", "new production", "regenerated production", and "bacterial production" early on in the text.

Number and quantity of references: Generally good, see more specific comments below. The manuscript could include more references for the release of N depending on the physiological state of diazotrophs since this is often stated as a key complicating issue, as well as more discussion about the lack of field evidence for N2 fixation producing a resident DON pool; see Hansell and Carlson, 2001; Knapp et al., 2005, etc. Also, since this is a review of potential complicating factors for interpreting C and N fixation data from diazotrophs, this review wonders whether it would be relevant to have a brief discussion of the potential bias in C and N fixation rates by trace metal contamination, and also by the extremely high [PO43-] in most Trichodesmium cultures?

Supplementary material: Not relevant/not a problem

Technical Corrections

p. 1050, line 3: "...little is known about the fate of this production"; this reviewer would recommend rephrasing as, "little is know about the fate of this N flux", or "little is known about the productivity resulting from/associated with N2 fixation".

p.1050, lines 5-7: instead of "Specifically, does new production from N2 fixation...", this reviewer suggests, "Specifically, does N from N2 fixation fuel autotrophic or heterotrophic growth, and thus facilitate carbon export from the euphotic zone, or does it contribute primarily to microbial productivity and respiration in the euphotic zone, respectively?".

p. 1050, line 19: drop "the stoichiometry of" before "particles", change "with" to "within"?

p. 1051, lines 4 - 6: Trichodesmium spp. should either be singular or plural; use either

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"occurs" and "it", or "occur" and "they" (preferably singular?).

p. 1051, line 11; "." needed after (Carpenter and Capone, 2006) reference.

p. 1051, line 14, "a" needed before "significant source"

p. 1051, lines 15-16: instead of "little is known about the fate of this production, despite the importance of diazotrophs to global C and N cycles", perhaps, "little is known about the fate of the resulting primary production associated with this N flux" is a more precise expression of the stated goal/question? Since the focus of the sentence is the new N introduced via diazotrophy, not C fixation, it seems the question should be the relationship of this N flux to production, not simply "production" from N2 fixation? Or, if the author truly wishes to emphasize production, this reviewer suggests including C fixation at the beginning of the sentence in addition to N2 fixation on line 14.

p. 1051, lines 19-21: instead of "Inputs of N and carbon via N2 fixation and associated carbon fixation...", perhaps, "Fluxes of N and carbon associated with N2 fixation have been measured... ...however the quantification of export fluxes remain poorly constrained"?

p. 1051, lines 22 - 16: Would it be consistent to include a sentence after the author's list of mechanisms of Tricho death such as, "These observations indicate N2 fixation may primarily fuel regenerated production, unless there is another as-yet unidentified pathway to export surface N fluxes from diazotrophy to depth"?

p. 1052, line 1, instead of "... the fate of production from N2 fixation", perhaps, "the fate of production supported by N2 fixation"? This emphasizes the need to differentiate between C and N fluxes, not just in this instance, but throughout the text...

p. 1052, line 6, Trichodesmium spp. should be singular, and thus so should "diazotrophs", no?

p. 1052, lines 12 - 15; should read, "is comparable in magnitude to the estimated nitrate flux"? Also, this statement should be qualified; Capone et al., 2005, use only

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the diffusive flux of NO3- up from below, not the mixing flux supplied by seasonal overturn; see many Jenkins references, and also Knapp et al., 2005, for a comparison of N2 fixation and NO3- up from below as sources, which indicate NO3- is the dominant source of new N in oligotrophic North Atlantic environments.

p. 1053, lines 14 -25: move this paragraph to end of introduction to keep in situ/biological N2 fix assay rate estimates discussion together?

p. 1053, lines 19 - 20: can the author supply a reference for the statement, "rates of N2 fixation vary according to physiological state"? This would be a very interesting observation for many readers to follow up on...

p. 1053, lines 28-29: perhaps including, "is thought to" before "measures gross N2 fixation" is an appropriate qualification - has this statement been independently verified? Also, a ref at the end of this sentence would be useful, even though this statement is elaborated upon in the subsequent text.

