Unusual massive phytoplankton bloom in the oligotrophic Lake Tanganyika

Christine Cocquyt[1,*], Pierre-Denis Plisnier[2], N'sibula Mulimbwa[3] & Muderhwa Nshombo[3,4]

[1]Meise Botanic Garden, Research Department, Belgium
[2]University of Liège, Chemical Oceanography Unit, Institut de Physique, Belgium
[3]Centre de Recherche en Hydrobiologie – CRH-Uvira, Democratic Republic of the Congo
[4]Université Officielle de Bukavu, Democratic Republic of the Congo
*Corresponding author: christine.cocquyt@botanicgardenmeise.be

Background and aims – Massive algae growth resulting in a phytoplankton bloom is a very rare event in the meromictic and oligotrophic Lake Tanganyika. Such a bloom was observed in the north of the lake in September 2018. Phytoplankton species composition during this bloom is compared to a documented bloom in 1955, and to the composition in September 2011–2013. Meteorological observations suggest hydrodynamics could explain the occurrence of the 2018 bloom.

Material and methods – Phytoplankton net samples were taken in the pelagic and littoral zone near Uvira during five consecutive days of the bloom in 2018. For the period 2011–2013, quantitative phytoplankton samples were obtained during a weekly sampling at the same sites. Samples were analysed with an inverted microscope and relative abundances of the algal species were compared.

Key results – *Dolichospermum flosaquae* (Cyanobacteria) initially dominated the bloom followed by high relative abundance of *Limnococcus limneticus* (Cyanobacteria) on the third sampling day in September 2018. In the pelagic zone an increase of *Nitzschia asterionelloides* (Bacillariophyta), and *Dictyosphaerium* and *Lobocystis* (Chlorophyta) was observed while in the littoral zone increasing abundances of dinophytes were noted. *Dolichospermum flosaquae* was also responsible for the bloom reported in 1955, but was only sporadically observed in the 2011–2013 samples. Although *Limnococcus limneticus* was present in 2011–2013, it never reached relative abundances as high as during the 2018 bloom. Meteorological data indicate that 2018 experienced different conditions compared to previous years: strong south-east winds from May to September with a more eastern direction of the wind, and a well-marked drop in atmospheric pressure between August and September.

Conclusion – After a very windy season, the combination of strong hydrodynamics, calmer lake conditions, and high solar radiation and air temperature in September 2018 was favourable for a massive Cyanobacteria bloom in the north of Lake Tanganyika.

Keywords – Algal bloom; *Anabaena flos-aquae*; *Chroococcus limneticus*; *Dolichospermum flosaquae*; East African Great Lakes; *Limnococcus limneticus*; phytoplankton; secondary upwelling.

INTRODUCTION

Lake Tanganyika, located in the western branch of the East African rift between 3°25′S and 8°50′S, has a length of about 650 km and an average width of 50 km. It is globally the second deepest lake (1470 m) after Lake Baikal (1640 m) and has a water volume of about 18,880 km³ (Coulter 1994).

With its north-north-west to south-south-east position, the lake's orientation is in the direction of the south-east trade winds during the dry season from May to September. From a biological point of view, Lake Tanganyika is known to be a hot spot for biodiversity (Groombridge & Jenkins 1998). Studies on speciation and radiation of, among other, fishes, molluscs, and ostracods can be found in the literature from

the end of the last century onward (e.g. West & Cohen 1996; Kornfield & Smith 2000; Seddon et al. 2011; Schön & Martens 2012). Investigations on algal biodiversity and species richness, mainly focused on diatoms, are also carried out (Cocquyt et al. 1993; Cocquyt & Vyverman 1994; Cocquyt 1998, 2000, 2006; Taylor & Cocquyt 2015), but molecular research was only recently started (Christine Cocquyt pers. comm.).

Lake Tanganyika is an important source of drinking water and water for other purposes such as agriculture. Regional inhabitants depend on artisanal fisheries as main source of animal proteins. The annual yield of Lake Tanganyika is estimated around 16,500–200,000 tons (Mölsä et al. 1999). However, fisheries are seriously threatened by climate change (Cohen et al. 2016). It is therefore not surprising that on 7 September 2018 panic arose among the local population around the north of Lake Tanganyika when the water suddenly turned green. This phenomenon was widely reported by the local media (e.g. *Congo Actuel* at Uvira in the Democratic Republic of the Congo (D.R. Congo), *IWACU Web TV* at Bujumbura in Burundi). The green colouring of the surface water finally disappeared on 13 September at Uvira (D.R. Congo). A link with pollution was suggested as a possible explanation for the phenomenon. However, Congolese and Burundian scientists reassured the population that it was "a completely natural phenomenon that may happen in September".

Indeed, intensive studies of the limnological cycles in the lake (e.g. Coulter 1991; Plisnier 1997; Plisnier et al. 1999) have led to a better understanding of the dynamics and mixing regimes in the water column of this lake. Massive phytoplankton blooms occur but are rare events in this oligotrophic lake. The first written reports of bloom events date from the mid-1950s (Symoens 1955a, 1955b, 1956a, 1956b). Symoens described dense algal blooms at the north of Lake Tanganyika near Uvira in September and October 1955. Since the mid-1970s frequent research has been conducted in the north of Lake Tanganyika (e.g. Hecky & Kling 1981; Coulter 1991; Plisnier et al. 1996, 2015; Plisnier 1997; Langenberg et al. 2003; Descy et al. 2005) and major phytoplankton blooms were rarely reported (Salonen et al. 1999).

