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Biogeosciences
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Interactive
Comment

Interactive comment on "Co-limitation by iron, silicate, and light of three Southern Ocean diatom species" *by* L. J. Hoffmann et al.

L. J. Hoffmann et al.

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Authors reply to the reviews on the manuscript "Co-limitation by iron, silicate, and light of three Southern Ocean diatom species" by L. J. Hoffmann et al.

There are a few major points in the experimental set up that lead to the rejection of the entire manuscript by the reviewers. However, both reviewer and the editor agree, that co-limitation is an important question for the ecological understanding of diatom growth in the Southern Ocean. We feel that our experimental set up is never the less suitable to tackle this interesting scientific question and in the following we explain our reason to use this approach and thereafter answer the specific remarks.

Both reviewers doubt that the choice of 20 μM Si/l for the low Si treatment can limit diatom growth and that the results of these experiments can be extrapolated to the

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low silicate regions of the open Southern Ocean. It seems that both reviewers are generally in doubt with culture work. Nutrient concentrations in culture experiments are normally much higher compared to natural systems. This is necessary since phytoplankton cell concentrations usually have to be very high in culture experiments to get enough biomass for different measurements. When comparing these experiments with natural systems not the absolute nutrient concentration is important but the nutrient concentration that is available for each cell. A natural system works as a giant chemostat and even very low nutrient concentrations can be sufficient for growth as they are supplied constantly for each cell. The following calculation shows that in our batch culture experiments 20 μM Si/l, the concentration used in our low Si treatments, is very low, taking the high cell density in the experiments into account.

The C. dichaeta strain used in this experiment has a cellular Si content of about 0.7 pM under favorable growth conditions (Hoffmann et al., submitted to Biogeosciences). This species had a start concentration of 11000000 cells/l in all treatments of our experiment. Therefore, 7.7 μM Si would be taken up at the first and additional 15.4 μM Si at the second cell division assuming normal silicification. In other words at a start concentration of 20 μM Si and a cell density of 11000000 cells/l this species could not even pass two complete cell divisions under normal silicification before all Si of the growth medium is taken up (7.7 μM + 15.4 μM = 23.1 μM). Another indication for Si limitation even at relatively high concentrations are the half saturation constants (Ks). The Ks values of Fe-limited diatoms reported in the literature vary a lot. Brzezinski et al. (2005) for example report Ks values of 4,4 +- 1,9 up to as high as 12,1 +- 3,6 μM for low Fe SO waters. This shows that Si concentrations can limit diatom growth even at much higher concentrations as commonly found in the SO north the Polar Frontal Zone. It additionally shows that Si concentrations in our low iron treatments can be limiting soon after the beginning of the experiment, when some of the initial Si concentrations have been used. Further, the morphological changes observed in our low silicate treatments are similar to those found by Harrisson et al. (1977) using chemostats. We therefore are confident that our basic findings can be extrapolated to natural systems. We will

include this discussion in the new version of the manuscript. The estimation of free iron concentrations in the growth medium is a procedure commonly used in similar laboratory experiments (Leynaert et al., 2004; Sunda and Huntsman, 1995; Sunda and Huntsman, 1997; Sunda and Huntsman, 2000; Sunda et al., 1991; Timmermans et al., 2001a; Timmermans et al., 2001b; Timmermans et al., 2005) (see also reply to comment # 6 of reviewer # 1). Our data are therefore comparable to and in line with other experimental work. The storage problem mentioned by reviewer # 1 does not affect the current data set. Total cell counts and morphological changes were not affected by fixation at all. As described in the authors reply to the comment # 10 of reviewer # 1 only data of chain length taken directly or within one week after fixation are presented in this manuscript. This short storage time did not affect chain length in our experiments.