p. 1054, line 3: remove comma after methods at end of line

p. 1054, line 4: remove comma after "other"

p. 1054, line 20: perhaps include a reference to Table 3 here?

p. 1054, line 23: remove "of" between "extrapolate" and "N2 fixation"

p. 1055, lines 8 - 11: "...these include factors resulting in underestimates of N2 fixation rates and rationalizations as to why Trichodesmium may have unusually high C fixation rates" - elaboration and specific examples would aid the reader.

p. 1056, line 1: Instead of "Another", perhaps starting the sentence with "An", since no other genomic findings have been discussed in the preceding sections....

p. 1056, line 9, remove "an" before "important"

p. 1056, lines 11 -15, perhaps including a reference to Eppley and Peterson, 1979,

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would be useful for the reader?

p. 1056, line 17: sp. should be spp.; also, either "nitrogen" or "N" is unnecessary at end of line 17.

p. 1056, lines 17 - 27: This reviewer suggests rephrasing some of the wording in this section. It may be helpful if the author explicitly defined what they consider to be "new" and "regenerated" production, and what forms of N support each, respectively, in the introduction of this manuscript. As per the traditional definition, and as is implied here, NH4+ and DON (including urea, amino acids, etc.) support "regenerated" production. However, if a large amount of NH4+/DON is released from diazotrophs and that NH4+/DON is used by phytoplankton that then are somehow exported from the euphotic zone, then NH4+ and DON can count as a "new" N source for "new" (or "export") production; this indeed seems to be the main thrust of this manuscript, as well as much other recent work. Also, if there is a large concentration gradient in DON, say as was observed in Karl et al., 1992, that surface to subsurface [DON] gradient can represent a flux of N from euphotic zone to depth ("exported" N ˜ "new N"), especially upon annual mixing. However, if there is no concentration gradient, and if that NH4+/DON "spins" infinitely in the "regenerated", suspended PON pool/in the euphotic zone, then it will indeed count towards the traditional definition of "regenerated" N supporting "regenerated" production. Additionally, while the author lists evidence for NH4+/DON release by diazotrophs, there is also field evidence suggesting that diazotrophs do not release NH4+/DON, or at least that it does not necessarily accumulate in surface waters, which seems that for balance's sake should also be included in this discussion section (see Hansell and Carlson, 2001, Knapp et al., 2005, etc.).

p. 1057, lines 19-21: can the author supply a reference for statement #2, "release products are rapidly taken up by organisms in oligotrophic environments"? Is this always, necessarily the case? As written, this would seem to contradict the observations the author has listed above, such as the accumulation of DON in surface waters as observed by Devassy et al., 1978, Karl et al., 1992, etc. Also, are there references for

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statement #3, metabolite accumulation?

p. 1057, lines 26 - 28: Again, definitions of what the author includes as "new", "regenerated", "net" and "gross" would be useful - while N released by diazotrophs may not accumulate in diazotrophic biomass and thus not could towards "net" fixation, it may still count towards "new" production - if N from N2 fixation represents a new, external source of N, and it contributes to production that is exported from the euphotic zone, then "gross" N2 fixation could still count towards "new" production, no?

p. 1058, line 5: is "recently fixed N" more precise than "recently reduced N2"?

p. 1058, line 9: unless the gross vs. net N2 fixation test has been independently confirmed, "excellent" is too strong a term to describe this estimate.

p. 1058, lines 23-26: please supply a reference for the variability in N release with physiological state and environment; this is referred to throughout the text, but we have yet to see a reference or have data discussed explicitly to support this claim.

p. 1059, lines 2 - 12: The author describes N release by diazotrophs as if this is an accepted fact, however, field evidence suggesting that DON is necessarily released, and/or accumulates, is inconsistent at best (Hansell and Carlson, 2001; Knapp et al., 2005). At this point, there is too little data to conclude either way that DON is or is not necessarily released by diazotrophs, and it would seem that a fair discussion would address both possibilities, and include all of the evidence regarding this question, in particular since much of the evidence for NH4+/DON release is from culture studies. In the end, all observations will have to be reconciled by a common, uniting theory, and so these observations deserve to be discussed, even if they seemingly complicate current explanations for diazotrophs and N cycling.

