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Biogeosciences Discussions

Interactive comment on "Phosphate availability and the ultimate control of new nitrogen input by nitrogen fixation in the tropical Pacific Ocean" *by* T. Moutin et al.

T. Moutin et al.

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We wish to thank reviewer 1 for his in-depth work on the ms. Most of the remarks have been taken into account as detailed below:

AR1: While this paper contains important interesting information I can't recommend it for publication in its current form. Overall, this paper needs more work. Some sections need to be rewritten because the text is not clear. The P pool is very well characterised. Nevertheless, the paper suffers of a lack of N2 fixation data.
RESP: The aim of the paper is essentially to present data describing P availability and its relationship with nitrogen fixation in the tropical Pacific Ocean. The complete description of the Nitrogen cycle (including N_2 fixation data measured during the

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BIOSOPE cruise) is presented in the supplementary paper of Raimbault and Garcia, Biogeosciences discussion 4, S1419-S1425, 2007 in the same special issue. This paper will refer to ours when comparing N2 fixation data and model estimation from the SP gyre.
In response to the observed lack of N2 fixation data, we now include the vertical profiles of N2 fixation data from the SP gyre and SW station (Garcia et al., 2007) in fig. 3.
AR1: The abstract needs to be improved. P data are not clearly linked to N2 fixation data. Some results do not appear in the abstract such as: there is no P limitation of N2 fixation in the south east Pacific ocean, temperature is probably a key factor in N2 fixation control in this area...
RESP: The abstract has been modified to take into account these remarks
AR1: Lines 5 and 8 replace phosphate by phosphorus
RESP: The element phosphorus P exists only in the PO4 form (oxidation number V) in water, despite its mineral (inorganic) or organic, particulate or dissolved, status. Therefore, the generic term phosphate is more appropriate than phosphorus and chosen by many authors working on this topic.
AR1: Line 11: ...remained above 100 nM in the upper layer (0-200m) and TDIP were more than 6 months (min value _200 day fig. 2e and 3h)
RESP: Correction done
AR1: line 15: ...during the summer season in the upper layer
RESP: We added “in the upper layer”
AR1: Introduction :
Page 2409
Line 7 : Karl et al., 2007 is not in the list of references
Line 4 to 9: the sentence is too long. Need to clarify in the text that the increase of N2 fixation rate with pCO2 is based only on culture experiments of Trichodesmium (see also Hutchins et al., 2007)
Line 10 : add : changes in atmospheric Fe inputs (Tagliablue et al., 2007, Biogeo-

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sciences discuss.,)
Line 12 : “an increase in diazotrophic populations” : does it mean an increase of biomass or diazotrophic species number ? please clarify it
Line 20 : While the atmospheric source of P is probably low it is definitely not zero as suggested in the text
RESP:
Line 7, it is in press.
Line 4 to 9: the sentence was shortened. We deleted “and even on the carbon dioxide concentration in areas where light and nutrients, such as P or iron (Fe), are not limiting (Levitan et al., 2007)” because it is confusing and the ms focuses on the tropical Pacific ocean where nutrients are limiting.
Line 10 : Tagliabue et al., 2007 was added
Line 12 : Done
Line 20 : We changed “no” by “a negligible”.
AR1: Page 2410
line 1 : ...add : N2 fixation rate
Line 16 : the reference Levitan et al 2007 is not correct
RESP:
Line 1 : rate was added
Line 16 : It has been added directly from ISI Web of Knowledge and verified. It seems OK.
AR1: Method Page 2411 : N2 fixation
Only 0.6 L was incubated for N2 fixation rate. 2 to 4 L are generally needed in oligotrophic areas to measure N2 fixation rate (15N2), e.g. Needoba et al., 2007 L&O. Therefore, I am really surprised that the authors can measure significant N2 fixation rate with a so small volume. Please comment
RESP: During the BIOSOPE cruise, uptake rates for 3 forms of nitrogen were performed simultaneously: nitrate, ammonium and diazote. For practical reasons, we choose to work with smaller volumes of water samples but defined a corresponding

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detection limit. All the procedures are detailed in Raimbault and Garcia, this issue. The dual isotopic enrichment analysis were performed on an Integra-CN mass spectrometer calibrated with glycine references following every batch of 10-15 samples, with a very low detection limit of 3 μg N (0.2 μmoles N, corresponding to that given by the manufacturer). The following relationship was obtained with a PN range between 0 and 150 μg: [Measured PN] = 0.9757[Theoretical PN]+2.7 with r2=0.9955.