Detailed authors reply to review # 1 by B. Quéguiner:

Quéguiner comment # 1: Abstract 1) Replace "The effect of combined iron, silicate, and light co-limitation was investigated in two Southern Ocean diatom species, Chaetoceros dichaeta and Actinocyclus, sp. and one cosmopolitan species, Chaetoceros debilis, all isolated in the Southern Ocean (SO). " by " The effect of combined iron, silicate, and light co-limitation was investigated in three diatom species, Chaetoceros dichaeta, Actinocyclus sp., and Chaetoceros debilis, isolated from the Southern Ocean (SO). " Ch. dichaeta is cosmopolitan and Actinocyclus " sp. " refers to a genus which is not endemic from Southern Ocean. Also do not use " endemic species " when refering to Ch. dichaeta and Actinocyclus sp.

Authors reply: We agree that we should be more careful in this context and will avoid the word "endemic species". However, C. dichaeta is to our knowledge not a cosmopolitan species. The literature indicates that this species clearly shows a circumpolar distribution (Assmy et al., accepted). It is true that there are a few papers that describe observations of C. dichaeta in temperate waters. But these observations are very rare and it is not certain today that the species described is really C. dichaeta since no genetic analysis has been performed. We will therefore refer to C. dichaeta

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as a species almost exclusively found in the Southern Ocean.

Quéguiner comment # 2: Introduction 2) " Diatoms can build up enormous blooms and, since there is only little frustule dissolution during the transport to the deep sea (Tréguer et al., 1989), they are responsible for almost all of the silica sedimentation in the SO (Abelmann and Gersonde, 1991). " Although I agree that the antarctic sediments are dominated by diatom frustules, the reasons are not unique and it does not only reflect slow dissolution. This is a controversial point as recent measurements have indicated high dissolution rates (which I personally don't trust) while other papers explain the biogenic silica accumulation by focusing processes.

Authors reply: We agree that this is a controversial point. We will extend the introduction and include other reasons discussed in the literature.

Quéguiner comment # 3: " The extremely deep mixing and the resulting low light intensities are discussed as a third main factor influencing algal growth in the SO (Mitchell et al., 1991; Timmermans et al., 2001; van Oijen et al., 2004). " Please add the classical paper by Nelson and Smith (1991).

Authors reply: We will include this reference.

Quéguiner comment # 4: " Here we present the first study examining the effect of iron, light, and silicate colimitation on two Antarctic diatom species Actinocyclus sp. and Chaetoceros dichaeta limitation and one cosmopolitan species Chaetoceros debilis, all isolated in the SO, in laboratory experiments. " - same as comment #1.

Authors reply: See reply to comment # 1

Quéguiner comment # 5: Material and methods 5) The notation of the different treatments by letters A to H is not easy for the reader. It would be better characterized as LFe/Llight/LSi to HFe/Hlight/Hsi with " L " standing for Low and " H " standing for High.

Authors reply: We agree that the notation used can be confusing and will change it as suggested.

Quéguiner comment # 6: “ In these treatments free iron concentration were 1.55nM Fe’ (all inorganic Fe species) estimated after Timmermans et al. (2001). ” Without any Fe chemical measurements how can you take fro sure that no contamination could have occurred ?

Authors reply: The estimation of free iron concentrations in culture experiments regarding the EDTA concentration and the iron concentration added is a method commonly used in similar experiments (Leynaert et al., 2004; Sunda and Huntsman, 1995; Sunda and Huntsman, 1997; Sunda and Huntsman, 2000; Sunda et al., 1991; Timmermans et al., 2001a; Timmermans et al., 2001b; Timmermans et al., 2005). To prevent iron contamination special trace metal clean lab procedures were used throughout the experiment as described in the “material and methods” section. We are sure that no iron contamination occurred in our experiments as Fv/Fm values in the low Fe treatments were low throughout the experiment. It is well known that Fv/Fm values increase within hours after iron addition. Therefore, iron contamination would have been observed very early. Additionally, iron contamination in some replicates would have resulted in higher growth after some time. Since standard deviation between the replicates are low and all low iron treatments showed significantly lower Fv/Fm and growth we can exclude iron contamination. We will include that a possible iron contamination was monitored using Fv/Fm values in the new version of the manuscript.