p. 1059, lines 21-23: awkward phrasing of sentence.

p. 1060, lines 5 - 6: awkward phrasing, "As for N, the amount of C released changed depending on light conditions and the physiological status of the cells" - please elabo-

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rate how this relates to N, and can a reference be supplied?

p. 1060, line 14: stating that cyanos release "C" compounds is unnecessary - simply stating that, "Cyanobacteria release compounds such as glycolate (ref), as well as amino acids containing both N and C (ref)" would be sufficient - in this "C release section", the reader does not expect the author will be discussing DIN compounds, so we expect these compounds will contain C.

p. 1060, line 20-22: is there a reference for the statement, "cyanobacteria in general can exude as much as 80% of the CO2 they fix as extracellular polymeric substances (mainly polysaccharides)"?

p. 1060, line 23: "was" should be "has"

p. 1060, lines 24-25: "Production of DOC ranged from 0.04 to 0.32 μg C col-1 h-1" - is this CDOM, or DOC? Same question for calculations immediately following...

p. 1061, line 2, no comma necessary after "globally"

p. 1061, lines 1 - 6: does the author have any suggestions for how to determine DOC release by diazotrophs? Is there a unique C isotopic signature for diazotrophs that can be exploited? Doesn't Carpenter, 1997, show that diazos have relatively high d13C? Would this be an effective strategy for tracking DOC release by diazos? Have there been any other studies of [DOC] gradients in space/time that may indicate C release by diazos? What about Hansell and Carlson, 2001, and HOT/ALOHA data? Can DOC release by diazos be resolved even if C:N ratios are uncoupled from Redfield ratios, as discussed above, and if diazos have highly variable C:N fixation/release rates such as the author documents?

p. 1061, lines 16-17: ref for bacteria and dinos as most common associates of diazos?

p. 1061, lines 17-22: please supply more refs for lack of grazing on Tricho. Also, do these observations suggest that N from N2 fixation is regenerated, or contributes to export production?

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p. 1061, line 25, should be "spp.", not "sp."

p. 1062, line 11; "varies" should be "vary"

p. 1062, lines 11-12; please give ref for "trophodynamics of Tricho vary depending on the form it takes and the amount of stable surface area and interfilamental space..."

p. 1062, line 13: should the first sentence of this paragraph be qualified with, "by Trichodesmium" at the end? There is a robust literature of trophic dynamics among plankton, especially using stable isotopes of C and N...

p. 1062, lines 23-25: please define "community productivity" - it sounds like this term is intended to be used as "regenerated production"; however, if "new N" is introduced to the system, under steady state, this must be balanced by a flux of N out of the euphotic zone, whether as a [DON] gradient or as a sinking flux, or by supplying the new production of other organisms that do eventually constitute a sinking N flux (this sounds like what the author is implying). Again, this relates to earlier comments in this review suggesting explicit definitions by the author of "new" and "regenerated" N, as well as "new", "export" and "regenerated" production.

p. 1062-63, lines 26-2: yes, indeed, much of the previous evidence for the importance of N2 fixation as a source of new N for export/new production cited in this manuscript is supported by the observations of low d15N in sediment trap material, including Karl et al., 1997. Also, Karl et al., 2002 and Knapp et al., 2005, show very low NO3- d15N in the shallow thermocline of the subtropical gyres, which is most easily explained by the addition of recently fixed N with a low d15N, indicating that as the steady state models suggest, the low d15N-N of newly fixed N is ultimately exported from the euphotic zone to depth, and thus that new N from N2 fixation ultimately supports new (as opposed to regenerated) production. The question, as this manuscript suggests, is by what mechanism is this N transferred, since few diazotrophs are found in sediment traps, and yet few organisms are thought to graze them...