The accuracy of our analytical system was regularly verified using reference materials from the International Atomic Energy Agency (AIEA, Analytical Quality Control Services), see table 1 at the end.

The mean delta^{15}N does not vary between 0.2 and 10 μmoles N (figures 1 and 2 at the end). The low background of the system enables us to analyse samples containing low nitrogen concentrations (0.2 μmole = 2.8 μg N), values often observed in surface oligotrophic waters.

Finally, the ^{15}N isotope enrichment of a sample is reported in terms of atom % excess ^{15}N or delta^{15}N over time, for the atom% ^{15}N or delta^{15}N in a sample that is not enriched, taken from the same phytoplankton population **and containing the same PN**. Therefore, the value of time zero enrichment is necessary and determined along with the samples (same volume as incubated sample) and were filtered immediately after isotope addition. For N_2 experiments, the time zero value, established from 8 samples, was 0.3676 $\pm$ 0.007%.

Due to the natural variation of delta^{15}N (-5 to 158240;), we considered results to be significant when ^{15}N excess enrichments were higher than 0.014 % (twice the standard deviation obtained from time zero samples), equivalent to delta^{15}N = 378240;. Finally, according to the experimental conditions, the detection limit for nitrogen fixation, calculated from significant enrichment (0.014% in excess) and lowest particulate nitrogen (0.2 μmole N) is estimated to be 0.12 nmol.l^{-1}.d^{-1} (for an initial $^{15}N_2$ enrichment $R_{N2} \approx$ 24%).

AR1: 24h incubation time: The Montoya 15N2 method of measuring nitrogen fixation has the advantage of using the actual substrate for the nitrogenase enzyme, rather

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than an analogue as in the acetylene reduction assay. It also has a number of serious drawbacks.

The most serious is that much of the nitrogen fixed by diazotroph is released as ammonium or DON on very short timescales, so it typically results in an underestimate of nitrogen fixation. New data suggests that as much as 20-80% of fixed nitrogen can be released over the course of a short incubation. This would of course lead to large underestimates of nitrogen fixation in this experiment. Was any attempt made to quantify DON or DIN release? Comment.

RESP:

It is true that N_2-fixation rates could be underestimated due to some DON or DIN release, as we have shown for nitrate and ammonium (Raimbault and Garcia, same issue).

A method now exists to determine DON losses during ^{15}N experiments and we have used it for our nitrate and ammonium uptake experiments. However it needs significant ^{15}N uptake, to significantly enrich the particulate pool, and then the dissolved organic pool.

In the present experiment, N_2 fixation rates were around 1 nmoles.l^{-1}during the incubation time given, and the initial $^{15}N_2$ enrichment was around 25%. Then the quantity of tracer fixed was 0.25 nmoles per liter. If we consider that the same quantity could be released in the DON pool (5000 nmoles.l^{-1}), the final enrichment in the organic pool would be equivalent to (0.25/5000) x 100 = 0.005 % in excess.

This enrichment in the DON pool is too low to be measured accurately using the available methods. So, even if some ^{15}N tracer is lost in terms of DIN or DON during the $^{15}N_2$ fixation experiment, there is no procedure available to detect it in oligotrophic waters, especially in the absence of large populations of diazotrophs. There is no information or data available thatshows significant DIN or DON release by diazotrophs (other than Trichodesmium) in open oligotrophic oceans.