Quéguiner comment # 7: “ The iron, silicate, and light conditions of the different treatments are shown in Table 1. The high silicate treatments were grown in 200 μM Si, which is the concentration commonly recommended in f/2 media for diatoms. The 10 times lower Si concentrations n the low Si reatments (20 μM Si) resulted in a NO3-Si(OH)4 ratio of 44, which is close to the ratio that can be found in low Si regions of the Southern Ocean, where Si concentrations are depleted to <1 μM (Brzezinski et al., 2005; Coale et al., 2004; Franck et al., 2000; Sigmon et al., 2002). ” This is a major problem with the experiment. The “ low ” silicic acid concentration is probably 20 times as high as the real low in situ concentration north of the PF while the high silicic

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acid concentration is 3 to 5 times higher thant the high in situ concentration south of the PF. Given the commonly reported high KS values of Fe-limited Southern Ocean diatoms, such a discrepancy between culture and natural concentrations makes any extrapolation to the natural ecosystem totally speculative.

Authors reply: Nutrient concentrations in culture experiments are usually higher than compared to natural systems to prevent nutrient limitation during the experiment. For limitation experiments it is definitely better to use chemostats and to maintain the cultures under limiting nutrient conditions during the whole experiment. This was not possible in our case as it would be very difficult, probably impossible, to prevent iron contamination in a chemostat system. We are aware that therefore our experiments do not provide natural conditions perfectly. However, as described in the initial statement in more detail, the high cell concentration in the experiment made it necessary to use higher nutrient concentrations. Further, the low Si concentrations in fact reduced growth resulted in morphological changes.

Quéguiner comment # 8: " Therefore Fv/Fm and cell counts of the treatments A, B, and F are also only shown until day 46 (Figs. 1 and 2). " I don't understand the reference to the figures 1 and 2 which are photographs of the cultures. References should be respectively 5 and 4.

Authors reply: We are thankful for this correction and will change the reference respectively.

Quéguiner comment # 9: " For determination of cell numbers 2 ml samples were fixed with 40 μl Lugol's Solution (iodine - potassium iodide solution 1%, MERCK) and stored at 3°C in the dark until analysis. " How long did the storage last ? Did you use acidic Lugol ?

Authors reply: We used buffered Lugol and the storage lasted up to four month.

Quéguiner comment # 10: " Fixation with Lugol's Solution broke cell chains after some

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months of storage, which was not expected by the authors. ” How can you rely on chain length estiùmation with such a problem ?

Authors reply: All data on chain length presented in the manuscript are collected directly after the samples were taken or within a week after fixation. No significant differences were found between the samples counted directly and those after one week of storage in the same treatment. We therefore are confident that we can rely on the chain length estimation presented. Some samples have been stored between 1 and 4 month. In these samples almost all chains were broken. We therefore excluded these data, which resulted in the incomplete dataset. We would like to emphasize that this problem only affected chain length estimation and not total cell numbers. We will reveal this in the new version of the manuscript.

Quéguiner comment # 11: “ Assuming a cylindrical shape of the cells, ˇE ” Chaetoceros cells are flatened and the section is not circular but elliptic ; so your estimation of cell volume is wrong.

Authors reply: We agree that Chaetoceros cells do not have a perfect cylindrical shape. According to Hillebrand et al. (1999) the best way to calculate cell volume would be to use the volume formula of an elliptic prism. To do so one needs the length of all three axis, the height of the cell, the apical and the transapical section length. Using light microscopy it is not possible to measure all of these three axis. Because of the spines, Chaetoceros cells are always positioned in girdle view when settled on a flat surface such as a microscope slide. Therefore, it is only possible to measure the height and the apical section of the cell. The length of the transapical axis can be estimated as 2/3 the length of the apical axis. This method has been used to determine cell volume of C. dichaeta by Assmy et al. (accepted). This assumption is of course also very error-prone especially when the cell morphology changes as we observed in our experiments. We can of course change the volume estimations but we believe that both ways are subjected to errors. To assume a cylindrical shape of the cell is a procedure also feasible according to Hillebrand et al. (1999) and also used in the literature

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(Montagnes and Franklin, 2001). Cell volumes estimated according to Hillebrand et al. (1999) are lower compared to those assuming a cylindrical shape. However, even though absolute cell volume is lower, the relative changes in cell volume between the treatments are the same. We will include this discussion in the “material and methods” section of the new version of this manuscript.