An increase of cyanobacterial blooms in freshwater ecosystems has been reported during the last decades (e.g. Paerl & Huisman 2009; Long et al. 2018). Anthropogenic nutrient loading and global warming with its impact on the vertical stratification in lakes and reservoirs seem to play an important role in this increase. Nitrogen (N) fixation is energetically costly and N-fixing cyanobacteria tend to dominate only TN:TP (total nitrogen:total phosphorous) values $\leq$ 22 (Havens et al. 2003). Experimental results showed that *Dolichospermum* (Ralfs ex Bornet & Flahault) Wacklin, L.Hoffm. & Komárek, on the other hand, is favoured with increases of phosphorous only (Moisander et al. 2012). Cyanobacterial blooms can potentially cause taste changes and odour nuisance. Moreover, under certain conditions cyanobacteria can produce toxins. *Dolichospermum*, together with *Microcystis* Lemmerm., belongs to the most toxic Cyanobacteria (Capelli et al. 2017; Aguilera et al. 2018; Chia et al. 2018) and is able to induce neuromuscular blockades

(Carmichael et al. 1975). Dinophytes are also known for their toxicity when massive development takes place (Zaccaroni & Scaravelli 2008).

It is thus important to investigate the algal taxa responsible for the 2018 bloom near Uvira (D.R. Congo) in the northernmost part of the lake. In this paper, we compare the dominant taxa during this bloom with those of the bloom of 1955 as described by Symoens (1955a, 1955b, 1956a, 1956b). We also compare the algal species composition with phytoplankton data from the same period of the year in 2011–2013 when no bloom was observed at Uvira. Finally, a hypothesis on the origin of the phytoplankton bloom event is presented. The hypothesis is based on meteorological observations and on the present knowledge of the limnological cycle in Lake Tanganyika from previous observations.

MATERIAL AND METHODS

Phytoplankton samples were taken by a team of researchers from the Centre de Recherche en Hydrobiologie (CRH-Uvira) at two sites in Lake Tanganyika off Uvira. The samples were collected using a phytoplankton net of a 10 μm mesh width. In the pelagic zone (3°24.945′S, 29°10.635′E), phytoplankton was collected at the surface on 10 Sep. 2018 and from the water column through a vertical haul from 60 m depth up to the surface every day between 11 and 15 Sep. 2018. Additional samplings close to the shoreline (3°25.020′S, 29°2.948′E) were conducted by horizontal hauls of 60 m at the surface between 12 and 15 Sep. 2018. Materials were fixed in situ with buffered-formalin (37%) and stored in plastic jars.

Materials for phytoplankton composition analyses were transported to Belgium and studied at Meise Botanic Garden with an inverted Olympus CKX41 light microscope, equipped with a UC30 digital camera, using a 100 × oil objective. Phytoplankton counts of cells and colonies ≥ 3 μm were completed according to the Utermöhl method (Utermöhl 1958). Samples were well homogenized and a subsample of 10 ml was put in a sedimentation chamber of 10 ml (Hydrobios). It was made sure that all phytoplankton was settled and no remaining organisms were floating in the sediment chamber after sedimentation of 24 hours. For each sample, the first unicellular taxa or colonies of all phytoplankton species observed during a random transect were enumerated up to at least 100 cells or colonies. Only 'living' cells were taken into account and 'dead' diatoms without plastids were not included in the present study. The number of individual cells for each colony was counted, resulting in a total between 3600 and 6800 individual cells for each sample studied. To discuss the phytoplankton composition, we use the individual cells for calculating relative abundances (expressed as %) as this gives a better idea of the importance of each taxon as colonies can be composed of a small or a large number of individual cells and, moreover, colonies can be broken into smaller chains during storage and transport.

For comparison with years without noticeable algae bloom formation at the surface, phytoplankton samples taken around the same period of the year in 2011, 2012, and 2013

in the frame of the CHOLTIC project (Plisnier et al. 2015) are discussed in this paper. Sampling sites and methods were the same as for the September 2018 campaign, except that the monitoring between 2011 and 2013 included a quantitative sampling with a known (100 ml), unconcentrated lake water volume. Prior to the fixation of the samples with 2.5 ml buffered-formalin (37%), two drops of an alkaline Lugol's solution were added. The number of individual cells for each colony were enumerated (except for *Aphanocapsa* Nägeli, *Aphanothece* Nägeli, and *Planktolyngbya* Anagn. & Komárek for which colonies were counted), resulting in a total between 950 and 3400 individual cells for each sample studied. For this study, the results of the cell counts of the quantitative investigation, and not the calculated biovolumes (Plisnier et al. 2015), were used to allow comparison with results issued from different sampling techniques.

Identification was done with standard works (e.g. Komárek & Fott 1983; Starmach 1985; Popovský & Pfiester 1990; Komárek & Anagnostidis 1999) and more specific literature on phytoplankton of Lake Tanganyika (e.g. Van Meel 1954; Hecky et al. 1978). Taxonomic updates were done using AlgaeBase (Guiry & Guiry 2021).

For the physico-chemical characteristics of the lake water, only temperature and pH at the surface and transparency are available for the pelagic sampling station off Uvira. Water temperature and pH were measured in situ with a multiparameter kit model HANNA multiprobe HI 9828. The pH meter had been previously calibrated. The water transparency was measured with a standard white Secchi disk (SD) of 30 cm diameter. During the 2018 bloom and during the monitoring in 2011, 2012, and 2013, the physico-chemical parameters were measured using the same methods. Student's t tests were done according to the tables in Sokal & Rohlf (1995), without transformation of the data.

Meteorological data were recorded using an automatic weather station (AWS) (DAVIS Vantage Pro 2+) installed at Uvira (3°23′S, 29°8.7′E) at the north of Lake Tanganyika. To ensure equipment protection, the AWS was installed at the height of ~5 m at the Centre de Recherche en Hydrobiologie (CRH-Uvira). The CRH-Uvira is located at a distance of 200 m from the lake shore. The following parameters were measured every 15 min: air temperature (°C), rainfall (mm), wind speed (m.s^{-1}), wind direction (degrees), atmospheric pressure (mbar), solar radiation (W.m^{-2}), and relative humidity (%). Available data include the period from January 2012 to December 2018. However, data for the year 2016 were not available and data from September and November 2017 were missing in addition to a few days, including the period from 5 to 13 Sep. 2018. For this paper, meteorological information is considered as only indicative because of the non-optimal location of the AWS and some missing periods of recording.

