Title

Need for harmonized long-term multi-lake monitoring of African Great Lakes

Journal

JOURNAL OF GREAT LAKES RESEARCH, 49(6)

ISSN

0380-1330

Authors

Plisnier, Pierre-Denis
Kayanda, Robert
MacIntyre, Sally
et al.

Publication Date

2023

DOI

10.1016/j.jglr.2022.01.0160380-1330

Journal of Great Lakes Research xxx (xxxx) xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Phytoplankton blooms and fish kills in lake Tanganyika related to upwelling and the limnological cycle

Pierre-Denis Plisnier [a,*], Christine Cocquyt [b], Yves Cornet [c], Nadia Poncelet [c], Muderhwa Nshombo [d], Gaspard Ntakimazi [e], David Nahimana [e], Lawrence Makasa [f], Sally MacIntyre [g]

[a] University of Liège, Chemical Oceanography Unit, Institut de Physique, Liège, Belgium
[b] Meise Botanic Garden, Research Department, Meise, Belgium
[c] University of Liège, Geomatics Unit, Department of Geography, Liège, Belgium
[d] Centre de Recherches en Hydrobiologie, Uvira, Democratic Republic of the Congo
[e] Université du Burundi, Centre de Recherche en Sciences Naturelles et de l'Environnement, Bujumbura, Burundi
[f] Department of Fisheries, Zambia
[g] Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, United States

ARTICLE INFO

Communicated by: Anthony Vodacek

Keywords:
Trade winds
East African Great lakes
Remote sensing
Local knowledge
Kelvin waves

ABSTRACT

Characterizing the processes which cause upwelling in the East African Great Lakes enables prediction of the spatial–temporal variability of phytoplankton blooms and increases in fish abundance or incidence of fish kills. The influence of the southeast trade winds on the limnology of Lake Tanganyika is well known. Upwelling occurs to the south and downwelling to the north from May to September and subsequent upwelling and blooms at the northern end of the lake. However, the influence of the shifts in wind speed and direction after the SE trade winds, including the Northeast trade winds, and any further internal wave driven upwelling requires investigation. Here we use images from remote-sensing during a 12 year period (2003–2014) to illustrate intense phytoplankton blooms at the southeast of Lake Tanganyika in April-May, a period characterized by relaxation of the Northeast trade winds. Phytoplankton blooms progressed around the lake after a massive cyanobacteria bloom at the northern end in September 2018; recent and historical observations and local knowledge show similar patterns. Lake Tanganyika limnological cycle is revised to include four main periods: two trade winds seasons and two inter-monsoon seasons (April-May and September-October) with lake-wide up and downwelling of the thermocline associated with the monsoons, and upwelling associated with subsequent internal waves in the inter-monsoon period which are linked with increased phytoplankton blooms and sometimes also fish kills.

1. Introduction

Amongst the African Great lakes (AGL), Lake Tanganyika fishery is the second largest after Lake Victoria with an estimated yearly fishery catch of 165,000–200,000 tons (Mölsä et al., 1999). High fisheries production is supported by new production, that is, increases in primary and secondary production enabled by fluxes of nutrients from deeper in the water column or from incoming river water. For Lake Tanganyika, inflows from river water are modest in comparison to the volume of lake water, and the upwelling associated with the southeast trade winds have been known to lead to increased fish production (Coulter, 1991). The high winds of the southeast monsoon cause upwelling to occur in other of the AGL which leads to increased nutrient fluxes and high productivity at that time (MacIntyre, 2013; MacIntyre et al., 2014, 2002; Talling, 1966, 1965). The annual cycle of monsoon (or trade) winds is a main driver of the seasonality and hydrodynamics of Lake Tanganyika (Spigel and Coulter, 1996) with early evidence linking the changing hydrodynamics to fisheries production (Cohen et al., 2016; Coulter, 1991, 1966a, 1966b, 1963; Plisnier, 1998). However, the dominant upwelling occurs only once each year, hence other mechanisms are required to sustain the fisheries over the year.

Increases in new production can occur when winds cause internal waves to upwell and/or break, causing mixing, or when heat losses are substantial and cause water from deeper depths to be entrained

* Corresponding author.
E-mail address: pierre-denis.plisnier@uliege.be (P.-D. Plisnier).

https://doi.org/10.1016/j.jglr.2023.102247
Received 16 March 2023; Accepted 17 October 2023
Available online 3 November 2023

(Reynolds, 2006; MacIntyre et al., 1999). The set up for the changing dynamics within L. Tanganyika depends largely on the trade winds. The patterns are as follows. Changes in trade winds result from the movements of the Inter-tropical convergence zone (ITCZ) (Nicholson, 2000). From April/May to September/October, the ITCZ moves to the north of the Lake Tanganyika basin and southerly winds prevail over the lake (Coulter and Spigel, 1991). From November to April/May, the ITCZ moves southward and becomes situated to the south of the Lake Tanganyika basin; northerly winds prevail during part of this period. In May-August, the SE trade winds tilt the thermocline downwards to the north while upwelling followed by considerable mixing is observed at the south of the lake. In the north, the upper mixed layer deepens and the thermocline is compressed (Coulter and Spigel, 1991). When the SE winds relax or stop, a secondary upwelling takes place in the north followed by an internal seiche (Coulter, 1963; Coulter and Spigel, 1991; Mortimer, 1952; 1974; Plisnier, 1996; Plisnier et al., 1999, 1996). In fact, on cessation of the SE trades, the thermocline compresses to the south and expands to the north, as indicative of a second vertical mode wave across the basin with first vertical mode internal waves thereafter until the SE trades once again begin (Huttula, 1997). Thus, the SE trade winds not only cause the thermocline to tilt across L. Tanganyika, on their cessation a variety of other internal waves are generated which persist over the annual cycle (Huttula, 1997).

The likelihood of increased primary production in coastal regions of the lake would be enhanced if the internal waves induced as the SE trade winds relax are rotational, e.g., Kelvin waves, such that upwelling occurred in coastal areas, or if they became non-linear which enhances mixing (MacIntyre et al., 1999; Horn et al., 2001). Coulter and Spigel (1991) addressed some of these questions. Assuming a two layered density structure, the periodicity of the first vertical mode waves are between 25 and 30 days (Coulter and Spigel, 1991). The calculated lifetime for these to decay is in excess of a year (Coulter and Spigel, 1991), thus they can be acted upon by subsequent wind events which can then cause either increases or decreases in amplitude. Antenucci (2005) provides arguments that whether internal waves are influenced by rotation can be determined by the Burger number, $S = c/L{\cdot}f$, where c is the wave celerity, L is the width of the basin, and f is the Coriolis parameter. For L. Tanganyika and using the value of $c = 0.55$ calculated by Coulter and Spigel (1991), the mean width of the basin, 50 km, and the Coriolis parameter for the north and south of the lake, gives $S = 1.4$ to the north and 0.48 to the south. Antenucci (2005) reports that internal waves have been found to be influenced by rotation for Burger numbers up to 2. Hence, in the north basin the tilted thermocline would occur across the width of the basin whereas it would be accentuated in coastal regions in the south basin. In other words, coastal upwellings are expected in this lake due to the influence of the Earth's rotation. At this time, time series temperature data from inshore and coastal regions of L. Tanganyika are lacking; however, this analysis indicates that Kelvin waves are likely within the lake. Biological and remotely sensed data can be used to further decipher the nature of the internal waves in L. Tanganyika.

Coulter and Spigel (1991) also addressed whether the internal waves induced in response to the SE trades become non-linear and break to induce mixing. The extent of thermocline tilting and the likelihood of mixing during and immediately after the monsoons can be predicted from the Wedderburn number (W) which is a ratio of the buoyancy forcing, (i.e., the stratification) resisting thermocline tilting by wind and the wind energy applied. It also takes basin morphometry into account (Imberger and Patterson, 1989). Values of W less than 1 indicate considerable thermocline tilting. and the likelihood that the ensuing internal waves would be non-linear and would break and induce vertical mixing. When values are less than ~ 0.5, internal bores are predicted to occur (Horn et al., 2001). These can traverse a lake and induce considerable mixing along the thermocline. Based on the density stratification within Lake Tanganyika and range of wind speeds in the southeast monsoon, Coulter and Spigel (1991) calculated that the Wedderburn number would range from 0.08 to 0.5. Spigel and Coulter (1996) calculated that W would have values close to 0.2. Consequently, the low values predict that the internal waves which form after the initial thermocline tilting will be non-linear and induce considerable mixing. Thus, depending on the extent to which nutrients increase with depth, these waves could lead to the increased nutrient fluxes that would support new production after the stronger winds of the monsoons abate.