Quéguiner comment # 12: Discussion 12) “The nutrient concentrations in culture media are usually much higher compared to natural conditions. This is necessary to reach sufficient biomass in a relatively small volume so that there is enough material for analysis. Nutrient concentrations that would be considered high in the field, such as the 20 μM silicate, were suitable for our low Si treatments due to the much higher biomass and showed to reduce algal growth in our experiments. ” This is purely speculative!

Authors reply: Our data show that growth of all three species tested in our low Si treatments was clearly Si-limited under favorable light and iron conditions. The observed morphological changes are similar to those observed in Si limitation experiments using chemostats (Harrison et al., 1977). We therefore are confident that our data are comparable to field conditions (see initial statement for a more detailed explanation).

Detailed authors reply to review # 2, anonymous:

Reviewers comment # 1: The low silicate level of 20 μM is not necessarily limiting for diatoms north and south of the Polar Front. Sedgwick et al. (2002) determined silicate concentrations of 0.5 μM and 1.2 μM north and south of the Polar Front. These authors used high-silicate treatments of 4.4 μM and 18.3 μM in incubations, respectively, while they had corresponding control (low) silicate treatments of 0.5 μM (north) and 1.2 μM (south) of the front. The length of incubation in their study was 5 (north) and 9 days (south). The ‘lowsilicate’ concentrations in the manuscript are in fact quite high silicate concentrations in the real ocean. In the high-silicate experiments by Sedgwick and colleagues the silicate concentrations did not decrease by more than a third of the initial concentrations. Thus, there is no justification for a high silicate concentration of

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20 μM in the 'low silicate' treatments (in contrast to the statement on p220 lines 26-27).

Authors reply: As described above, the absolute Si concentrations in batch culture experiments can not directly be compared with the concentrations in natural systems. The much higher biomass in our experiments has to be taken into account. Sedwick et al. (2002) used natural phytoplankton community for their experiments and therefore worked with a much lower biomass. The chlorophyll concentrations reached at the end of their experiments were between 10 and 15 μg Chl /l , which is about as high as our start values (between 6,4 μg Chl/l for Actinocyclus and 19,4 μg Chl/l for C. debilis). Additionally these experiments included many different phytoplankton groups beside diatoms that do not take up silicate when growing. This is also a reason why in these experiments only a third of the initial Si concentrations has been taken up while we needed much higher concentrations for Si uptake in pure diatom cultures.

Reviewers comment # 2: The high silicate concentration of 200 μM is a very high concentration, which is not found in Southern Ocean surface waters (WOCE Southern Ocean Atlas, 2005).

Authors reply: It is true that these concentrations are not fund in natural Southern Ocean waters. However, 200 μM Si is the concentration generally recommended for diatoms growing in f/2 media to prevent Si limitation during batch culture experiments. This concentration was not chosen to be directly comparable to natural conditions but rather to guarantee growth throughout the experiment without Si limitation.

Reviewers comment # 3: No justification for the choice of light levels is given. Combining the abstract with Table 1 suggests that the high light level of 90 umol photons /m2/s corresponds to the light in an actively mixed layer of 28 m. However, it is not clear if this is an average light level integrated for the daytime hours and depth range, nor at which latitude and season such a light level is found and whether the light level is for days with clear or overcast skies. The absence of such information makes it difficult to judge how relevant the light level is. Gervais et al. (2002) found depth averaged irradiance

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of 100-150 umol photons /m2/s on most days of the EisenEx experiment (in the Polar Frontal Zone, north of the Polar Front) in November 2000, with higher levels of 38-80 umol photons /m2/s on two days. From this it appears that the low light level is on the low end of the light levels in parts of the Southern Ocean in spring, while the high light level exceeds that in the springtime EisenEx experiment.