RESULTS

Phytoplankton composition during the bloom in September 2018

The cyanobacterium *Dolichospermum flosaquae* (Bréb. ex Bornet & Flahault) Wacklin et al. (fig. 1A, B) was the dominant species in the surface sample taken on 10 September 2018 in the pelagic zone of Lake Tanganyika. This taxon was recently transferred to the genus *Dolichospermum* (Wacklin et al. 2009) and is better known under its synonym *Anabaena flos-aquae* Bréb. ex Bornet & Flahault. *Dolichospermum flosaquae* accounted for 85.3% of all phytoplankton cells and was followed in relative abundance by the cyanobacterium *Chroococcus limneticus* Lemmerm. (fig. 1C). In 2010, this species was transferred to the genus *Limnococcus* (Komárek & Anagn.) Komárk.-Legn. et al.: *Limnococcus limneticus* (Lemmerm.) Komárk.-Legn. et al. The relative abundance of *D. flosaquae* as enumerated in the first sample taken on 10 September, increased slightly the following day, and then dropped on 12 September (fig. 2A, supplementary file 1). On the other hand, the relative abundance of *L. limneticus* increased and reached a maximum on 12 and 13 September, to more than 70%. Besides cyanobacteria, the diatom *Nitzschia asterionelloides* O.Müll. and green algae species belonging to *Dictyosphaerium* Nägeli (fig. 1D) and *Lobocystis* R.H.Thomps. were also observed in the samples with relative low abundances (fig. 2A, supplementary file 1).

The cyanobacteria in the samples taken at the sampling site close to the shore (fig. 2B) showed the same trend as in the pelagic zone. The relative abundance of *D. flosaquae* on 12 September was, however, much more important near the shore compared to its abundance in the pelagic zone on the same day. The abundance of this cyanobacterium decreased gradually to 15 September, while *L. limneticus* increased from 12 to 14 September. *Nitzschia asterionelloides* and *Dictyosphaerium*/*Lobocystis* spp. were present with comparable relative abundances as in the pelagic zone. Dinophytes, belonging to the genus *Peridinium* Ehrenb. (fig. 1E), were also observed near the shore with increasing relative abundance up to more than 20% on 15 September (fig. 2B, supplementary file 1).

Species richness during the five sampling days increased in the pelagic zone from nine taxa in the counted cells/colonies the first day to 26 taxa on 14 September. In the littoral samples an increase was observed from 23 taxa on 12 September 2018 to 34 taxa on 15 September. Phytoplankton species richness increased in the pelagic zone mainly due to the introduction of more chlorophytes (supplementary file 1), although these green algae were always present in very low relative abundances. On the other hand, diatoms were responsible for higher species richness in the littoral zone (supplementary file 1), but also here, species were represented in very low relative abundances.

Phytoplankton composition at the end of the dry season (August–September) in 2011, 2012, and 2013 in the pelagic zone

Dolichospermum flosaquae was absent between late August through September in 2011, 2012, and 2013. Only on 20 Sept. 2011, a relative abundance of less than 0.1% was noted. In contrast, *Limnococcus limneticus* peaked in September 2011 and 2013, while in 2012, its relative abundance never reached 15% (fig. 3A–C, supplementary file 2). The small cyanobacterium *Synechococcus elongatus* (Nägeli) Nägeli, observed in all samples, was the dominant species on 26
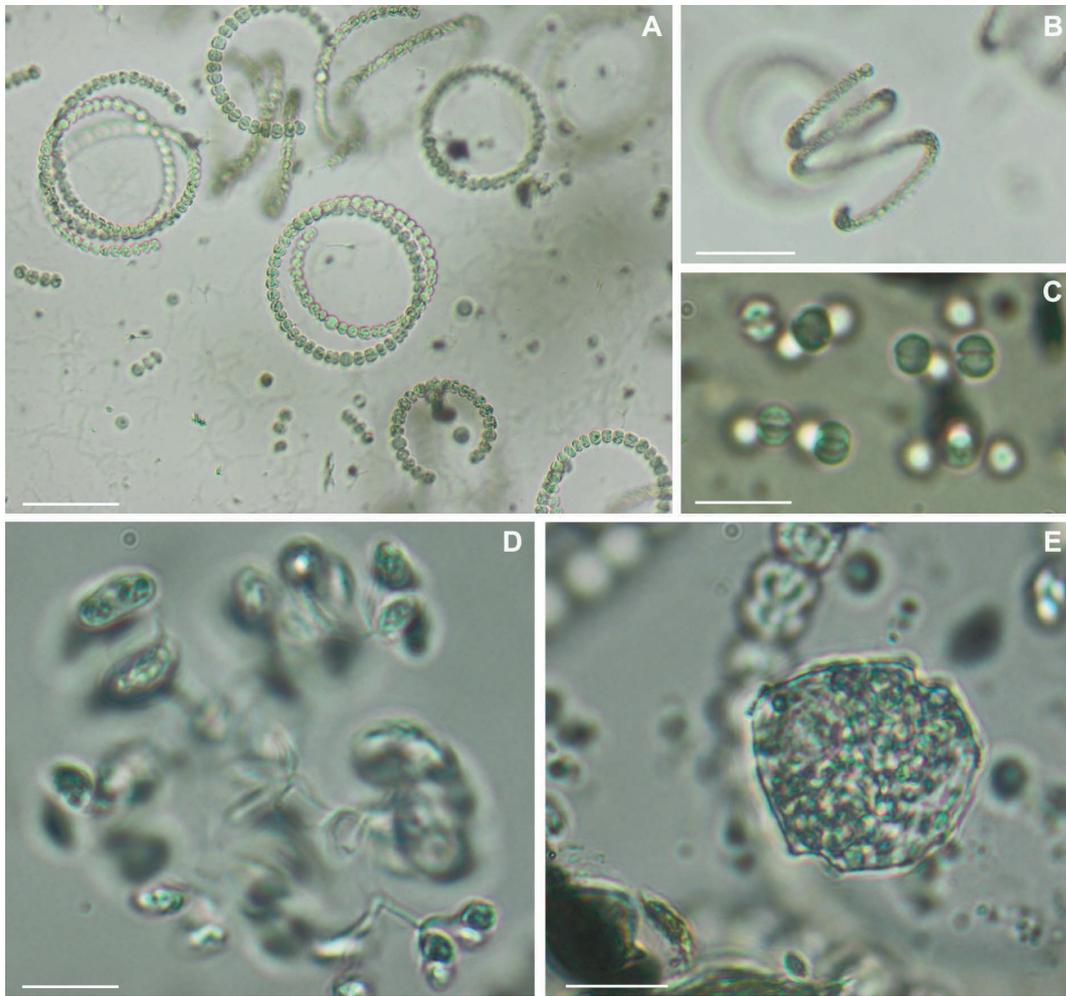
▲ **Figure 1** – Light microscopic micrographs of the dominant algae taxa observed in Lake Tanganyika during the phytoplankton bloom of September 2018. **A–B**. *Dolichospermum flosaquae* (Cyanobacteria). **C**. *Limnococcus limneticus* (Cyanobacteria). **D**. *Dictyosphaerium ehrenbergianum* (Chlorophyta). **E**. *Peridinium* sp. (Dinophyta). Scale bars: A, B = 50 µm, C–E = 10 µm.