As discussed by Slawyk et al. (2000) and by Raimbault et al. (2000), DON loss during ^{15}N experiments can not exceed 50%, when tracer is added to the inorganic com-

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partment. Higher release rates of ^{15}N tracer could lead to large losses of particulate nitrogen leading to a dramatic decrease in biomass.
Moreover, in oligotrophic systems, it is obvious that a tight coupling exist between autotrophs and heterotrophs. A large quantity of organic matter released by primary producers (essentially carbohydrates) is immediately taken up by bacteria, mostly collected on GF/F filters. We can hypothesize that the same coupling exists for nitrogen in a system where this element is dramatically depleted.
Slawyk et al. 2000. Use of ^{15}N to measure dissolved organic nitrogen release by marine phytoplankton (reply to comment by Bronk and ward). *Limnol. Oceanogr.*, 45 :1884-1886.
Raimbault et al. 2000. Comparison between chemical and isotopic measurements of biological nitrate utilization: further evidence of low new production levels in the equatorial Pacific. *Mar. biol.*, 136:1147-115
AR1: Please detail in the text if you made duplicates
***RESP:** We didn't make duplicates. During a cruise, choices have to be made between sampling in duplicates or having twice as many depths. We definitively chose to sample more depths as duplicates (when done) revealed small variations. Sometimes, triplicates or even more samples are analysed to measure the SD between samples on a single Niskin bottle.
AR1: Line 19: What samples (i.e. what type and weight) did you used for the determination of background natural abundance?
RESP: Some T0 experiments were performed to determine the natural background or, rather, the initial enrichment in the same conditions as for incubated samples. Surface samples were enriched with ^{15}N-tracer, and immediately filtered without an incubation step. Procedures and results are described in Raimbault and Garcia, same issue. For the labelling ^{15}N-tracer experiment, we prefer to use T0 values obtained using the same PN and the same quantity of tracer instead of the conventional natural background.
AR1: Page 2412 : P pools

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DIP : please detail in the text if you made duplicates for DIP measurements and provide the standard deviation
PP : Detail in the text if you made duplicates. What is the detection limit for PP? 20 nmol L-1? what is the pressure of filtration ?
DOP : please detail in the text if you made duplicates and provide the uncertainty of DOP estimates
RESP: See also ***RESP:**
DIP : We added this sentence :"Only one sample was analysed per depth with the exception of the S-gyre station where triplicate samples were collected". We provided the SD for Arsenate because no significant variations were observed in the concentrations with depth. This was not the case for DIP. Here, all DIP measurements at the S-gyre station were reported fig. 3(e) which gives a better representation of what was measured.
PP: We added this sentence. "Only one sample was analysed per depth with the exception of the S-gyre station where duplicate samples were analysed. From calculations : 1000 mL of filtered water concentrated to a final volume of 25 mL has a concentration factor of 40, and a detection limit of 0.5 nmol L-1. We added:" Considering a concentration factor of 40 (final volume = 25 mL), the limit of detection was 0.5 nmol L^{-1}." We added :". . . at very low pressure. The pressure was increased to get a drop by drop filtration and never exceeded 0.1 bar".
AR1: Page 2413: TDIP please detail in the text if you made duplicates and provide the standard deviation
RESP: We made duplicates, it is written Line 24: DIP turnover time was measured in 50 mL duplicate sub-samples from each bottle. We provide only the means because a SD from duplicates is not statistically meaningfull.
AR1: Page 2414:
Pressure of 0.6 bars: this high filtration pressure could potentially damage cells leading an eventual release of 33P in the dissolved phase. A consequence of this would be an underestimation of radioactivity on the filter. Comment.

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RESP: It is true, but this the only possible method for separating the 33P in the dissolved phase from 33P in the particulate phase.The method has been regularly employed since its first use (Thingstad et al. 1993). This author showed that increasing the pressure to 0.6 bar at the end of the filtration does not lead to significant loses of material if the filtration is stopped without breaking the vacuum (possible with Millipore manifold system) and not followed by any rinsing procedure (water or other solutions). Our recent results,using a dual-labelling (^{14}C and ^{33}P) technique confirms this experimental result.

Duhamel, S., Zeman, F. and T. Moutin, 2006A dual-labelling method for the simultaneous measurement of dissolved inorganic carbon and phosphate uptake by marine planktonic species. Limnology and Oceanography: Methods 4: 416-425.

AR1: Have you withdrawn the blanks from samples counts?

RESP: Yes, it is written Line 6-7

AR1: What is the mean and maximum blank values (percentage of the radioactivity in the samples) ?

RESP: Sample counts were 10 times higher than the blank values. The confusing sentence Line 20-24 was modified as follows: Sample counts were at least 10 times greater than the blanks, less than 10 % of the radioactivity in the samples was consumed and incubations did not exceed several hours in order to minimize the increase in bacterial production caused by confinement.