Considerable effort has been expended to address the impact of the southeast (SE) trade winds in hydrodynamic studies of Lake Tanganyika (Delandmeter et al., 2018; Gourgue et al., 2011, 2007; Huttula, 1997; Naithani and Deleersnijder, 2004; Naithani et al., 2007, 2003; Podsetchine et al., 1999). The upwelling to the south is evident by the spreading of isotherms and ultimately mixing to $\sim$ 150 m and the downwelling of the epilimnion to the north by SE winds is evident by its deepening and the sharp thermocline below it (Coulter and Spigel, 1991; Huttula, 1997). When the SE trade winds decrease and the thermocline upwells to the north, nutrient fluxes are expected to increase in this lake in which internal loading of phosphorus and silica dominates (Hecky et al., 1991). The massive increase in abundance of phytoplankton and protozoa to the north at the end of the SE monsoon would be one manifestation of this large flux (Hecky and Kling, 1981).

Lakes are sentinels for climate change (Adrian et al., 2009; Williamson et al., 2008). Lake Tanganyika, the longest (673 km) and second deepest (1470 m) freshwater lake in the world and with the trade winds directed along its length, is a prime example of a lake sensitive to changes in climate (O'Reilly et al., 2003; Tierney et al., 2010; Verburg et al., 2003). With nutrients increasing strongly with depth, variable depths of upwelling associated with the SE and NE trade winds mainly will moderate nutrient supply and may similarly affect the amplitude of the internal wave field which subsequently develops. Given the need for greater understanding of these linkages, the aim of this paper is an improved understanding of the main hydrodynamics events of Lake Tanganyika and their recurrence over the annual cycle. We establish these linkages using a variety of observations including phytoplanktonic blooms and fish kills considered proxies of upwelling and mixing. A multidisciplinary approach has been used by including observations from local knowledge, from the literature spanning the last 119 years, from high frequency temperature data, and from remote sensing. Special attention was given to the timing and location of events possibly linked to the first, second, and third vertical mode waves which are predicted after cessation of the stronger winds, their potential to rotate around the basin (Kelvin waves), and any associated mixing. The results are then synthesized in a sequence of events updating a previous hypothesis on the annual limnological cycle (Plisnier et al., 1999). The long-term objective is to provide information to improve modeling of the lake's hydrodynamics as a necessary step toward applied forecasting models (fisheries, hydrology, health,etc.) for the benefit of the population and the sustainable use of the lake's ecosystem services.

2. Site description and methods

2.1. Lake Tanganyika

Lake Tanganyika is a tropical lake occupying a deep and narrow trough of the western branch of the East African Rift Valley between 3°30′-8°50′ S and 29°05′-31°15′ E with an approximate surface area of 32,600 km^2. Lake Tanganyika is stratified and meromictic (Beauchamp, 1939; Coulter and Spigel, 1991; Kufferath, 1952). Its stratification is largely dependent on the density gradient from changes in temperature. Throughout most of the lake, a persistent epilimnion varies in depth between 0 and 100 m covering a metalimnion varying in thickness but occasionally extending up to 250 m depth. Waters are anoxic below about 70 m at the north and 240 m at the south (Coulter and Spigel, 1991). There is evidence for a persistent shorebound current moving clockwise around the lake (Caljon, 1991; Coulter and Spigel, 1991).

In Lake Tanganyika, periodicity of internal waves is between 23 and

33 days (Coulter, 1968, 1963; Naithani et al., 2003; Plisnier et al., 1999; Podsetchine and Huttula, 1996). This periodicity is in quasi-resonance with the wind oscillations and is largely dominated by a one node in the neighborhood of the middle of the lake (Naithani et al., 2002). The amplitude of thermocline oscillations, 15 to 45 m for Lake Tanganyika, and periodicity depend on wind stress, stratification and thermocline depth. In addition to the main oscillations, spectral analysis of temperature data indicated the existence of peaks around 3, 6 and 12 days (Naithani et al., 2002).

Lake Tanganyika is oligotrophic. Its primary production is closely linked to the availability of nutrients in the euphotic zone. Nitrate concentration starts to increase around 44 m and phosphate around 34 m at the stations of Kigoma and Kipili (Edmond et al., 1993). Ammonium increases below about 100 m, where the water column is often anoxic. The increased concentrations are likely a result of remineralization as pH begins to decline by 50 m. Deep waters are thus rich in silicate, phosphorus and nitrogen (Edmond et al., 1993; Hecky et al., 1991; Plisnier et al., 1996). The average nutrient concentration increases between the surface and 300 m depth by 8 times for PO_4^-, 14 times for NH_4^+ and 15 times for SiO_2 (Plisnier, 1996) (Fig. 1). Pulses of higher nutrient concentration have been observed in the epilimnion in relation to internal waves (Plisnier and Coenen, 2001; Plisnier et al., 1999). A main southern upwelling during the southeast monsoon extends to 100 m and deeper (Huttula et al., 1997). The extent to which probable Kelvin waves would transport water from deeper depths is unknown. Phytoplankton in Lake Tanganyika are currently represented by a cyanobacteria-chlorophytes-diatoms community (Cocquyt and Vyverman, 2005). Interannual changes in phytoplankton biomass vary with the monsoons, and the succession of species begins even as the wind speed begin to increase (Hecky and Kling, 1981). The pelagic mesozooplankton community of Lake Tanganyika is simple being dominated by one calanoid species and three cyclopoid species (Coulter, 1991; Kurki et al., 1999).

Lake Tanganyika is threatened by climatic change and anthropogenic activities including pollution and overfishing (Plisnier et al., 2018). The warming of the lake could induce an increased thermic stability with less mixing and a decreased primary production (O'Reilly et al., 2003; Verburg et al., 2003). Overfishing could be present although fisheries data are rare or missing (Sarvala et al., 2006). An increased sedimentation along the shores could threaten various organisms and fish particularly (Cohen et al., 1993). Pollution from various sources, including petroleum exploitation, remain a major risk for Lake Tanganyika as for all other African Great Lakes (Abila et al., 2016). The residence and flushing time of Lake Tanganyika are respectively 440 and 7000 years which makes the lake and it's high biodiversity very sensitive to pollution risks (Coulter, 1992). This lake is a biodiversity hotspot sheltering more than 840 aquatic plant and 1318 aquatic animal species (LTBP, 2000). This increases the importance of an improved understanding of the lake's hydrodynamics which could help managers in various ways including simulating spreading of pollutants.

2.2. Observations of phytoplankton blooms and fish kills

Although there is no consensus in the literature on the quantitative definition of a bloom (Hopkins et al., 2021; Kutser, 2009), we define one as the rapid growth of one or more phytoplankton species leading to an increase in its biomass (Richardson, 1997). This definition was applied to the few historical blooms or "peaks" that have been described in Lake Tanganyika since the earliest observations (Van Meel, 1954). Plankton biomass at Lake Tanganyika increases rapidly during blooms by a factor of 2 or 3 (Bailey-Watts, 2000; Chale, 2004; Narita et al., 1986) and sometimes 4 or 5 folds (Ferro and Coulter, 1974; Hecky and Kling, 1981).

Three types of field observations related to plankton blooms and other events considered as proxies of upwelling, here also called hydrodynamic mixing, are reported in this paper:

- Observations based on local knowledge of surface waves, plankton blooms and fish kills were collected at various occasions between 1994 and 2022 from about 40 fishermen from Zambia (Mpulungu area) and Tanzania (Kigoma area) in addition to some observations from inhabitants, visitors or researchers. Mainly older fishermen, having a greater experience, were interviewed. Only observations that all or most of the fishermen agree on are reported here.
- Soon after a Dolichospermum *flosaquae* (Cyanobacteria) bloom, observed at Uvira on September 7, 2018 (Cocquyt et al., 2021), different bloom events and a fish kill were reported at various sites around the lake.
- Published observations as well as unpublished reports (from annual reports by Fisheries Departments or from various research projects) were consulted, particularly regarding the occurrence of plankton blooms and fish kills. Other events that can also be considered as indicators of upwelling were gathered such as limnological observations (physico-chemical characteristics in upper layers normally observed deeper), unusual fish abundance or floodings along the lake shores. The documents that were consulted spanned over the period 1904–2023. The information gathered in this paper include thus various limnological monitoring periods lasting several years with