► **Figure 2** – Relative abundances (expressed in %) of the dominant algae taxa in net samples of Lake Tanganyika between 10 and 15 Sep. 2018 as obtained from cells counts. **A**. Pelagic water column off Uvira. **B**. Surface water near the shore at Uvira.
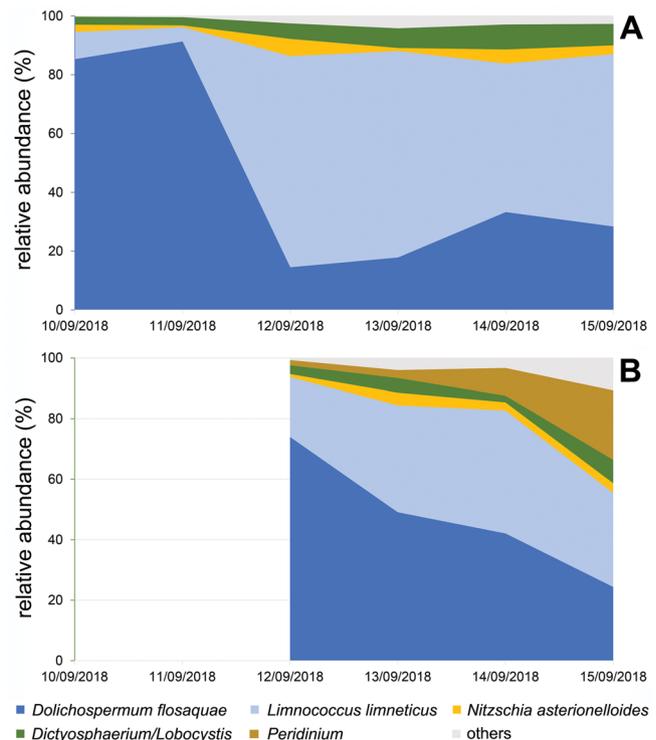
Aug. 2011, while *Anathece clathrata* (West & G.S.West) Komárek et al. (synonym of *Aphanothece clathrata* West & G.S.West) was the relative most important on 28 Aug. 2012.

Nitzschia asterionelloides was observed in most the samples, but its relative abundance showed only a small peak on 11 Sep. 2012 (fig. 3A–C, supplementary file 2).

Chlorococcum Menegh. spp., *Dictyosphaerium/ Lobocystis* spp., and *Coelastrum reticulatum* (P.A.Dang.) Senn were the most important green algae followed by a taxon resembling *Plectodictyon*, *Didymocystis comasii* Komárek, *Monoraphidium nanum* (Ettl) Hindák, and *Desmodesmus bicellularis* (Chodat) S.S.An et al. (included in "others" in fig. 3A–C; supplementary file 2).

Species richness per counted cells in the pelagic zone from the end of August to the end of September varied between 22 and 33 in 2011, between 33 and 43 in 2012, and between 31

and 45 in 2013 (supplementary file 2). The highest number of species was observed within the chlorophytes, more specifically 16 species within the Chlorellales, on 4 and 28 Sep. 2012.