AR1: Line 11: could you please add a reference for P monoesters?

RESP: We used the Strickland and Parsons, 1972 procedure to measure the labile DOP within the gyre. It is written line 10. Then, we assume that the labile DOP is mainly composed of P monoesters: it is a classical assumption as P monoesters are the simplest form of dissolved organic molecules that can be found in aquatic waters.

AR1: Labile DOP: please detail in the text if you made duplicates and provide the uncertainty

RESP: It is written Line 13: At each station from the NW edge to the centre of the gyre, 50 mL triplicate surface samples. . . The mean SD of each triplicate was 16 nmol

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L-1. Because the labile DOP measurement depends on DIP measurements whose DL is 20 nmol L-1, the labile DOP DL could not be lower. Then, we compared our results with this number (Paragraph 3.1.1.). In any case, the labile DOP as defined (Strickland and Parson, 1972) was close or below the DL and then unmeasurable. This result is very important because some authors working on DOP uptake by phytoplankton (after APA) consider in their calculation that all DOP pool is available which is far from the truth as demonstrated here (See also Moutin et al. 2005).

Moutin, T., N. Van Den Broeck, B. Beker, C. Dupouy, P. Rimmelin & A. Le Bouteiller. 2005. Phosphate availability controls Trichodesmium spp. biomass in the SW Pacific ocean. Mar. Ecol. Progress Ser. 297, 15-21.

AR1: Page 2415:

Line 3: Clarify what is P*

RESP: We modified the paragraph as follows: The recently defined variable P* (Deutsch et al., 2007) was calculated: P* = PO_4 – NO_3/rr (rr = Redfield ratio = 16), PO_4 = DIP in this study. While nutrient uptake by non-N_2-fixing organisms will on average consume NO_3 and PO_4 in a proportion that conserves P*, N_2 fixation will extract PO_4 alone, driving a water parcel towards lower P* (Deustch et al., 2007).

AR1: Result

Page 2415

Line13: Do chlA values confirm the low biomass estimated with PP?

RESP: Yes, we added: . . . , as confirmed by total chlorophyll a concentrations reaching 0.017 mg m^{-3} in surface waters in the centre of the gyre (Ras et al. 2007).

J. Ras, H. Claustre, and J. Uitz. Spatial variability of phytoplankton pigment distributions in the Subtropical South Pacific Ocean: comparison between in situ and predicted data. Biogeosciences Discuss., 4, 3409-3451, 2007

AR1: Line18-19: the detection limit for labile DOP is 20 nM, please clarify then how you could give 4.7 nM of labile DOP?

Please include in the text the labile DOP data. Are they all below detection limit? What is the spatial distribution of this parameter? Comment

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RESP: This result is obtained by difference as explained in the method section Line 18 p. 8. The result 4.7 nM with a SD of 15 nM is thus possible and as noticed, close or below the detection limit of 20 nM.
We have provided the labile DOP data (table 2 at the end) but not in the paper as we do not think it is necessary. As explained in the paper, these concentrations are close or below the detection limit throughout the gyre, when measured without a marked spatial distribution. It is one of the major results of our paper. It is not as important to know whether labile DOP contributes significantly to the DOP pool outside the gyre because the DIP/DOP pool values are higher.
AR1: Line 23: undetectable ($<$ 3 nmol L-1)
Page 2416:
Please include the mixed layer depth data and also the max chla depth
RESP: we have included the depth of the chla max when talking about PP: No maximum value was obtained from the deep chlorophyll maximum (180 m). We have no particular reason to include the MLD here.
AR1: Could you explain the variability of DIP measurements at 250m (fig 3e)? please comment
Replicates gave a higher variability at this depth but there is no explanation.
AR1: Line 5: 3.5 μmol.m-4 ?check units
RESP: It is the slope between concentration (μmol m-3) and depth (m), thus μmol.m-4 is OK.
AR1: Line 17: if the PP detection limit is 20 nmol L-1, please clarify then how you could give 9.3 nmol L-1
Line 19 : same remark for 1 nmol L-1
RESP: PP detection limit is 0.5 nmol L-1 as iis now stated in the method section.
General remark: It is possible to obtain a value (above the blank reagent for example) but under the detection limit (classically 3 times the blank reagent in chemistry).
AR1: Page 2416-17-3.1.3
Please add that in the upper layer, the maximum values of DIP (and for TDIP) are