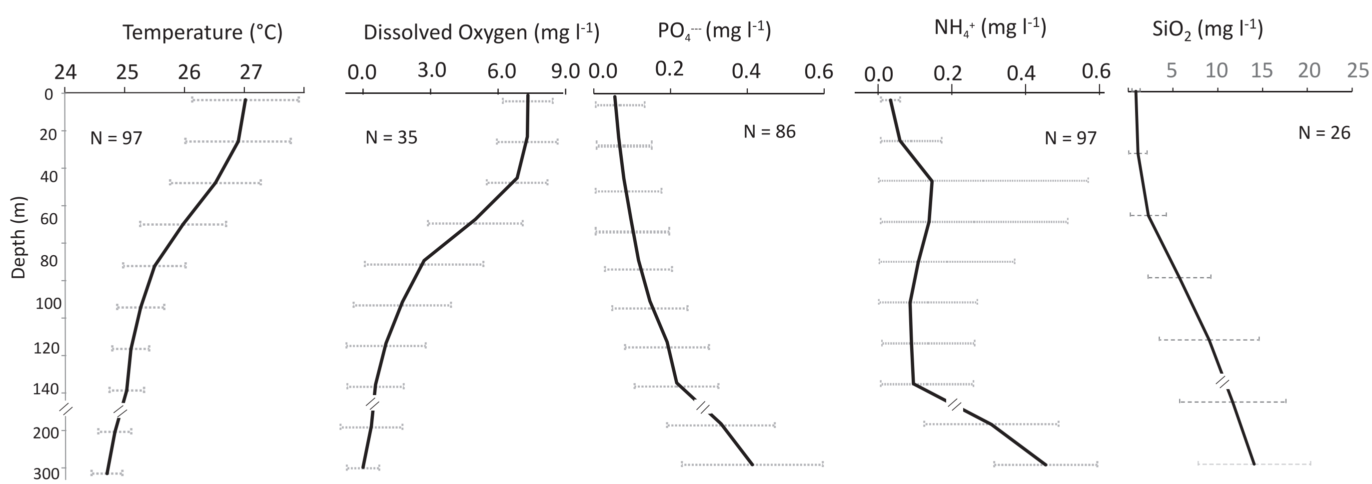

Fig. 1. Vertical profiles (0 to 300 m) of Lake Tanganyika measured from three sites regions (Bujumbura, Kigoma and Mpulungu). Average and standard deviation of temperature, dissolved oxygen, phosphates, ammonia and silica measurements in 1993–94. Note, these profiles are lake-wide averages. Nutrient concentrations begin to increase and anoxia develops below about 60 m in the north and deeper in the south. Profiles for different locations are presented in Plisnier et al. (1999).

systematic weekly, bi-weekly or monthly sampling. The reported events linked to mixing during inter-monsoon periods can be considered as representative of the seasonal upwelling variability over all months of the year.

2.3. Lake water temperature measurements in the north of the lake in 2005–2006

Two Tidbit © thermistors were installed at 1 m and 40 m depth in the north of Lake Tanganyika at 03°23.129′ S, 29°19.139′ E at the distance of about 3.5 km from the shore on a cable of the REGIDESO (Régie de production et de distribution d'eau et d'électricité, Burundi). Hourly data were recorded. The thermistor installed at 1 m depth was operational from March 9 to December 31, 2005. The thermistor installed at 40 m depth recorded temperature from March 9, 2005 to December 27, 2006. The accuracy was 0.2 °C and resolution was 0.02 °C.

2.4. Measurement of chorophyll a

Chlorophyll *a* (chl a) was measured using standard methods with a fluorometer (Turner Designs T7-1A 03/95) in Kigoma and a spectrophotometer in Mpulungu after acetone extraction. Samples from both stations were also analysed for chl a using HPLC analysis (Descy et al., 2006; Plisnier et al., 2015). Pigment data processing used the CHEMTAX software (Mackey et al., 1996). Details of the processing method are given in Descy et al. (2005). Those data were used to assess the performance of methods to estimate satellite chl a.

2.5. Remote sensing observations

Moderate Resolution Imaging Spectroradiometer (MODIS) data were processed to generate raster Time Series (TS) of Lake Tanganyika surface chl a concentration (chl a) for the period from July 2002 to December 2014 in the context of a past project (CHOLTIC) (Plisnier et al., 2015).

MODIS Level 1A data (Reprocessing 5) covering the area of Lake Tanganyika were downloaded (http://oceancolor.gsfc.nasa.gov/) and cropped to this area (last accessed on December 2014). Only MODIS Aqua (crossing the equator in ascending node at 13:30 Local Time) was used as the NASA Ocean Biology Processing Group does not encourage the use of MODIS Terra for Ocean Color (OC) processing due to calibration problems (Franz et al., 2007).

Level 1A was chosen to reduce the parallax effect on the geometric consistency due to altitude and high value of satellite zenith angle near the margins of the field of view. SeaDAS 7.1 software was used to extract geolocation and compute calibrated radiance and biogeophysical variables. Terrain height correction was enabled to compute geolocation files and Rayleigh radiance. Default stray light and cloud masking were disabled at this stage.

Level 2 products were computed. They include biogeophysical parameters such as remote sensing reflectance in all visible wavelengths, chl a sensor and solar zenith angles and other useful ancillary information (e.g. flags). Pixel value was evaluated based on sensor and solar zenith angles geometry to exclude specular reflection and observation incidence angle higher than 40°. MODIS Atmosphere cloudmask (35_L2 from MODIS-Atmosphere group) was applied to keep only 'clear' or 'probably clear' sky pixels. Five aerosol models for the atmospheric correction are indicated in the Electronic Supplementary Material (ESM) (Appendix S1). The seven most relevant bio-optical algorithms to estimate satellite chl a are indicated in ESM Appendix S2. Those were tested in combination.

To measure the performance of those combinations, in situ chl a data were matched up with satellite estimates applying the following criteria: maximum time difference of 6 h, minimum coastal distance of 1 km and maximum spatial distance of 4 km between the in situ observation and the associated pixel in case of masked value. In situ values have been associated either directly with the matched pixel value or the median extracted in a 5-by-5-pixel window around the pixel to eliminate the effect of noisy values. Only observations matching up for all the combinations tested were retained. Performance metrics were computed using the protocol described by Campbell and O'Reilly (2006).

Some main methodological limitations of the determination of surface chl a by remote sensing, need to be mentioned:

1) Empirical OC algorithms have been developed for open ocean clear water case and are sensor specific. Lake Tanganyika water seems to be comparable to this case (Horion et al., 2010; Loiselle et al., 2009). Lake Tanganyika presents generally clear waters with Secchi disks values generally between 8.7 and 12.8 m (Plisnier et al., 1996). Moreover, regarding sensor specificity, SeaDAS software was originally implemented to process SeaWIFS products. However, NASA has been updating the software for existing ocean color sensors such as MODIS with powerful atmospheric correction functionalities.
2) Some configurations of sun illumination and sensor view angles induce water surface effects like sun glint and whitecaps for particular wind conditions or specular reflection that prevent any measurement of bio-optical properties of water column. The performance of masking procedures is linked to the combinations of aerosol models and bio-optical algorithms.
3) Observation zenith angle threshold has been set to a large value which is less adapted to capture water column bio-optical properties. Multi-path light from mountainous slopes can affect water color near the coast with this setting.
4) Sediments from river water could disturb the measurement of chl a using remote sensing techniques. Although colder river rapidly sinks below the surface, satellite data obtained near the coasts must be interpreted with caution. However, no large river inflows occur near the major blooms observed in April-May. Also, the density of human population in the SE of the lake is very low and the agriculture is mainly traditional. Consequently, this area of the lake does not have appreciable erosion and concomitant perturbation by sediments as in the north.
5) The contribution of atmosphere to the satellite signal recorded in short visible wavelengths of light is very much higher than contributions coming from water inducing uncertainties (De Vis et al., 2022; Ruddick et al., 2000). At Lake Tanganyika, atmospheric properties are more spatio-temporally variable than in open ocean. Seasonal variability of aerosol optical depth is high (https://earthobservatory.nasa.gov/global-maps/MODAL2_M_AER_OD). During the wet season, temporal variability is high in daily periods with possible clear sky. Also, the contribution of the surface of the water to the satellite signal linked to wind speed (waves, glint, whitecaps) varies greatly in space and time which is poorly represented by meteo-reanalysis used.
6) High cloudiness, especially in the northern basin and during the wet season (Horion et al., 2010), produces very incomplete and noisy satellite chl a estimates. Even using a specific cloud mask, this problem impacts the quality of the satellite products with observable border effects.
7) Satellite chl a estimates systematically show a better correlation with fluorometer/spectrophotometer field measurement than with HPLC, the standard in OC science, although the number of simultaneous observations was limited.
8) Satellite observation times do not necessarily correspond to the response of maximum phytoplankton concentration since deep maxima are also observed (Descy et al., 2010).
9) MODIS 1 km resolution (at nadir) is large with respect to the small and ephemeral bloom patches. In the margins of the field of view (higher satellite zenith angle) resolution is degraded. The use of finer spatial resolution sensors should surely be a better solution to detect such blooms. But the use of those sensors doesn't allow frequent observations with similar angle of observation (no oblique orientation of the sensor using forward–backward camera and right and left

tilting of the platform) because of narrow field of view and orbit geometry. This solution is also not compatible with the ephemeral nature of those blooms. Furthermore, medium (decametric) and high (metric) spatial resolution sensors are characterized by lower spectral resolution and smaller signal to noise ratio that are not compatible with OC parameters computation.