Phytoplankton composition at the end of the dry season (August–September) in 2011, 2012, and 2013 in the littoral zone

Dolichospermum flosaquae was not observed in the plankton close to the shore between the end of August and the end of September in 2011, 2012, and 2013. *Limnococcus limneticus* peaked on 10 Sep. and 29 Sep. 2011 and on 3 Sep. 2013, while in 2012 its maximum relative abundance did not exceed 10% (fig. 3D–F, supplementary file 2). Other cyanobacteria showed a one-off peaked such as *Aphanocapsa delicatissima* West & G.S.West, *Anathece clathrata*, *Microcystis natans*
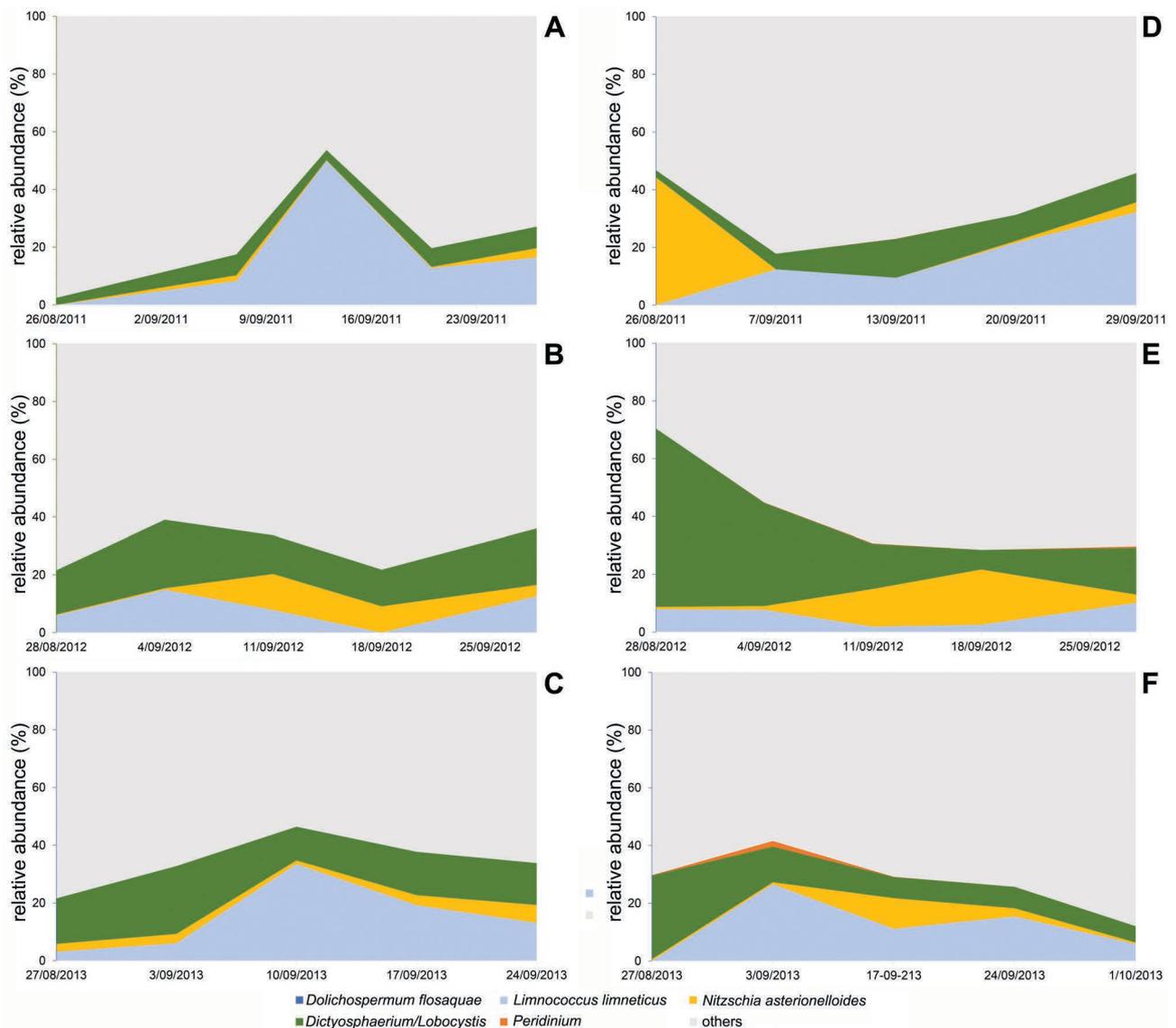
Figure 3 – Relative abundances (expressed in %) of the dominant algal taxa in the surface waters of Lake Tanganyika off Uvira between the end of August and the end of September in the pelagic zone for 2011 (**A**), 2012 (**B**), and 2013 (**C**), and in the littoral zone for 2011 (**D**), 2012 (**E**), and 2013 (**F**) as derived from quantitative cell counts.

Lemmerm. ex Skuja, and *Synechococcus elongatus* on 7 Sep. 2011, 1 Oct. 2013, 27 Aug. 2013 and 13 Sep. 2011 respectively (fig. 3D–F, supplementary file 2).

Nitzschia asterionelloides reached its maximum relative abundance on 26 Aug. 2011 and on 18 Sep. 2012, while in 2013 its relative abundance was not higher than 10.6%.

The relative abundances of *Dictyosphaerium*/*Lobocystis* spp. peaked in 2012 and at the end of August 2013, while other chlorophytes such as *Didymocystis comasii*, *Monoraphidium nanum*, and cf. *Plectodictyon* showed some small peaks (fig. 3D–F, supplementary file 2).

Between the end of August and the end of September 2011, 2012, and 2013, dinophytes were only sporadically observed.

Species richness per counted cells in the littoral zone from the end of August to the end of September varied between 26 and 37 in 2011, between 40 and 52 in 2012, and between 42 and 52 in 2013 (supplementary file 2). The highest number of species was observed within the chlorophytes, at the end of August and the end of September 2012.

Physico-chemical observations

Water temperature, pH, and SD transparency were measured at the surface in the pelagic zone and compared with previous studies (Plisnier et al. 1999, 2015; Langenberg et al. 2008). The average water temperature ($26.9°C \pm 1.25$) was not different from the surface water temperature measurements in the north of the lake during the months of September in 1993–1995 ($26.2°C \pm 0.27$) and 2011–2013 ($26.1°C \pm 0.20$). There were significant differences between pH during the phytoplankton bloom in 2018 (9.5 ± 0.40) compared to pH measured in the same period in 1993–1995 (8.8 ± 0.23) (no surface bloom periods) but no significant differences for the same month in 2011–2013 (9.2 ± 0.10, 9.1 ± 0.18, 9.5 ± 0.35). It is not known whether this reflects a change in methodology or whether it is related to different environmental conditions. The SD transparency data, on the other hand, was significantly ($p < 0.01$) lower in September 2018 (7.9 m ± 0.61) than in previous years in the same month: 12.6 m ± 1.51 (2011), 11.5 m ± 1.73 (2012), and 10.3 m ± 2.50 (2013).

