Biogeosciences

Discussions

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Interactive comment on "Thermocline depth and euphotic zone thickness regulate the abundance of diazotrophic cyanobacteria in Lake Tanganyika" *by* Benedikt Ehrenfels et al.

Anonymous Referee #1

Received and published: 30 June 2020

General comments The manuscript presents a conceptual model for the development heterocytous cyanobacteria in Lake Tanganyika, involving the position of the thermocline and euphotic depth. The data were acquired during two cruises on the lake, carried out at the end of the rainy season and at the end of the dry season. The model is presented as possibly explaining "blooms" of cyanobacteria in N-deficient surface water systems. However, the authors apparently ignored key aspects of the present phytoplankton assemblage of Lake Tanganyika and some claims are not based on sufficient data (such as N vs. P limitation). Specific comments Regarding the methods, those for physical and chemical analyses are correct and yielded apparently consistent data. On the contrary, the phytoplankton analyses, being based on concentrating the

phytoplankton on a 10 μm plankton net could not give a correct sample for quantitative phytoplankton analysis: Lake Tanganyika comprises taxa in a large size range, with a substantial, often dominant part of nanoplankton < 10 μm and of picoplankton (< 2 μm). Even though in the methods it is clear that this sampling method focused on medium to large sized phytoplankton, in the results, such a statement as "The phytoplankton community in Lake Tanganyika was dominated by chlorophytes, diatoms, and cyanobacteria . . ." is misleading. See also below the remark about the correlation of PC and PE data with cyanobacteria biomass. In addition to this serious technical problem, there are two main issues in this study, in addition to various potential shortcomings (see other remarks below). The first is the assumption (lines 52-53) that "cyanobacteria can dominate the phytoplankton community during periods of pronounced stratification when nutrients are scarce (Cocquyt and Vyverman, 2005)". This is not untrue, but the cyanobacteria that dominates the phytoplankton in present Lake Tanganyika are not the heterocytous taxa but picocyanobacteria (Synechococcus spp.), which have quite different characteristics. Briefly, they are not as efficient N-fixers as the heterocytous taxa, and their small size allows high growth rates and high nutrient uptake rates, which make them specialists of oligotrophic conditions. This is an issue throughout the manuscript, which does not mention these picocyanobacteria, which make 41 - 99 % of total phytoplankton biomass (Stenuite et al., JPR, 2009). The paper by Cocquyt & Vyverman, by contrast, being based only on LM examination, does not account for "algae" < 5 μm, and therefore gives a biased view of the phytoplankton assemblage of the present lake. Actually, the heterocytous taxa (mainly Dolichospermum, formerly Anabaena) are presently detected relatively rarely in Lake Tanganyika, as shown by analyses of samples collected over a few years (Descy et al., Hydrobiologia, 2010), as well as by remote sensing, which allowed to detect surface "blooms" (Horion et al., 2010). It seems that they occur much less frequently than in the past, which may be a consequence of the lake's oligotrophication (Verburg et al., 2003). A second issue relates to the assumption that N is the main limiting factor of phytoplankton growth in the lake (line 72-73), which is in contradiction with evidence based on seston elemental