The values of satellite chl-a TS were extracted computing the median in a 5x5 window around the pixel corresponding to the in situ sampling position. This method obviously smooths the TS with regard to a nearest neighbour approach and probably also reduces the temporal variance with regard to in situ values TS that has not the same spatial signification. But this is not systematically observed with all aerosol model/bio-optical algorithm combinations.

Future field observations in some lake regions, such as in the SE of the lake in April-May, could re-enforce the interpretation of the chl a estimates from remote sensing observations. Those in situ measurements could include bio-optical components of lake water (dissolved organic matter, mineral suspended matter) to confirm water case I. The satellite products TS should be completed and possibly produced with more adapted OC algorithms and atmospheric correction (models and ancillary data).

3. RESULTS

3.1. Local knowledge related to hydrodynamic events

The main winds known by all fishermen are the trade winds. In the south of the lake, two additional important events are identified during inter-monsoon periods by specific names: Those are the surface waves "Chimbanfula" and "Yalafula". Winds are said to cause waves of varying intensity and strength and therefore are called by the same names. Those events and local information are presented as they occur sequentially during an annual cycle:

(1) S/SE WINDS in May-June to August-September ("Kapata" in Zambia, "Kusi" in Tanzania).

The SE trade winds are described by all fishermen who were interviewed as "very strong" in Zambia while in the Kigoma area (Tanzania) they are perceived as less strong than the NE (Kaskazi) winds. Fishermen in Zambia indicate a relation between years of heavy rains and stronger SE (Kapata) winds. Those winds generally blow there for 2 to 4 days and about 3 times a month. In the 1970's, it was reported that they could blow continuously up to 7 days.

(2) "CHIMBANFULA" WAVES (Zambia) from September to November/December (Fig. 2).

"Chimbanfula" means "the waves that bring the rains" and seems specific to the south of the lake. Coming from the north, they are observed during an inter-monsoon period soon after the SE trade winds cease and before the first rains accompanying the NE winds season. They are described as "very strong" surface waves. Differently from "Yalafula" waves (below), some fishermen indicate that the Chimbanfula waves can happen two to four times per month and can be observed during several months some years. Fishermen indicated that, as for the winds and various events in the lake (blooms, fish kills, etc.), those waves used to be much stronger before the 1980's. A fisherman indicated that those waves were then able to destroy fields and carry heavy stones out of the lake. Today, fishermen still remove their boats from the lake when those waves start. At the south of the lake, the direction of the waves is indicated by some fishermen as rather from the east than from the north.

(3) N/NE WINDS from November to March/April ("Kaskazi" in

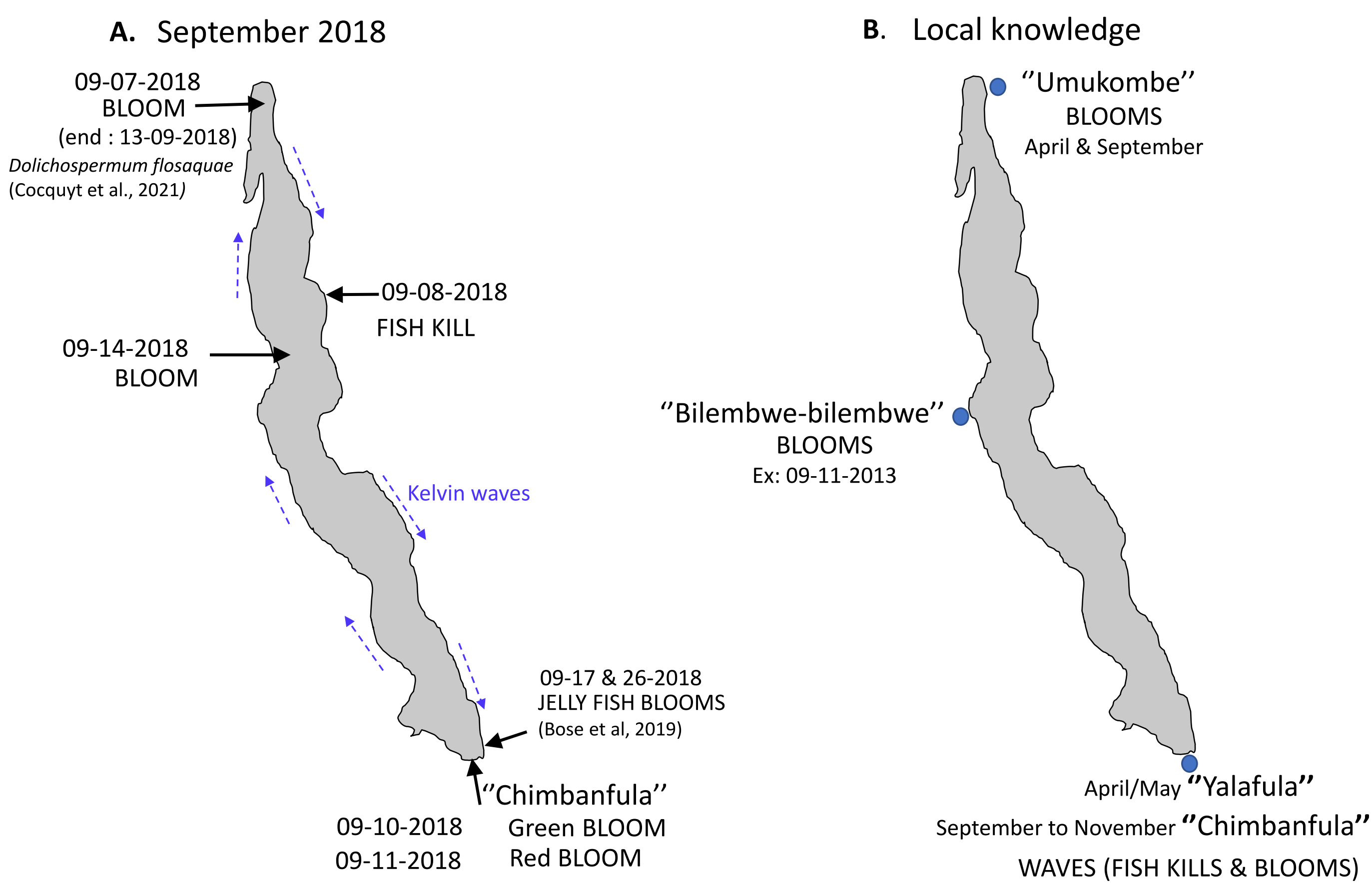

Fig. 2. (A) Plankton blooms observed around the lake in September 2018, an inter-monsoon period . The probable Kelvin waves propagation is indicated with blue dashed arrows. (B) Local names related to surface waves or planktonic blooms around Lake Tanganyika. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Zambia and Tanzania,"Kasikazi" in Burundi, also "Muhozi" in Zambia).

Fishermen don't have a unique perception of the strength of these trade winds that are described by some as "strong" but "weak" by others. It could indicate a marked intraseasonal and/or interannual variability (possibly also spatial variability). In Kigoma, those winds/waves are called "Kifunda" when they are extra strong which is not observed every year (Wekesa, 2001). In the same area fishermen noted that those winds generally last about 2 to 3 days. One fisherman indicated that it can cause fish kills about once in five years and that it kills fish in shallow sites. Phytoplankton blooms and good fish catches are noted about 2 to 3 days after those winds. Near Kigoma, a fisherman indicated that in 1978 this wind caused shipwrecks of 3 big passenger boats and 10 small boats. There was one oral report that, in 1995, it caused the big passenger boat 'Mwongozo' to capsize while enroute to Burundi. Fishermen in Burundi noted that those winds start to blow after the dry season with the start of the rainy season. Their speed gradually decreases from January to March. At the end of this period, in April, the lake is indicated as "almost calm" in Burundi (Nahimana et al., 2008; Petit, 1995).