Meteorological observations

In 2018, average air temperature at Uvira was 24.7°C, while the minimum recorded temperature was 18.8°C and the maximum 33.9°C (supplementary file 3). Differences with other years were significant ($p < 0.001$), except for 2013 ($p < 0.02$). Average solar radiation was significantly lower in 2018 ($p < 0.001$), except for the comparison with 2012 which was not significant. The average wind speed was significantly higher in 2017 and 2018. Available data from 2018 indicate that rainfall was then higher (> 963 mm) compared to the other years (685 mm in 2012 and 855 mm in 2013) (supplementary files 3 and 4). Although no precipitation data were available for September 2018, some rain was observed in September 2018 during and after the bloom (Muderhwa Nshombo & N'sibula Mulimbwa, pers. obs.).

Wind directions (2011–2018) at Uvira are mainly from the south-east (SE), which is partially caused by the SE trade winds from May to September, and partially by inshore winds in relation to the location of Uvira at the north-western end of the lake (supplementary files 4 and 5). Details on monthly wind speeds are provided in supplementary file 6. Stronger SE winds and a more easterly direction were observed during most of 2017, and mainly after the month of May in 2018.

DISCUSSION

Secondary upwelling in the north of Lake Tanganyika

At Lake Tanganyika, two major seasons are identified: a cold and dry season from May to September with mainly south-east trade winds and a warmer season with weaker and more variable winds. In the northern part of the lake, rainfall is interrupted in mid-January by a short dry period although this is not noticeable every year; and the heaviest rains are generally observed in March/April. The inter-seasons are generally in September/October and April/May corresponding respectively to the latitudinal and seasonal migration of the Intertropical Convergence Zone (ITCZ) in the Lake Tanganyika area. The inter-season period of September/October is also the period when, historically, important blooms of cyanobacteria had been observed in the north of Lake Tanganyika (Symoens 1956a, 1956b; Dubois 1958; Hecky & Kling 1981, 1987).

The annual limnological cycle of Lake Tanganyika explains the increase of nutrients from deeper waters at the end of the dry season (September). SE trade winds, blowing between May and August/September, induce an upwelling at the southern end of the lake (fig. 4). The thermocline is then tilted because warm upper water layers of the epilimnion are accumulated by the SE winds toward the north of the lake (Coulter 1991; Plisnier et al. 1999; Langenberg et al. 2008). The thermocline tilting towards the north of the lake corresponds to an accumulation of potential energy in the north of the lake.

At the inter-season period around September, when the ITCZ reaches the Lake Tanganyika area, the wind pressure decreases and the potential energy accumulated in the north of the lake is released. It is known that deeper nutrient-rich water rises toward the surface when layers of water tend toward re-equilibration (Mortimer 1974). This increase in nutrients near the thermocline was indeed clearly observed from the physico-chemical measurements but no planktonic blooms were visible at the surface in 1993–1995 (Plisnier et al. 1999). When SE winds are particularly strong during the dry season, a strong increase of primary production and a planktonic bloom are expected at the lake surface. Strong SE trade winds in 2018 most likely induced a strong tilting of the thermocline and the *Dolichospermum flosaquae* bloom observed in September, just after the dry season winds, is likely the consequence of an upward movement of hypolimnion nutrient-rich water at this moment of the year as water layers oscillate to recover initial depths (Mortimer 1974; Plisnier et al. 1999). Nutrient loading of anthropogenic impact or erosion are in this case not responsible for the

cyanobacteria bloom as often observed in aquatic ecosystems (Paerl & Huisman 2009; Long et al. 2018). Rivers flowing into Lake Tanganyika are colder than the surface water of the lake and quickly sink into the hypolimnion (Capart 1949; Pierre-Denis Plisnier, pers. obs.). The observed warming of the lake is expected to increase its thermic stratification, lower the lake mixing and lead to a decreased primary production (O'Reilly et al. 2003).

Comparison of the phytoplankton composition at Uvira during the bloom of September 2018 with the data of August/September 2011, 2012, and 2013

Dolichospermum flosaquae, the dominant species during the first two days of observations in the pelagic zone during the September 2018 bloom, was not observed in the pelagic nor in the littoral zone during the surveys from end of August to the end of September 2011, 2012, and 2013. On the other hand, *Limnococcus limneticus* peaking on the 3rd and 4th sampling day of the 2018 bloom, was also observed in September 2011, 2012, and 2013, but never reached similar high relative abundances independently of sampling techniques. In the littoral zone, other cyanobacteria such as *Aphanocapsa delicatissima*, *Anathece clathrata*, *Microcystis natans*, and *Synechococcus elongatus* developed but never in such an amount that it resulted in a visible bloom.

In years without observed bloom of blue green algae, the relative abundances of green algae became more important as shown by the phytoplankton analyses from September 2011, 2012, and 2013. During those three years, Chlorophyta represented up to 82.9% of all observed phytoplankton cells in the surface waters of the pelagic zone. *Dictyosphaerium* and *Lobocystis* species, the most important Chlorophyta observed in the September 2018 bloom with a maximum relative abundance of 8.5%, peaked on 4 Sep. 2012 and 3 Sep. 2013 with relative abundances of 23.7% and 23.5% respectively.

