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Primary production in a tropical large lake: The role of phytoplankton composition

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HIGHLIGHTS

- We provide a 7-year dataset of primary production in a tropical great lake.
- Specific photosynthetic rate was determined by community composition.
- Annual primary production varied between 143 and 278 mg C m^{-2} y^{-1}.
- Pelagic production was highly sensitive to climate variability.

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ABSTRACT

Phytoplankton biomass and primary production in tropical large lakes vary at different time scales, from seasons to centuries. We provide a dataset made of 7 consecutive years of phytoplankton biomass and production in Lake Kivu (Eastern Africa). From 2002 to 2008, bi-weekly samplings were performed in a pelagic site in order to quantify phytoplankton composition and biomass, using marker pigments determined by HPLC. Primary production rates were estimated by 96 in situ ^{14}C incubations. A principal component analysis showed that the main environmental gradient was linked to a seasonal variation of the phytoplankton assemblage, with a clear separation between diatoms during the dry season and cyanobacteria during the rainy season. A rather wide range of the maximum specific photosynthetic rate (P_{Bm}) was found, ranging between 1.15 and 7.21 g carbon g^{-1} chlorophyll *a* h^{-1}, and was best predicted by a regression model using phytoplankton composition as an explanatory variable. The irradiance at the onset of light saturation (I_k) ranged between 91 and 752 μE m^{-2} s^{-1} and was linearly correlated with the mean irradiance in the mixed layer. The inter-annual variability of phytoplankton biomass and production was high, ranging from 53 to 100 mg chlorophyll *a* m^{-2} (annual mean) and from 143 to 278 g carbon m^{-2} y^{-1}, respectively. The degree of seasonal mixing determined annual production, demonstrating the sensitivity of tropical lakes to climate variability. A review of primary production of other African great lakes allows situating Lake Kivu productivity in the same range as that of lakes Tanganyika and Malawi, even if mean phytoplankton biomass was higher in Lake Kivu.

1. Introduction

Contrary to common assumptions on the constancy of ecological conditions in tropical lakes, pelagic primary production may vary considerably in African great lakes, at different time scales, from seasons to centuries (Melack, 1979; Cohen et al., 2006). At long time scales, Indian Ocean surface temperatures, determining rainfall, are the primary influence on East African climate (Tierney et al., 2013), which largely determines water column processes in the great Rift lakes (e.g. Johnson and Odada, 1996; Plisnier, 2000; MacIntyre, 2012). At a seasonal scale, the main driver of pelagic primary production is the alternation of wet and dry seasons, with changes in relative humidity and wind velocities: typical wet season conditions induce thermal stratification of the water column, which reduces nutrient supply in the euphotic zone. Dry season conditions tend to reduce the temperature–density gradient and higher wind velocities result in deep vertical mixing of the water column, increasing nutrient supply in the euphotic zone, inducing a dry season phytoplankton peak (Hecky and Kling, 1987; Spigel and Coulter, 1996).

Phytoplankton composition also depends on the alternation of stratified conditions in the rainy season with the deep mixing that occurs in the dry season: the seasonal mixing event not only increases the supply of dissolved nutrients in the euphotic zone, but also results in a rise of the ratio between mixed layer depth (Zm) to the euphotic layer depth

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(Zeu) (Sarmento et al., 2006). In these conditions, phytoplankton is subjected to potential light limitation, leading to diatom dominance (Reynolds, 2006a). By contrast, in the shallow mixed layer of the rainy season, the lower Zm:Zeu ratio selects for high-light adapted phytoplankton such as green algae and cyanobacteria. The trade-off between high light and nutrient limitation in the rainy season and low light and high nutrients during the dry season has been documented in classic studies in African lakes (e.g. Hecky and Kling, 1987; Kilham et al., 1986) and is a key to understanding shifts in phytoplankton composition in these lakes.

Estimates of annual primary productivity in tropical lakes have been usually based on measurements of phytoplankton photosynthesis carried out over sufficiently long periods to capture the seasonal variations of incident light, water transparency, temperature, nutrients and phytoplankton biomass. Examples of this approach can be found in Lewis (1974) in Lake Lanao (Philippines), in Talling (1965) for several East African lakes, in Hecky and Fee (1981), Sarvala et al. (1999) and Stenuite et al. (2007) for Lake Tanganyika, in Guildford et al. (2007) for Lake Malawi and in Silsbe et al. (2006) for Lake Victoria. Such studies derived photosynthetic parameters (P_{Bm}, the maximum specific photosynthetic rate, and Ik or α, a measure of the photosynthetic efficiency) from in situ incubations. If the irradiance at the onset of light saturation (Ik) describes the regulatory response of the phytoplankton photosynthesis to the light climate, P_{Bm} relates to the efficiency of the light harvesting system. Main environmental factors influencing P_{Bm} in cultures are temperature and nutrient availability (Geider and MacIntyre, 2002). A reduction of P_{Bm} is observed in nutrient-limited algae (Geider et al., 1998; Greene et al., 1991). At the community level, it has occasionally been demonstrated that larger cells sustain higher P_{Bm} than smaller cells (Cermeño et al., 2005; Peltomaa and Ojala, 2010), but field studies attempting to relate the compound photosynthetic response on the taxonomic composition of the phytoplankton assemblage are rare (Segura et al., 2013). However, phytoplankton composition matters, as shown by experimental studies on pure cultures, which have provided evidence of significant variation of photosynthetic parameters among taxonomic groups (Falkowski and Raven, 2007; Kirk, 1994; Reynolds, 2006a).