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recorded at S-gyre station when compared to the other stations.
RESP: It is added
AR1: At the SW station during summer, how do you explain the DIP decrease and the "no variation" of DOP and PP ?
RESP: It could be explained by an export of PP out of the photic zone
AR1: Please compare PP concentrations at S-gyre and N-gyre stations with those at SW
RESP: We completed the following sentence: The PP concentrations at the N-gyre station were higher (by a factor of 1.5) than those in the more oligotrophic S-gyre station and close to or lower than those at the SW-station.
AR1: Line 15: add : near the sea surface at N-gyre station
RESP: Done
Page 2417 3.2
AR1: N2 fixation is a central parameter in this paper. However, the paper suffers of a lack of N2 fixation rate data. The three profiles (1 Chilean coast station and 2 S-gyre station) would provide very useful and necessary data. Please, include this new figure. If the same data are available for SW and N-gyre, please include them also.
RESP: We include N_2 fixation rate data to complete fig. 3.
AR1: Bonnet et al., 2007, Biogeosciences were unable to measure nitrogen fixation rate in their experiments with the same protocol used in this paper, even after iron and/or phosphate additions. Please discuss
RESP: It is true that we are unable to detect N_2 fixation following the addition of P or Fe during the Bonnet et al's experiments
The ^{15}N experiments and the analytical procedure were the same as those used during in situ experiments. However the sampling method was different. During direct measurements of N_2-fixation (present work), samples were collected at different depths using Niskin bottles. Samples were immediately spiked with $^{15}N_2$-tracer and rapidly placed in an incubator, (generally less than 30 minutes after sampling). For Bonnet et al's experiments, samples were collected at 30 m using a peristaltic pump

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equipped with Teflon tubes. Then, large volume samples were treated over a long duration (several hours) in the dark or under very low light intensities. ^{15}N-tracer and incubations started some hours after sampling for t0 samples, and one day after sampling for the others. During these experiments we did not detect significant ^{15}N-enrichment in particulate nitrogen. Table 3 gives the ^{15}N enrichment (delta^{15}N) obtained during the experiments. Some T0 samples, those treated more quickly than others show some delta^{15}N higher than 378240;, a value we consider to be significant during our experiment. The other samples exhibit lower values, due to the absence of N2-fixation or due to uptake of another form of nitrogen as ammonium artificially added to the N-samples.

AR1: Please, explain the large observed variability in the N2 fixation flux at the S-gyre station: 48 and 135 μmol N m-2 d-1 at the S-gyre station?

RESP: We observed the same variability in nitrate and ammonium uptake. It may be due to changes in light intensity because of cloudy weather:

12/11/2004: mean Irradiance intensity was 26 E.m-2.s-1 and N2 fixation around 48 μmol N m-2 d-1

14/11/2004: mean Irradiance intensity was 44 E.m-2.s-1 (value generally registered along the cruise) and N2 fixation around 135 μmol N m-2 d-1

We added : ... and 48 and 135 μmol N m^{-2} d^{-1} at the S-gyre station (from 2 *in situ* depth profiles between 0 and 200 m taken on two different days). A doubling of the mean irradiance intensity and similar variations of ammonium and nitrate uptake rates were also observed.

AR1: line 19 : add : in surface waters

RESP: Done

AR1: line 20 : Please include the data for the Marquesas islands station and depth

RESP: Done with the range for surface water

AR1: line 21: what depth ?

RESP: "Surface waters" was added

AR1: line 23 : Is 40m the mixed layer depth at Chilean coast station?