In contrast to their abundance in the littoral zone towards the end of the phytoplankton bloom in September 2018, the dinophytes were only sporadically observed in the studied September samples of 2011, 2012, and 2013. However, the different sampling techniques most likely had an influence on the number of dinophytes observed. An overestimation is very likely in net samples because the dinophytes are much larger than the other phytoplankton cells present and therefore more concentrated. In the quantitative cell counts, on the other hand, dinophytes are easily underestimated because a limited number of cells are counted, which is in favour of the small phytoplankton taxa such as coccoid green algae and cyanobacteria.

The lowest species richness per counted cells was noted during the first sampling days in September 2018 when
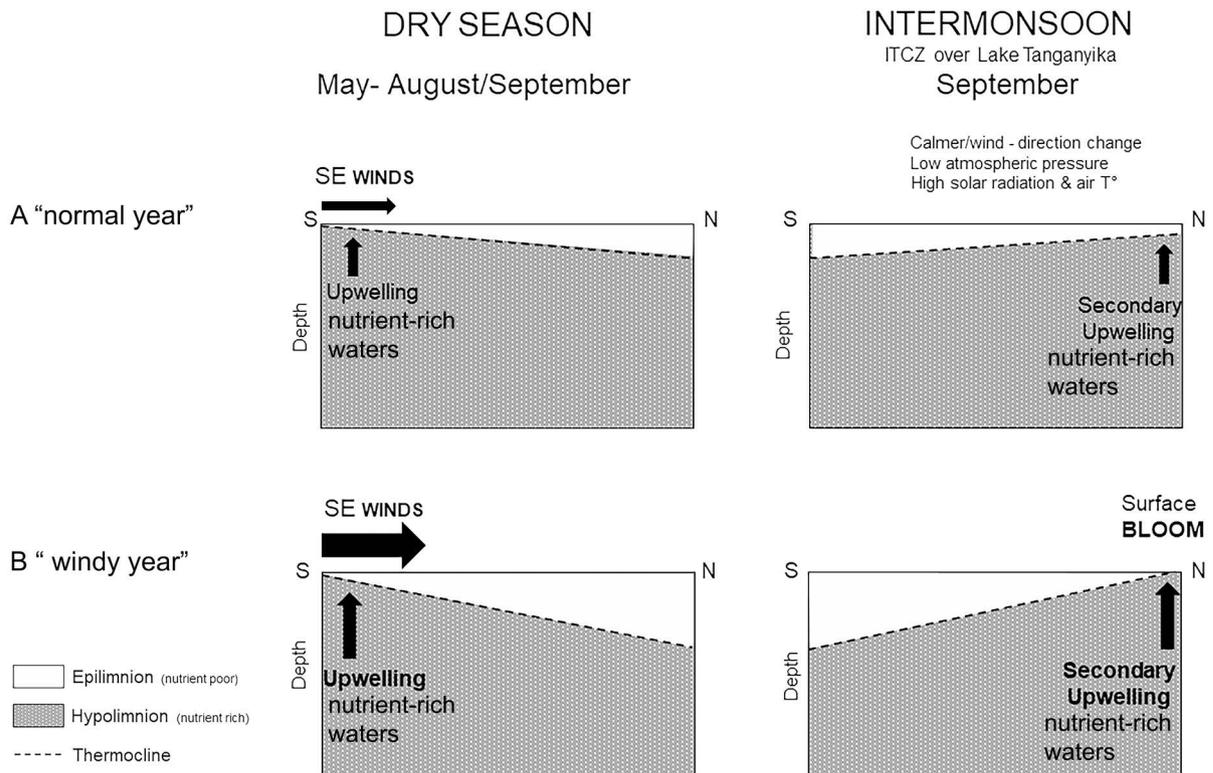
Figure 4 – Schematic representation illustrating a "normal" and a "windy" year in a longitudinal profile section of upper Lake Tanganyika. **A**. "Normal year": weak SE trade winds induce a weak tilting of the epilimnion; the secondary upwelling takes place in September in the north but no surface plankton bloom is observed. **B**. "Windy year": strong SE trade winds induce a strong tilting of the epilimnion; during the secondary upwelling at the inter-monsoon period hypolimnion nutrient-rich waters reach the euphotic layer inducing a visible surface plankton bloom.

Dolichospermum flosaquae caused the green colour of the surface water of Lake Tanganyika. As the phytoplankton bloom decreased, so did the number of cells of the dominant species, while more diverse phytoplankton species were observed.

Comparison with historical planktonic blooms in the north of Lake Tanganyika

The phytoplankton bloom observed by Symoens in Lake Tanganyika in 1955 started during the first week of September. A thin, intense green layer was formed on the surface of the lake during the windless time of the day, and sometimes continuous over several hectares (Symoens 1956a, 1956b). The maximum extent of the bloom was reached between 9 and 12 September. The SD transparency dropped from 12.5 m and 10 m on 24 and 29 August respectively to zero during the bloom. The phytoplankton bloom disassociated rather quickly and on 16 September, a transparency of 6 m was noted, increasing to 7.5 m and 8.5 m on 20 and 23 September respectively.

The cyanobacterium *D. flosaquae* (as *Anabaena flosaquae* in Symoens 1956a, 1956b) was the only organism responsible for the 1955 bloom and was observed down to 3 to 4 m below the surface. There was no mention that this species was replaced by massive development of *Limnococcus limneticus* as observed in the 2018 bloom.

In 1955, a second bloom was observed in October with extreme dense concentrations of *D. flosaquae*, followed by a third, less important bloom in November (Symoens 1956a, 1956b). The timing between those three blooms in 1955 is certainly linked to the internal wave periodicity in the lake (Coulter 1991). After the September bloom in 2018, no observations of surface blooms in October and November were reported near Uvira in the north of Lake Tanganyika.