(4) "YALAFULA" WAVES (in Zambia) from April to May (Fig. 2).

The waves called "Yalafula," mean "the waves that end the rains". They come from the north during an inter-monsoon period. This corresponds to the end of the NE trade winds before, and possibly simultaneously, with the starting of the SE trade winds. Fishermen describe them as very strong surface waves during a complete day (some years 2 or 3 days) and indicate that those waves are observed only once during the year.

In Zambia, fishermen indicate that SE winds ("Kapata") or NE winds ("Kazikazi") in addition to "Chimbanfula" and "Yalafula" waves may all be tied with plankton blooms. As soon as the winds blow, the water turns green. When "Kapata" and "Chimbanfula" events are strong, fish kills may be observed. Those take place very close to the shore up to a distance of about maximum 50 m. Fish kills are not observed everywhere. For example, along the Tanzanian coast, at Kipili (7°26'29" S, 30°35'59" E), those are not observed contrarily to the nearby Kirando (Fishermen and Mupape, pers. com.). Fish collected from fish kills are not toxic and may be consumed. This suggests that the cause of the death is probably upwelling of anoxic waters. Fishing is good after the winds have been blowing, especially Kapata and fairly Kazkazi. When Kapata wind is blowing heavily, many fish swim against the current coming to the shore. Calm days and good fishing follow the Kapata wind, especially for *Stolothrissa tanganicae* and *Limnothrissa miodon* (clupeids) but also for *Lates* spp. Plankton blooms or "green events" have another name in Kalemie (D.R. Congo), where they are called "Bilembwe-bilembwe" (Deladerrière, pers.com). In Burundi, "green events" are called "Umukombe". Those are generaly observed in April and September and are followed by good fishing (fishermen, pers. com.). Many other local winds are known by fishermen around the lake but are not reported here.

The oldest written record of local knowledge at Lake Tanganyika is noted by the explorer Henry Morton Stanley during his circumnavigation in 1876 to search for inlets and outlets. On July 4, 1876, he asked at the south of the lake (currently Mpulungu in Zambia): "Where does the water of the lake go to?". He was answered "It goes north, then it seems to come back upon us stronger than ever" (Stanley, 1889). This could be interpreted as the first report of relaxation of tilted layers toward the north of the lake by the SE trade winds inducing a "returning" surface wave in the south at the end of the SE trade winds season.

A main result from local knowledge is thus the identification of 4 periods during an annual cycle: two periods related to the trade winds alternate with two inter-monsoon periods characterized by important mixing related events (waves, blooms, fish kills…).

3.2. Local observation in September 2018

In September 2018, a major phytoplankton bloom was observed at the north of the lake (Cocquyt et al., 2021). This bloom was mainly caused by the cyanobacteria *Dolichospermum flosaquae*, the current accepted name for *Anabaea flos-aquae*. It was observed in surface waters of Uvira from September 7 until September 13. The green coloration of the lake water was particularly well observed along the shores (Fig. 3a). During this phenomenon, juveniles of *Stolothrissa tanganicae* and *Lates stappersii* became about three times more abundant in the local markets. An increase of shrimps abundance was also noted. One day after this northern massive bloom, a fish kill took place at Jakobsen Beach near Kigoma, Tanzania. Many small dead fish were observed in the afternoon (between 2 and 6 pm) on September 8, at 5 to 10 m from the shore (Denayer, pers. com.) (Fig. 2a). Two days later, on September 10, strong waves known as "Chimbanfula" were observed at the southern end of the lake (Mpulungu in Zambia). It was accompanied by a "green bloom" the same day and a "red bloom" on September 11. Four days later, on September 14, the crew of the Maman Benita boat observed in the northern area of the lake between Kalemie (D.R. Congo) and Kigoma (Tanzania) a huge bloom on their way (Akilimali, pers. com). Later, in the South of the lake (Mutondwe Island near Mpulungu), two jelly fish *Limnocnida tanganyicae* blooms were observed, on September 17 and again on September 26th (Bose et al., 2019) (Fig. 2a).

3.3. Historical occurrence of mixing events

We now investigate the monthly occurrence of events linked to mixing in publications and data from previous projects and earlier research to identify when they occur during the annual cycle. Any identified patterns will then be compared with the seasonality of the trade winds. It is known so far that the SE trade winds are indeed strong drivers of mixing (Coulter, 1991; Plisnier et al., 1999).

Upwelling and related hydrodynamics events are expected to induce: phytoplanktonic blooms, fish kills, exceptional abundance of organisms or peaks in their reproduction stage, surges, flooding events along the lake shores, and mixing observed from limnological measurements. In addition, a sharp change of wind direction or speed is likely to be linked with such events. Each of those type of events is detailed below:

3.3.1. Phytoplankton blooms

Since observations have been recorded in Lake Tanganyika, five phytoplankton blooms were reported in April/May (Table 1) and twenty-three in September/November (Table 2). Two peaks of increased primary production are well observed in the south of the lake during the two inter-monsoon periods (Bergamino et al., 2010).

Abundant phytoplankton were noted in the large bays with marked periodicity (Van Meel, 1954). Currents associated with thermocline movements bring very deep water close to the shore which then gradually expands offshore (Coulter, 1977, 1963; CLIMFISH project, unpublished data). During the September 2018 massive bloom in the north of the lake, which lasted for 7 days, the relative abundance of *Dolichospermum flosaquae* was much more important near the shore compared to the pelagic area (Cocquyt et al., 2021) . It was noted that a jelly fish bloom in September 1995 was about 10 times denser near the coast than at 15 km offshore (Salonen et al., 2012). Wind-driven upwelling events occur at several locations along the eastern and western coasts (Huttula et al., 1997). Some intense phytoplankton blooms may appear suddenly and may be observed for less than 24 h (Fig. 3 b).

Out of 27 reported plankton bloom events, taxonomical information was provided for 20 blooms including 17 filamentous cyanobacteria blooms (16 *Dolichospermum* and 1 *Anabaenopsis*). A higher reporting frequency for Cyanobacteria probably resulted from their visibility at the lake surface. Up to now, toxicity has not been reported during cyanobacteria blooms at Lake Tanganyika.

The duration of blooms may vary. A period of 7 days has been observed several times (Cocquyt et al., 2021; own obs.). However, short blooms also take place (Horion et al., 2010). Those are sometimes recurrent. Two or three pulses were observed with a periodicity of about 3 weeks (Beauchamp, 1939; Hecky and Kling, 1981; Symoens, 1956,

Table 1
Overview of events as proxies of type 1 mixing at inter-monsoon in April-May-June in Lake Tanganyika (B = phytoplankton bloom, FK = fish kill, L = limnology, F = fish, Z = zooplankton, FL = flooding, DO = dissolved oxygen, BI = Burundi, DRC = Democratic Republic of the Congo, TZ = Tanzania, ZB = Zambia, LTR = Lake Tanganyika Research project/FAO-FINNIDA, MS = Muderhwa Nshombo, LM = Lawrence Makasa).