Pigment-based analysis of phytoplankton composition may provide an adequate framework to relate community composition to photosynthesis parameters. Phytoplankton pigments, determined by high performance liquid chromatography (HPLC) analysis, have been used widely for assessing biomass at the class level, with many applications in marine, estuarine, and freshwater environments (e.g., review in Sarmento and Descy, 2008). The assessment of algal abundance from pigment concentrations uses different techniques, involving ratios of marker pigments to chlorophyll *a* (Chl*a*) (Mackey et al., 1996). As it is based on a fast, automatic and reliable analytical technique, the pigment approach has been largely used in oceanographic studies and monitoring programs (Jeffrey et al., 1997), as well as in large lake studies (Descy et al., 2005; Fietz and Nicklish, 2004; Fietz et al., 2005; Sarmento et al., 2006).

We applied a pigment approach in Lake Kivu, a great and deep (maximum depth of 489 m) meromictic lake of the East African Rift (Fig. 1). Lake Kivu is located north of Lake Tanganyika, at 1463 m above sea level. The mixolimnion (i.e. the upper layer of a meromictic lake) alternates between periods of complete mixing down to maximum 65 m and periods of stratification during which nutrients become depleted in the euphotic zone (Sarmento et al., 2006; Schmid and Wüest, 2012). Whereas moderate to severe P-limitation of phytoplankton prevails during most of the year (Sarmento et al., 2009, 2012), N-limitation may occur in the stratified rainy season, as denitrification takes place within the oxic–anoxic transition zone (Llirós et al., 2012). By contrast, the monimolimnion, i.e. the lower layer that never mixes with surface waters, is rich in nutrients and dissolved gases (Degens et al., 1973; Schmid et al., 2005). Pelagic primary production in Lake Kivu exhibits substantial variation at the seasonal scale, but also between years

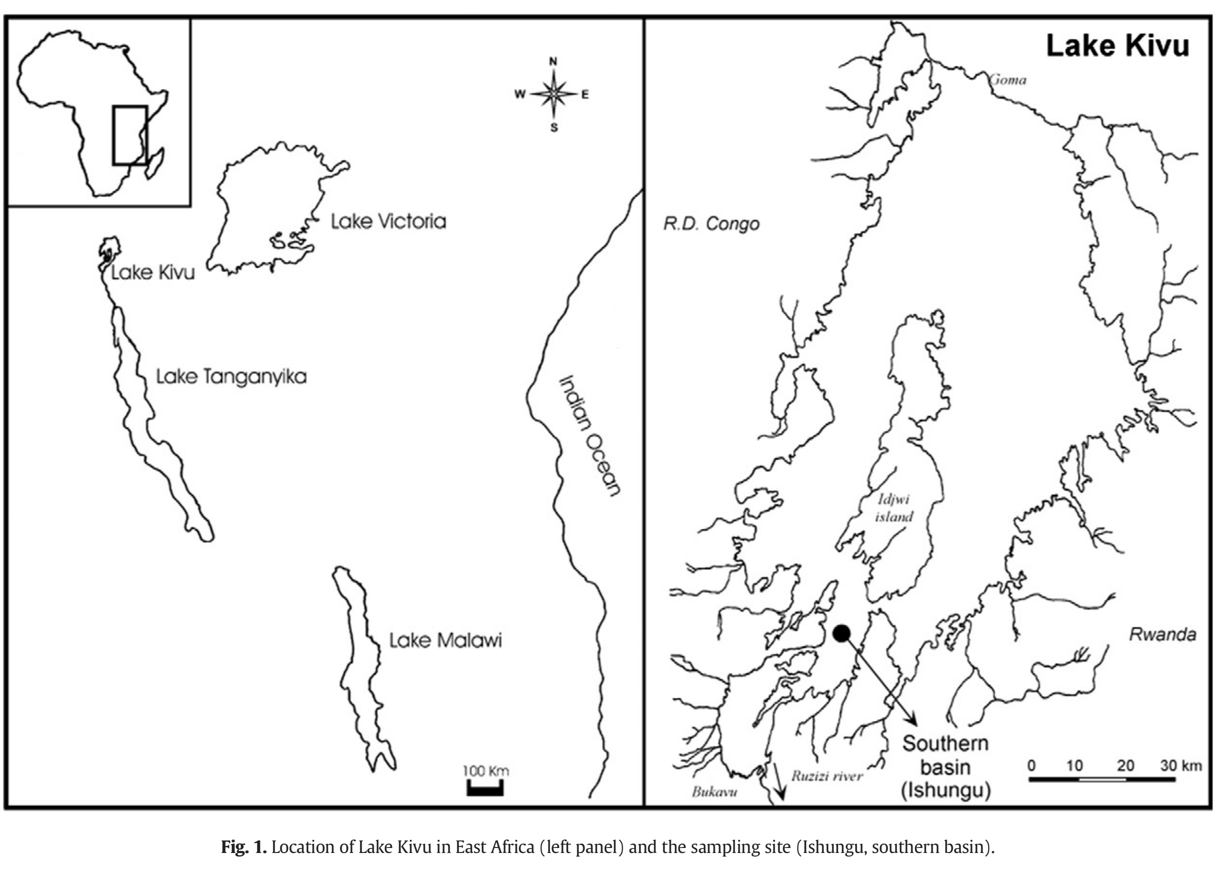

Fig. 1. Location of Lake Kivu in East Africa (left panel) and the sampling site (Ishungu, southern basin).