ratios (which is a more reliable indicator of phytoplankton nutrient status than a deficit estimated from a ratio DIN : SRP). According to Stenuite et al. (2007), who used particulate C, N and P analyses to assess nutrient limitation over several years in 2 sites in Lake Tanganhyika, P limitation was more frequent than N-limitation, and neither nutrient could be considered as severely limiting. Both statements convey the impression that N-fixation is a key process controlling productivity in the present lake, whereas there is evidence that, as a result of global warming and increased stratification, the lake's productivity has decreased as a result of decreased P availability (Verburg et al., 2003, 2006), with consequences on fish yield, although this is still a matter of debate (Verburg et al., 2006; Sarvala et al., 2006). Interestingly, the increased P availability may have been the cause for the reported decline of heterocytous cyanobacteria, as their P requirements are typically high. An alternative conceptual model for Dolichospermum may be different from the one proposed in the paper: indeed, several authors have emphasized that the typical timing of surface "blooms" in Lake Tanganyika is the transition between the dry and the rainy season, in October-November, when they have exploited the SRP-rich conditions of the dry season, possibly by storing polyphosphate granules; only when the lake re-stratifies, they can outcompete the other phytoplankton, at least for a time, using the advantages of buoyancy due to their gas vesicles and of efficient N fixation with their heterocytes. "Blooms" occurring at other times, as in the moderately nutrient-limiting conditions of the middle and end of the rainy season, may be explained by migration below the thermocline to take up and accumulate SRP. Low Fe availability at high pH may be an additional controlling factor of N-fixation, as suggested by experimental nutrient additions in tropical lakes, and grazing resistance may be an additional factor of success of these large-sized phytoplankters. An interesting analogue to heterocytous cyanobacteria development in an oligotrophic tropical lake can be found with the case of Trichodesmium in the ocean, which has been given a lot of attention. The conceptual model for Trichodesmium also involves N-fixation (with diazocytes, not heterocytes), control of growth by SRP and Fe, and vertical migration regulated by light and nutrient requirements (Bergman et al., 2012).

Other remarks 73-74: "This large tropical lake is permanently stratified and characterized by a nutrient-rich hypolimnion overlaid by an oligotrophic epilimnion" Poor depiction of the lake ... better to mention that it is meromictic, and that the mixolimnion is stratified during the wet season and mixed during the dry season, with a large spatial variability.

106: "This sampling approach has been adopted in previous studies (e.g. Salonen et al., 1999; Stenuite et al., 2009)": Yes but long time series with adequate sampling frequency are better suited to capture temporal variability, particularly when studying relatively rare "bloom" events. Combination with remote sensing data is ideal, given the very large spatial heterogeneity (see Horion et al. 2010) 135: "We calculated the N deficit according to the Redfield stoichiometry of phytoplankton ..." Very rough indeed, as it depicts only the situation at the time of sampling; moreover, a concentration ratio is not a supply ratio, and only nutrient supply vs. demand from phytoplankton determines nutrient status 178 : "The N deficit (98 % of all observations) persisting throughout the water column (Fig. S2) implies that primary productivity was N limited": far from sure, see above 205: "The phytoplankton community in Lake Tanganyika was dominated by chlorophytes, diatoms, and cyanobacteria (Fig. 2) with lower contributions from dinophytes, while euglenophytes were rare. Diazotrophic cyanobacteria, of which Dolichospermum sp. was the main taxon (we found only a few colonies of Anabaenopsis tanganyikae colonies in the South), were most abundant in the North and centre of the lake, where the primary thermocline was below the euphotic zone (Apr/May only) or deeper than ∼40 m (Fig. 2 & 4)". Again, the statement implies that cyanobacteria were all efficient diazotrophs, which was likely not the case. Cryptophytes were overlooked. 276-277 "An additional ecological driver for diazotroph abundance may operate by mutualistic interactions between diazotrophs and diatoms" and below (285-290). This rather wild assumption is just based on "contact" between cyanos and diatoms, which may have resulted from the sampling procedure. This has nothing to do with the endosymbiosis of Richelia with large diatoms in the sea. 330: "Our results also show that the fluorometric determination of extracted phycocyanin and phycoerythrin provides

an excellent proxy for the abundance of filamentous cyanobacteria" This statement is plainly false, as both phycobilins are also present in picocyanobacteria, which dominate the phytoplankton in the present lake. The fact that PC and PE concentration correlated with filamentous cyanobacteria abundance was very likely pure chance. Table S2 contains several misspelling of taxa names, likely some wrong identifications and a mis-classification (Sphinctosiphon is a cyanoprokaryote, not a green alga).

Interactive comment on Biogeosciences Discuss., https://doi.org/10.5194/bg-2020-214, 2020.