Year	Month	Date/site	Type	Observations	References
1946–1947	4	Not specified	B	Second maximum of phytoplankton abundance observed in April (much less important than at the end of the dry season).	Van Meel, 1954
1961	5	Mpulungu (ZB)	L	Breakdown of stratification inshore observed from temperature and DO isopleths.	Coulter, 1963
1973	4	Kigoma (TZ)	L	Mixing events observed from DO, temperature and conductivity measurements.	Ferro and Coulter, 1974
1990	4 or 5	Rumonge (BI)	FK	Fish kills of *Lates stappersii* along the beaches.	Petit (pers. com.)
1993–1996	4/5	Kigoma (TZ)	Z	Clear reproduction peak of Cyclopoids.	Kurki et al., 1995
1994	3 to 5	Bujumbura (BI)	L	Turbidity “layer” near the thermocline.	Plisnier et al., 1996
1994	4 or 5	Minago (BI)	FK	Fish kills of *Lates stappersii*.	Petit (pers. com.)
1996	5 & 6	05–28-1996 06–18-1996 Mpulungu (ZB)	FK	Fish kill of *Lates stappersii*.	LTR sampling
1996	5 & 6	Bujumbura (BI)	B	Deep chl a peaks (60 to 100 m).	Langenberg et al., 2002
1997	4	Not specified	L	Internal wave propagating along the main axis of the lake (surge).	Huttula, 1997
1998	6	Mpulungu (ZB)	B	Blooms of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*).	Bailey-Watts, 2000
1999	5	Kigoma (TZ)	B	Peak of chl a (2.5 $\mu g.l^{-1}$).	Chale, 2004
2002–2005	4/5	Southern Lake Tanganyika	L	Increase in phytoplankton production.	Bergamino et al., 2010
2004	4/5	Mpulungu (ZB)	Z	Mesozooplankton peak.	Descy et al., 2006
2005	5	Bujumbura (BI)	FL	Flooding of shorelines.	Tack (pers. com.)
2005–2006	5	Mpulungu (ZB)	B, F	*Stolothrissa tanganicae* appearing simultaneously in the catches as coastal plankton blooms developed both years.	Plisnier et al., 2009
2017	5	05–19-2017 North-Burundi	FL	Flooding of the beaches threatening the Imbo plains.	Iwacu, 2016
2020	4	04–04-2020 Mpulungu (ZB)	FL	“Yalafula” waves (one day) - damages to the market and shops.	Own observation (LM)
2020	4	04–17-2020 Uvira (DRC)	FL	Flooding before heavy rains. Increase of lake level by about 1 m; destructions resulting in > 20 deaths and 400 destroyed houses.	Own observation (MS)
2020	4	04–17-2020 Gatumba (BI)	FL	Flooding at the northern end. “The lake throws up”	https://imazpress.com/france-monde/le-lac-tanganyika-vomit-leau-monte-et-deplace-les-populations
2020	6	06–01-2020 Ubwari (DRC)	FK	Fish kills and injured fish, particularly *Tilapia* spp.	Actualite.cd, 2020
2021	5	05–11-2021 05–24-2021 Uvira (DRC)	FL	Flooding from big waves of the lake and from the Ruzizi (May 11) Flooding up to 50 m from the shores by lake waves. No rains were noted those days (May 24).	OCHA, 2021; Radio Okapi, 2021

Table 2
Overview of events as proxies of type 2 mixing at inter-monsoon following the SE trade winds season mainly in September, October and November in Lake Tanganyika (B = phytoplankton bloom, FK = fish kill, L = limnology, F = fish, Z = zooplankton, FL = flooding, WD = wind direction, DO = dissolved oxygen, BI = Burundi, DRC = Democratic Republic of the Congo, TZ = Tanzania, ZB = Zambia, LTR = Lake Tanganyika Research project/FAO-FINNIDA, GN = Gaspard Ntakimazi, LM = Lawrence Makasa, PDP = Pierre-Denis Plisnier).

Year	Month	Date/site	Type	Observations	References
1904	10	Not specified	B	Bloom of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*).	West, 1907
1938	9	09-14-1938 Kigoma (TZ)	B, L, Z, WD	Bloom of Cyanobacteria during a period without wind followed by a zooplankton peak. Wind changes from SE to NE. Two pulses of nutrient-rich hypolimnion water toward the surface (3 weeks period). "Submarine wave" (surge).	Beauchamp, 1939
1947	10	Uvira (DRC)	B, L	Bloom of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*). DO deficit of 70 %.	Van Meel, 1954
1955	9	Uvira (DRC)	B, Z	Bloom of *Dolichospermum flosaquae* (as *Anabaena flos-aquae*). Three pulses from September to November (period of about 3 weeks). Abundance of copepods, shrimps and jellyfish.	Symoens, 1955, 1956; Dubois, 1958a
1956	9	09-21-1956 Uvira (DRC)	B	Bloom of *Dolichospermum flosaquae* (as *Anabaena flos-aquae*).	Dubois, 1958a
1960	11	11-21-1960 Mpulungu (ZB)	B	Dense phytoplankton bloom close inshore and gradually extending offshore	Coulter, 1963
1961	08	08-22-1961 Mpulungu (ZB)	L	No oxygen below 80 m. Migration of fish above the anoxic zone	Coulter, 1963
1961	11	21-11-1961 Mpulungu (ZB)	B, L	Rising of isotherms. Release of nutrients close to the shore. Dense bloom inshore gradually extending offshore.	Coulter, 1963
1972	9	Burundi	F	High catches of *Stolothrissa* followed by damping.	Bazigos, 1973
1973	9	Bujumbura (BI)	L	Rapid rise of thermocline.	Ferro and Coulter, 1974
1974	10	Lake cruise	L	Internal wave surge derived from temperature and DO measurements.	Chapman et al., 1974
1975	9/10	Bujumbura (BI) Central lake	B	Phytoplankton blooms. First pulse: diatoms (especially *Nitzchia*), green algae and protozooplankton. Second pulse: Cyanobacteria (mainly *Dolichospermum flosaquae* as *Anabaena flos-aquae*) that also was prominent in the phytoplankton of the central lake area.	Hecky and Kling, 1981
1975	10	10-10-1975 Kigoma (TZ)	B	Bloom of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*).	Hecky and Kling, 1981; Ferro and Coulter, 1974
1981	9/10	09-21-1981 10-2-1981 Mahale (TZ)	B, Z	Blooms of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*). Abundance of shrimps. High reproduction of *Diaptomus*, shrimps and possibly cyclopoids.	Narita et al., 1986
1981	9/10	Uvira (DRC)	Z	High reproduction of Diaptomus, shrimps and possibly cyclopoids.	Narita et al., 1986
1990–1994	9 to 11	Burundi	F	Abundance of juveniles clupeids.	Petit, 1995
1993	9	Mpulungu (ZB)	FK	Fish kill of *Boulengerochromis* sp.	Plisnier et al., 1996
1993	9 to 11	Bujumbura (BI)	F, L	Pulse catches of clupeids and perch. High values pulsing toward the surface (temperature, conductivity…).	Plisnier & Coenen, 2001Plisnier et al., 1999
1993–1996	10/11	Kigoma (TZ) Mpulungu (ZB) Bujumbura (BI)	Z	Clear reproduction peak of Cyclopoids	Kurki et al., 1995
1994	9	Bujumbura (BI)	L	High values pulsing toward the surface (pH, temperature, nutrients).	Plisnier et al., 1999
1995	9	Mpulungu (ZB)	Z	Bloom of jellyfish. Medusa density was roughly 3,000 ind./m^{-3} near the coast, but an order of magnitude lower at 15 km offshore.	Salonen et al., 2012
1995	10	10-17-1995 Mpulungu (ZB)	B	Bloom of dinophytes.	Own observations (PDP)
1995	10	South	B	Massive blooms of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*).	Salonen et al., 1999 Langenberg et al., 2002
1996	11	Central lake area	B	Massive blooms of Cyanobacteria (*Dolichospermum flosaquae* as *Anabaena flos-aquae*) occurring kilometers long and approx. 50 m wide.	Salonen et al., 1999
1998	10	Kigoma (TZ)	B	Peak of chl a (5 $\mu g.l^{-1}$).	Chale, 2004; Bailey-Watts, 2000
2002	9	Kigoma (TZ)	B	Peak of chl a.	Descy et al., 2005
2002–2005	8/9	Northern Lake Tanganyika	L	Increase in primary productivity.	Bergamino et al., 2010
2002	9	09-13-2002 09-23-2002 Mpulungu (ZB)	L	"Chimbanfula" waves.	CLIMLAKE project, own obs.
2003	9	Kigoma (TZ)	B	Peak of chl a and *Anabaenopsis tanganyikae*.	Descy et al., 2005; Cocquyt et al., 2005
2004	9	Mpulungu (ZB)	B	Phytoplankton bloom (1 day).	CLIMFISH project, own obs.
2004	10	Kasenga (TZ)	F	Deep-dwelling fish near the surface at the coast.	Nielsen, pers. com.
2004	11	11-26-2004 Mpulungu (ZB)	FK, B	Phytoplankton bloom (coast and pelagic 3 days later, observation of *Lates* spp.).	CLIMFISH project, own obs.