Species switch during the cyanobacterial bloom in Lake Tanganyika

Species switches in cyanobacterial blooms are well known and documented (Long et al. 2018). *Microcystis* spp. blooms for instance are favoured by higher temperatures, higher nutrient (TN, TP) contents, and reasonable light (Pick 2016; Long et al. 2018), while *Pseudanabaena limnetica* is favoured by lower temperature (< 20°C) as observed during a monitoring in the Hongfeng Lake reservoir (Guizhou Province, China) (Long et al. 2018). Moreover, *Microcystis* spp. and *Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault are significantly correlated with high pH (9–11) (Laamanen et al. 2002; Hu 2011 in Long et al. 2018) and pH > 8.5 in the surface waters of the Hongfeng Lake reservoir (Long et al. 2018). In tropical Africa, *Microcystis aeruginosa* blooms are indeed common in Ugandan crater lakes where N is abundant and the pH is alkaline (Nankabirwa et al. 2019).

The switch from *Dolichospermum flosaquae* to *Limnococcus limneticus* as dominant taxon in a cyanobacterial bloom is not common at all. In temperate regions in Europe, a succession from *D. flosaquae*, together with *Woronichinia naegeliana* (Unger) Elenkin (as *Coelosphaerium naegelianum* Unger) and *Aphanizomenon flosaquae* in early summer (July) concentrated in the top 4 m of the water column (the first two taxa largely confined to the surface, the latter generally deeper), to a second cyanobacteria maximum in late summer and autumn including *L. limneticus* was reported in Lake Erken (Sweden) (Fogg et al. 1973). However*, L. limneticus* was not the dominant taxon, but among other species such as *Microcystis* spp., *Snowella lacustris* (Chodat) Komárek & Hindák (as *Gomphosphaeria lacustris* Chodat), *Aphanothece* Nägeli sp., and *Aphanocapsa* Nägeli sp. (Fogg et al. 1973). The dominance of *D. flosaquae*, a nitrogen-fixing cyanobacteria, in the September 2018 bloom in Lake Tanganyika points to a deficiency in N in the water column at the start of the phytoplankton bloom. The hypothesis that *Dolichospermum* is favoured by increasing phosphorous only as experimentally established by Moisander et al. (2012) cannot be verified due to the scarce available data of the September 2018 bloom. Information on TN, TP, and physico-chemical characteristics of the lake water at the surface and in the water column during phytoplankton blooms in the lake are necessary to explain the switch from the dominant *D. flosaquae* to the dominance of *L. limneticus*. Up to now, it is not known if this species switch from *D. flosaquae* to *L. limneticus* is generally occurring in phytoplankton blooms in Lake Tanganyika, because it was not reported for earlier blooms. Moreover, during phytoplankton blooms, the dominant species composition can only be observed from daily sampling during the entire period of these blooms.

CONCLUSION

The phytoplankton bloom with green colouring of the surface water as observed near Uvira in September 2018 is a rare phenomenon in Lake Tanganyika. The lake's annual limnological cycle explains an increase in phytoplankton productivity in the north of the lake due to upwelling of nutrient-rich deep waters at the end of the dry season in September. These upwellings are usually not strong enough to produce visual surface blooms. The available meteorological data provided more insight on possible causes of this exceptional bloom. Strong south-east winds during the dry season of 2018 (May–September) imply a strong tilting of epilimnion waters toward the north of Lake Tanganyika followed by a strong upwelling at the end of the period with strong SE winds (September). Moreover, there was a well-marked drop of atmospheric pressure at that moment indicating the passage of the ICTZ. At the same time, high solar radiation and air temperature were observed. Those conditions are favourable to increased water stability linked to cyanobacteria blooms (Paerl & Huisman 2009). The unusual meteorological conditions in 2018 probably explain the occurrence of a massive cyanobacteria surface bloom, which is a rare event in the generally oligotrophic Lake Tanganyika.

SUPPLEMENTARY FILES

Supplementary file 1 – Number of species per major algae group (italics), and relative abundance (expressed in %) of the dominant algae species as obtained during the semi-quantitative counts of the pelagic (P) and littoral (L) samples gathered during the phytoplankton bloom in Lake

Tanganyika off Uvira (D.R. Congo) between 10 and 15 Sep. 2018.

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Supplementary file 2 – Number of species per major algae group (italics), and relative abundance (expressed in %) of the dominant algae species as obtained during the quantitative counts of the pelagic and littoral samples gathered between the end of August and the end of September 2011, 2012, and 2013 in Lake Tanganyika off Uvira (D.R. Congo).

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Supplementary file 3 – Meteorological data for the years 2012, 2013, 2014, 2015, and 2018, as obtained from the weather station at Uvira (D.R. Congo), summarized as average (Av), maximum (Max), minimum (Min), and standard deviation (SD) for air temperature (°C), relative humidity (%), wind speed (m.s⁻¹), wind direction (°), atmospheric pressure (mbar), solar radiation (W.m⁻²), and rainfall (mm). The total number of observations on which these data are based are given for each year.

https://doi.org/10.5091/plecevo.2021.1890.2535

Supplementary file 4 – Annual cycles (monthly average) for the years 2012, 2013, 2014, 2015, 2017, and 2018 for **A**. Wind speed in m.s⁻¹. **B**. Atmospheric pressure in mbar. **C**. Air temperature in °C. **D**. Solar radiation in W.m⁻² measured at Uvira (D.R. Congo).

https://doi.org/10.5091/plecevo.2021.1890.2537

Supplementary file 5 – Annual data of wind speed (m.s⁻¹) and wind direction for the years 2012, 2013, 2014, 2015, 2017, and 2018 at Uvira (D.R. Congo).

https://doi.org/10.5091/plecevo.2021.1890.2539

Supplementary file 6 – Monthly data of wind speed (m.s⁻¹) and wind direction for the years 2012, 2013, 2014, 2015, 2017, and 2018 at Uvira (D.R. Congo).

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