Authors reply: The light intensity of 90 μmol photons /m2/s, that we chose for our high light experiments, corresponds to the mean light intensity in 1 to 28 m depth as described on page 224 line 20 and page 225 line 2 during the whole EIFEX experiment (50°S and 2°E January - March 2004) integrated for daytime hours. The lower light intensity of 30 μmol photons/m2/s corresponds to the mean light intensity in 16 to 42 m depth during EIFEX. These data correspond very well to the light levels in similar depth measured during the EisenEx experiment. All available light levels during the EisenEx cruise showed an average of 75 μmol photons /m2/s in 3 to 30 m depth and 25 μmol photons /m2/s in 16 to 75 m depth (Strass, unpublished data.)

Reviewers comment # 4: The iron concentration in the low iron treatments is not indicated. No justification is given for the choice of the high iron level. Strzepek and Harrison (2004) use a dissolved inorganic iron concentration of 0.4-0.7 nM [Fe'] in their iron replete treatments. The level in this study (1.55 nM [Fe']) is 2-4 times that level.

Authors reply: Strzepek and Harrison (2004) give no information about the biomass in their experiments, so a direct comparison to our study is difficult. It is possible that a lower iron concentration would have also increased growth and Fv/Fm of the species tested in our study. However, it was not our intention to determine which iron concentration is exactly needed by each species but to compare cells growing under iron, light and silicate limitation with those growing under nutrient replete conditions.

Reviewers comment # 5: The absence of information on how the nutrient and iron levels evolve during the incubations makes it difficult to interpret these results. It is questionable whether ‘the low iron and low light conditions represent typical Southern

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Ocean conditions' (page 216 line 16).

Authors reply: We agree, that additional measurements of the nutrient and iron levels during the experiment would have been useful to interpret the results. However, the current complexity of the treatment already led to 72 bottles (8 treatments with three replicates each for three species). Diatoms, isolated in the Southern Ocean, grow best in natural Antarctic seawater and we therefore decided to use this as growth medium. Since it is very time-consuming to sterile-filter seawater under trace metal clean conditions onboard a research vessel we only had limited quantities of this incubation water. This forced us to carefully choose important variables to tackle our research question. It was therefore not possible to take samples for additional measurements.

Reviewers comment # 6: The duration of some of the experiments (up to 77 days) is long compared to the studies by Sedgwick et al. (2002) (5-9 days).

Authors reply: Some Southern Ocean species like Actinocyclus can grow very slowly. Long experiments like ours are therefore common and also reported by Timmermans et al. (2004).

Reviewers comment # 7: The conclusions and parts of the abstract are not justified by the data: The statement that all species are co-limited by iron and silicate is flawed (abstract lines 7-9). The high-iron high-silicate treatments F and H (Figure 4) do not systematically show higher cell numbers for all species than the high-iron low-silicate treatments (E, G). Of course one might argue that the silicate concentration in the low-silicate treatments is non-limiting. The suggestion that grazing indirectly effects species composition (via different levels of these nutrients, presumably Si and Fe) (abstract lines 14-15) is not justified by these experiments which exclude grazers.

Authors reply: There must be some kind of misunderstanding. The treatments F and H had high iron but LOW silicate (see table 1) and they do show lower cell numbers for all species compared to the high iron and HIGH silicate treatments E and G. The only exception is for C. dichaeta and Actinocyclus which did not grow at all under the

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high light conditions in treatment G and H and therefore show no significant difference between these two treatments. It is true that we did not include grazers in our study and therefore can not directly estimate the effect of nutrient limitation on grazing. However, we found clear effects of nutrient availability on chain length and frustule morphology. Frustule stability and chain length are known to be an important mechanism protecting diatoms cells against grazers (Hamm et al., 2003). We consider it therefore logical to draw these conclusions. We have indicated in the text that this aspect is a speculation based on our observations.