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p. 1063, line 8: "Bacterial" instead of "Bacteria"?

p. 1063, lines 23-30: Is thymidine and/or leucine uptake indicative of bacterial colonization/productivity? More context, please. Also, please define "bacterial productivity".

p. 1064, lines 6-12: Are the amino acid oxidase and peptide hydrolysis activity observed unique to bacteria, or might we expect these types of activity to be supported by other co-occurring organisms, such as plankton? Also, are the rates quoted here higher than are otherwise observed in the oligotrophic ocean, where organisms are generally nutrient stressed, or higher than in other marine regions? Are these rates unusually high? Some context for the rates would be useful for the reader, since one assumes that some degree of protein/amino acid cycling occurs in all systems; otherwise, these molecules would accumulate rapidly, which is certainly not observed for amino acids and protein in the ocean.

p. 1064, line 24: remove "population"?

p. 1065, lines 1-3: again, other (indirect) evidence of trophic transfer of N from diazotrophs to other organisms is the low d15N observed in sediment trap material (and thus in the export flux), as well as the low d15N of NO3- observed in the N. Atl and N. Pac subtropical gyres' thermocline.

p. 1065, lines 25-26: please supply a reference for the statement, "... although isotopic evidence suggests that there are other grazers of Trichodesmium" - is this a reference to the d15N of organismal biomass? To the d15N of some form of N in the ocean? Please specify...

p. 1066, lines 21-26: would it be worthwhile to suggest measurements of C and N fixation by diazotrophs not be reported in units of "per colony", but in volume units (i.e., per liter, meter cubed)? Is there a better metric the author can suggest the community use rather than "per colony", since that seems to have serious liabilities (e.g., what is a colony)?

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Table 1: Although the footnote says the rates are converted from daily to hourly rates, the caption says it's unclear whether or not N2 fixers should be expected to fix at night; why not leave rates in per day? Wouldn't this obviate the problem? Otherwise, aren't up to 50% errors being introduced into the data in this table? Also, is there any way to convert out of "per colony" units, and into volume units, to remove the arbitrariness of "per colony"?

Table 2: Instead of "C2H2:N2", perhaps "C2H2:15N2" is more precise?

Table 2: What about data from Montoya et al., 1996?

Figure 1: The beginning of the caption says the schematic represents N cycling in the oligotrophic ocean, however, by definition, "HNLC" regions (as depicted in panel "b") are not low nutrient (oligotrophic); they are "High Nutrient Low Chlorophyll" regions, presumably limited by Fe, etc. This is also mis-phrased in the caption for panel b. Simply rephrasing the beginning of the caption as "Nitrogen and carbon cycling in different oceanic regimes" would be a more general, appropriate description of the cartoon. Is panel B necessary? Is it referred to anywhere throughout the text? Perhaps it is simpler and more relevant to only compare/contrast panels A and C in this figure... If panel B stays in, please insert "CO2" after "sequestration of atmospheric" in the caption.

Figure 1, panel A: This reviewer suggests the arrow in the subsurface point the other direction; in the subsurface, it is assumed that PON/POC are remineralized to NO3-/DIC, while in the surface, NO3-/DIC are incorporated into biomass (PON/POC).

Figure 1, panel C: what is the process represented by the flux of N2 from the surface ocean to the atmosphere? Does this represent denitrification? Is this relevant to this text? Figure 1, panel C caption: if something is "new production", it necessarily results in sequestration of C via an export flux. Perhaps calling the flux "new N" is more appropriate, although even that must still exit the euphotic zone w/ a balancing export flux, otherwise the system is not in steady state. Again, this relates to the on-going

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semantics theme of this review.

Perhaps Figure 1 is unnecessary? Figure 2 seems to incorporate relevant themes. In particular, if there was an arrow from the subsurface bring NO3- and DIC up from the subsurface to the surface, Figure 2 could due double duty for both Figs 1 and 2...

Figure 2: perhaps adding a label above each cartoon, "New" above the left panel, and "Regenerated" above the right panel, would help describe the schematics?

Interactive comment on Biogeosciences Discuss., 3, 1049, 2006.