(*continued on next page*)

Table 2 (*continued*)

Year	Month	Date/site	Type	Observations	References
2005	8/9	08-30-2005 Mpulungu (ZB)	B	Phytoplankton bloom (3 days).	CLIMFISH project, own obs.
2006	9	09-16-2006 Mpulungu (ZB)	L	"Chimbanfula" waves (2 days).	CLIMFISH project, own obs.
2012	9	09-25-2012 Nsumbu (ZB)	L	"Chimbanfula" waves.	Allafrica.com, 2021
2013	9	Kalemie (DRC)	B,L	Coastal bloom (turbidity AM: 600 NTU; PM: 5 NTU). Phenomenon locally called "Bilembwe-Bilembwe".	Deladerrière -MSF, pers. com.
2018	9	09-07-2018 Uvira (DRC)	B	Bloom of Cyanobacteria *Dolichospermum flosaquae* (7 days).	Cocquyt et al., 2021
2018	9	09-08-2018 Kigoma (TZ)	FK	Fish kill along the shore at Jacobson Beach.	Denayer, pers. com.
2018	9	09-10-2018 Mpulungu (ZB)	B	"Chimbanfula" waves (3 days). Phytoplankton bloom (green on 09–10, red on 09–11).	Lake Tanganyika Research Unit, pers. com.
2018	9	09-17-2018 09-26-2018 Mpulungu (ZB)	Z	Blooms of jellyfish (near Mutondwe Island).	Bose et al., 2019
2020	10	10-23-2020 Mpulungu (ZB)	L	"Chimbanfula" waves (3 days).	Own observations (LM)
2022	9	Bujumbura (BI)	B	Bloom known as "Umukombe".	Fishermen and own observations (GN)

1955). The blooms observed by Hecky and Kling (1981) appear, from their Fig. 3, to have lasted less than 7 days with a biomass increase of about 4 times in that period. Five pulses of phytoplankton blooms have been reported lasting between one and two weeks and lessening in intensity in relation to the previous one (JFRO, 1962) corresponding to a pulse and damping hypothesis (Plisnier and Coenen, 2001). It is probable that various limnological and meteorological conditions simulated using a hydrodynamic model could clarify the bloom pattern and its variability.

3.3.2. Fish kills

For the period 1960–2020, 4 fish kills were reported in the months of April/May (Table 1) and 3 fish kills in the months of September/November (Table 2). All types of fish species have been observed during these fish kills. In April-May 1990, exhausted large *Lates stappersii* were dying along the beaches of Burundi. Children were collecting more fish on the beaches than fishermen on the lake. This phenomenon was observed along long distances (possibly > 10 km) of beaches (Petit, pers. com). The migration of fish above the anoxic zone suggests that the fish kills were caused by anoxia (Coulter, 1963).

3.3.3. Abundance/reproduction of organisms

We note in published observations some exceptional abundances and reproduction peaks of various organisms (zooplankton, fish) during inter-monsoons: in April/May (Table 1) and in September/November (Table 2). Phytoplankton blooms induce a greater abundance of copepods, shrimps and jellyfish (Symoens, 1956, 1955) and also a higher reproduction rate of copepods of the genus *Diaptomus*, shrimps and possibly cyclopoid copepods (Narita et al., 1986). A clear seasonal peak of cyclopoids was observed during the inter-monsoon periods of April-May and October-November between 1993 and 1996 (Kurki et al., 1999). The abundance of juvenile clupeids was noted at the north of the lake between September and November (Petit, 1995). An increase of *Stolothrissa tanganicae* clupeid catches, at the onset of the dry season in May/June, has been noted at the same time as plankton blooms (Plisnier et al., 2009). Peaks of abundance or mature *Stolothrissa* activity occurred in May-June and September-December (Coulter, 1970; Matthes, 1967).

3.3.4. Surge

A surge (progressive wave) has been reported three times in Lake Tanganyika from limnological measurements, each time during inter-monsoon periods (Tables 1 and 2). Once the trade winds decrease or stop, the thermocline upwells at the north end of the lake and downwells to the south initiating internal waves. As reported below, these waves have features indicative of being non-linear, some of which take the form called surges (Horn et al., 2001; Mortimer, 1974). Additionally, the low Wedderburn numbers computed for the lake indicate that such waves are expected on relaxation of the wind. As the internal waves progress along the lake, localized mixing can occur. In September 1938, Beauchamp (1939) observed, at the inter-monsoon period when SE winds shifted to NE winds, a reversal of the current in the epilimnion, a fast thermocline depth change and a considerable mixing that could only be explained by the development of a subsurface wave since completely calm conditions prevailed. Coulter and Spigel (1991) indicated that the density redistribution following relaxation of the south wind probably gives rise initially to a surge moving back and forth along the longitudinal axis that could cause "local severe mixing". A surge could also be deduced from temperature and dissolved oxygen (DO) distributions (Fig. 4) as observed during a research cruise in October 1974 (Chapman et al., 1974). This surge induced flow of anoxic water from 100 m to nearly 50 m depth, and with the considerable shear associated with these waves, considerable mixing would be expected (Dorostkar and Boegman, 2013). In April 1997, during another inter-monsoon period, an internal wave propagating along the main axis was also observed (Huttula, 1997).

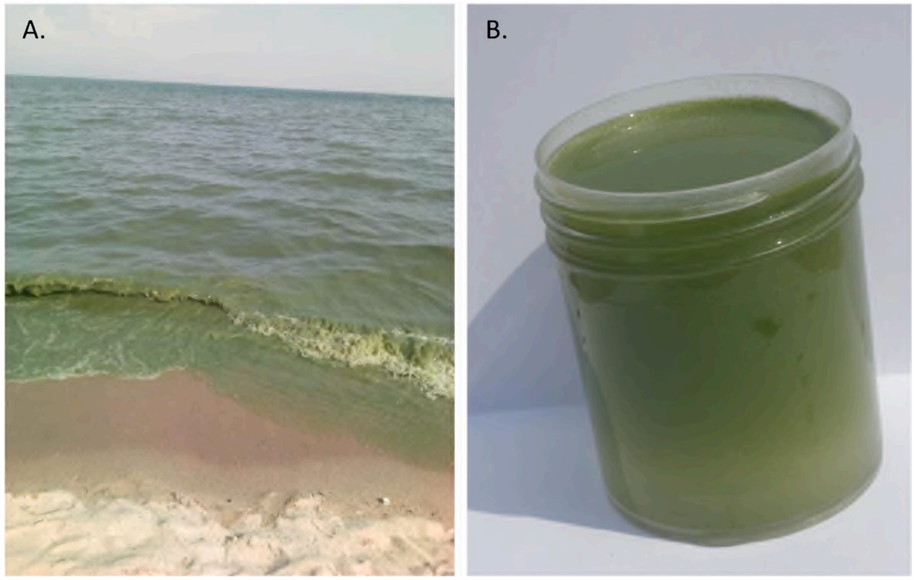

Fig. 3. (A) Photo of a major Cyanobacteria bloom observed during 7 days in September 2018 in the north of Lake Tanganyika (Cocquyt et al., 2021). (B) Photo of a water sample from a short (<24 h) but intense phytoplankton bloom at Kalemie (D.R. Congo) on September 9, 2013. In the morning, the water turbidity reached 600 NTU. A few hours later, at the beginning of the afternoon, the bloom (locally called "bilembwe-bilembwe") was no longer observable and the turbidity went back to previous values of 5 NTU (H. Deladerrière, pers. com.). Both phytoplankton blooms happened at the end of the SE trade winds season just before the rainfalls. Strong mixing is expected during inter-monsoon periods along the coasts particularly as expected from probable Kelvin waves impacts supported by a clockwise sequence of events observed in September 2018 (cf. Fig. 2 A). (Photos: (A) W. Akilimali, (B) H. Deladerrière).

3.3.5. *Flooding*

Flooding of coastal areas was reported several times in April-May, during the inter-monsoon period (Table 1). On April 4, 2020 the lake invaded the beach market at the southern end of the lake (Mpulungu) and a few days later (April 17), it invaded the northern end of the lake as reported in Gatumba (Rusizi plain, Burundi). The local press indicated that the lake was "throwing up". The same day, flooding was observed in the nearby Uvira at the north of the lake. The lake level increased by about 1 m and this took place before heavy rainfalls. Waves (possibly surface seiches) appeared to have induced those flooding which are more pronounced when the lake level is high during its annual cycle and particularly some years in relation to the atmospheric circulation (Bergonzini et al., 2004). Rains are mainly observed from November to April. Specific meteorological conditions could probably also reinforce surface waves and the amplitude of basin scale waves including any Kelvin waves at other moments of the year.