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Line 24: Is 200m the mixed layer depth at the S-gyre station ?
RESP: No, it corresponds to the maximum depths where we sampled and the approximate euphotic zone depth.
AR1: Line 25 : low N/P, provide values
Line 26 : "ample Fe concentrations are found". . . please include the values and the associated reference(s)
RESP: Done
AR1: Page 2418 : I agree with the light control of the N2 fixation flux. Nevertheless, iron bioavailability can also be a control factor.
RESP: Yes. It was just a remark here in the results section. Discussion concerning iron bioavailabilty is found in paragraph 4.2.2
AR1: Karl et al., 1992 and 2007 are not in the list of references
We deleted Karl et al., 1992 and changed Karl et al., 2007 by Karl et al., in press.
AR1: Could please compare your data with those found in other publications like Needoba et al., 2007, Falcon et al., 2004.
RESP: We added : "The N_2 fixation rates measured inside the SP gyre are close to the averaged 0.25 $\pm$ 0.05 nmol N L^{-1} d^{-1} measured in oligotrophic waters of the NP Ocean where water temperatures are typically below 20-25˚C (Needoba et al., 2007). Integrated rates in the SP gyre are similar to those reported by Falcon et al., 2004 for the tropical NA in summer (62 μmol N m^{-2} d^{-1}, SE = 21, n=30) and February 2001 (167 μmol N m^{-2} d^{-1}, SE = 49, n=30) and in the subtropical NP (84 $\pm$ 50 μmol N m^{-2} d^{-1})."
AR1: Page 2419
I did not find Raimbault and Garcia, 2007. I found Raimbault et al., 2007. Is it the same paper?
RESP: It is not the same paper. The paper Raimbault and Garcia (2007) is now available in the Biogeosciences discussion.
AR1: Page 2420 :
No Trichodesmium were recorded in the study area. Precise in the text that Bonnet

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et al., 2007 found the presence of extremely low numbers of Group A cyanobacterial phylotypes (see Table 2 in this paper).
RESP: We added that comment to paragraph 3.2
AR1: Page 2423 - temperature
Could you please add the ODV map of temperature.
Line 18 : I do not agree with your sentence “temperature does not restrict diazotroph growth”. Breitbarth et al., 2007 have shown an effect of temperature on growth rate and nitrogen fixation rate of Trichodesmium.
In the abstract, it is written “During the BIOSOPE cruise, N2 fixation rates were higher within the cold water upwelling near the Chilean coast.” Could you please provide the temperature data in this area. How do you explain this high flux within the cold water upwelling?
RESP: The sentence “temperature does not restrict diazotroph growth” was deleted. It is clear that Trichodesmium abundance is clearly related to temperature and that blooms of this species require temperatures above 25°C. We provide temperature data and show that maximum N2 fixation rates are observed when the lowest temperatures are measured. It is likely that other N2 fixing organisms do not have the same temperature dependence as Trichodesmium spp.
AR1: Line 25: Paerl, 1994 is not in the list of references
RESP: Done
AR1: Page 2425:
Line 18: Have you made a statistical test to compare P* and N2 fixation rate?
RESP: No but we take into account this remark and determine the following relationship N2 fixation = 6.37P*-0.41 (n=136, r2=0.49), significant using a non parametric Pearson test ($p<0.001$).
AR1: Page 2427:
Please add a reference for Mediterranean sea
RESP: We added (Bonnet & Guieu, 2006) who wrote:” The occurrence of high nitrogen fixation rates during the period of high DFe concentrations indicate that

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atmospheric DFe may participate in the nitrogen fixation process."

AR1: Figures

Figure 1:

Increase red line thickness. Please, use another color for Aloha and SW stations which are not part of the BIOSOPE cruise.

RESP: We changed the colour for the Aloha and SW stations and added Latitude but didn't increase red line thickness as it is not possible with the program which generates the map and it does not seem to be obligatory.

AR1: Figure 2 :

Change the scale for nitrate concentration because it is very difficult to see any changes especially in the center of the gyre. Are you sure that the units of nitrate concentration are expressed in μM ?

RESP: Done. Yes, nitrate concentrations are expressed in μM. We have added the isoconcentration 0.05 μM for a clearer understanding of the figure.

Figure 3 :

AR1: Could you include the references for Aloha and SW data?

We added the website where references and data could be obtained.

Fig e : +S&P, _ magic : not clear

Table :

Table 1 : Please provide the references for Aloha and SW data ?

Done

Tables and figures: see Reply Part 2

Interactive comment on Biogeosciences Discuss., 4, 2407, 2007.