Reviewers comment # 8: The authors speculate that the frustule deformation is a useful biological marker in sediments (e.g abstract lines 15-17). However, they do not indicate if such deformation has been observed in sediments.

Authors reply: Presenting these figures on a Poster at the ASLO Ocean Sciences Meeting in Hawaii 2006, a few colleques working with sediments were thankful to see this type of experiments since they told us, that they regularly observe malformed cells in their sediment cores.

Reviewers comment # 9: The observation that the (very) high light conditions have a negative impact on growth does not imply that diatoms do not suffer from low light availability, notably at levels below the low light treatment in these experiments (abstract lines 18-22).

Authors reply: This is true. However, the high light levels are comparable to those found in the upper 28 m of the Southern Ocean (SO) during EIFEX and therefore represent a light regime SO diatoms are commonly exposed to. As described on page 224 line 24-27 "Assuming surface irradiances between 100 and 500 μmol photons /m2/s, phytoplankton cells would be exposed to mean light intensities of 30 μmol photons /m2/s when constantly mixed between the surface and 44 m and down to calculative more than 200 m respectively." The low light levels therefore already represent a relative low irradiance.

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Reviewers comment # 10: Page 214, lines 15-17. Where and when were the diatoms isolated (month, latitude, geographic area)? Where the diatoms isolated in the non-iron enriched waters?

Authors reply: The diatoms were isolated during EIFEX (21 Jan 2004 - 25 Mar 2004) at 50°S and 2°E inside the iron fertilized patch. In the home laboratory the cultures were maintained under iron limiting conditions until the experiment.

Reviewers comment # 11: Several interpretations of the experiments are dubious or possibly not statistically significant. Certainly the reader is easily lost in the large number of treatments and parameters for three different species, especially as the effects on the diatoms are not clear cut. Here some examples: Page 216. Figure 2. The suggestion that high silicate concentrations lead to cell elongation is not clear for C. dichaeta in iron replete conditions. The cell length of diatoms is not clearly different in figures E versus F and of G versus H (given the different scale of Figure E).

Authors reply: We should have explained in more detail what we mean with cell elongation in this context. What we meant was not the absolute length of a cell but the ratio of length to width. Cells grown under Si limitation show a more elongated shape. We want to emphasize, that the pictures shown in figure 1, 2, and 3 are only examples. All cells grown under Si limitation were elongated but absolute cell sizes showed a relatively high variance as shown in figure 7. We consider to include a figure that shows the length : width relationship in a new version of this manuscript.

Reviewers comment # 12: Page 216 16-21 and Figure 4. It is difficult to judge differences in cell numbers between the treatments as the scales of Figure 4 vary widely, especially for C. debilis. Whilst struggling with the scales I would conclude that cell numbers of C. debilis are high in the ‘low-silicate’ treatments A, E and G, moderate in C, and low in the high silicate treatments B, D, F, H. Furthermore C. dichaeta should be excluded from the analysis given the small number of samples.

Authors reply: We agree that it is difficult to deal with the different scales. However,

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there is a misunderstanding with the different treatments. Treatment A, C, E, and G are HIGH silicate treatments and treatment B, D, F, and H are LOW silicate treatments (see table 1). Even though there are only very few data available for C. dichaeta we feel that the information is important and should be shown. For example, the observation, that C. dichaeta shows almost no growth under high light conditions confirms the conclusion, that Southern Ocean species are adapted to low light intensities. Since the labeling of the treatments has led to several misunderstandings we will change it for better characterization to LFe/Llight/LSi to HFe/Hlight/HSi.

Reviewers comment # 13: Page 219-220. In the discussion on chain length it is not clear whether the differences between the treatments are significantly different. The interpretation of these experiments needs careful thought. There could well be interesting science in them, but this is not obvious from the current manuscript.

Authors reply: We agree, that the interpretation might be difficult and will use appropriate statistic to make this argument clear before resubmission of this manuscript.

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