3.3.6. *Mixing observed from limnological measurements*

Limnological observations (N = 17) indicated probable upwelling during inter-monsoon periods in April/May (Table 1) and September/

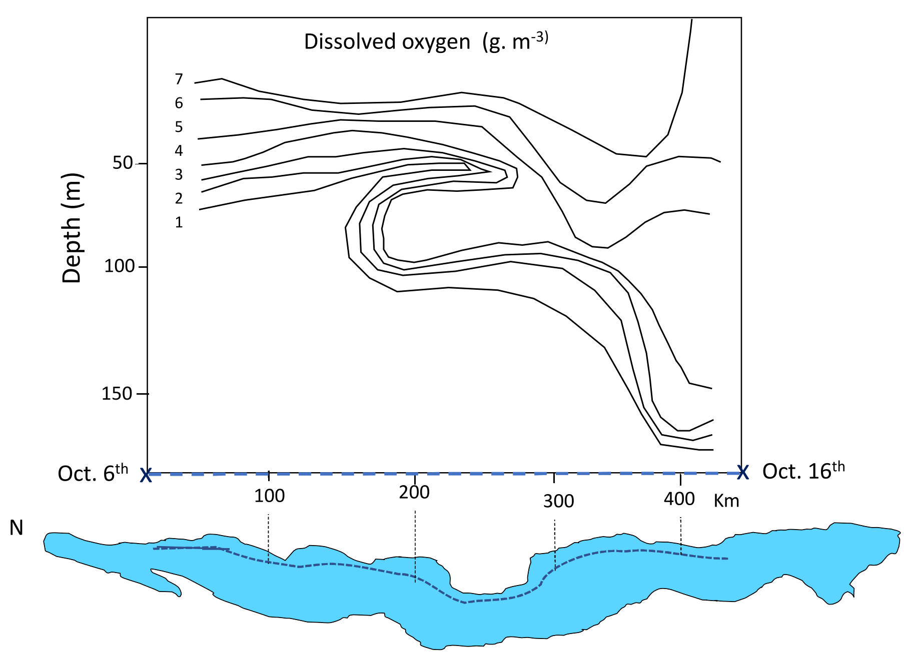

Fig. 4. Dissolved oxygen distribution in Lake Tanganyika up to 175 m depth along a north–south transect at 8 km from the Tanzanian shore. The transect extended about 425 km southward starting from the border with Burundi. Measurements on the southern trip were made at daily intervals through the period 6–16 October 1974 (Chapman et al., 1974).

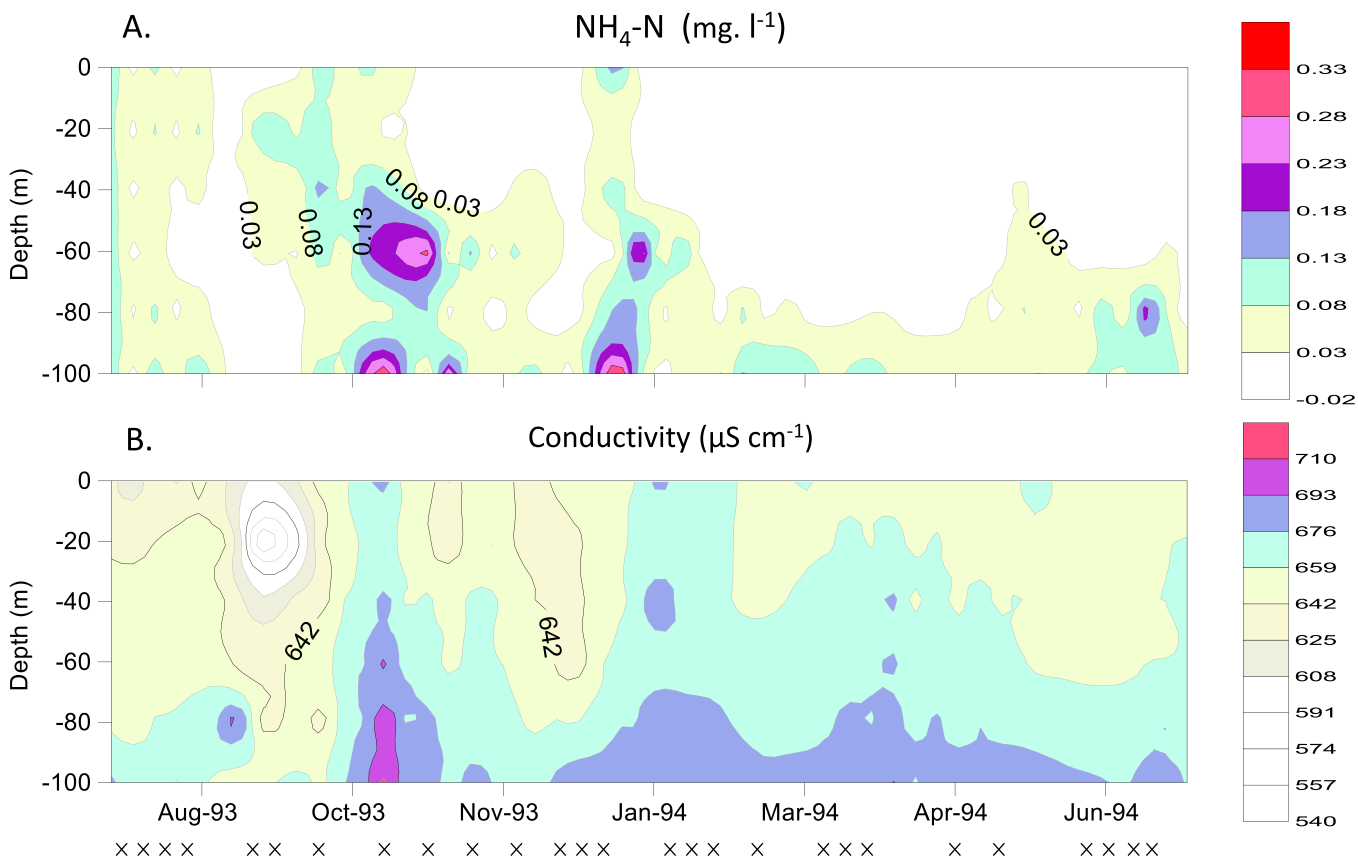

Fig. 5. (A) Ammonium and (B) conductivity of upper layers (0 to 100 m) in the north of the lake near Bujumbura (Burundi) showing deep water upwelling during the inter-monsoon period of October 1993. X indicate sampling dates at each 20 m depth from 0 to 100 m (data from FAO/FINNIDA in Plisnier et al., 1996).

November (Table 2). Those include a rapid rise of deep waters toward the surface (observed from 24 h cycle with observations every 6 h) characterized by colder water temperature, lower DO concentration, higher conductivity and lower pH in the upper lake layer, all characteristics of deep waters. Increased nutrient concentrations are rarely observed near the surface as they are rapidly taken up for primary production. Elevated values of ammonia and specific conductivity have been observed in near-surface water as well as between 60 and 100 m as in October 1993 and January 1994 at Bujumbura (Burundi) in the north of the lake (Fig. 5). The higher specific conductivity, characteristic of deeper waters, in October corresponds to the inter-monsoon period following SE trade winds. Various blooms have been observed in the same period in the north of the lake (Cocquyt et al., 2021) which probably result from a secondary upwelling (Plisnier et al., 1999). In January, when a small dry and colder period is known in the north of the Lake, a decreased water stability then could have allowed internal waves to have a stronger impact in upper waters at this moment which, requires more investigations.

3.3.7. *Wind changes*

A sudden mixing event was reported in September 1938 (near Kigoma) when the winds shifted from SE to NE (Beauchamp, 1939). The first appearance of the north winds then may be taken as marking the end of the cool dry season and the onset of the warmer rainy season, although there may be no rains for several weeks. In early May 1961, a brief breakdown of the stratification occurred when there was little wind stress (Coulter, 1963). A change of wind speed/direction (i.e. wind decrease/relaxation) can drive oscillations along density surfaces (Tables 1 and 2). An abrupt frequency change of oscillation of the thermocline was also detected in August– September at the end of dry season that was interpreted as a possible result from the abrupt change in wind speed and direction (Naithani et al., 2002). It is thus noted that the few observations of abrupt wind changes occurred only at the end of a trade wind season inducing enhanced internal wave amplitudes.

The observations above are considered proxies of mixing. Those are presented in a graph showing their accumulated occurrence in relation with the month of their observation (Fig. 6). In this graph, a bimodal curve is well observed indicating that the monthly occurrence of events related to mixing in Lake Tanganyika is higher during the two inter-monsoon periods: (1) around April/May and (2) from September to November. The details of each event are presented in Tables 1 and 2.

It is noted that an additional period of mixing is identified with phytoplankton blooms and fish kills sometimes but rarely ($N < 10$) reported around July-August in the main southern upwelling area (Table 3). Those events likely corresponded to the apex of an internal wave reaching the surface during the upwelling as identified in 1993–1994 (Plisnier and Coenen, 2001).

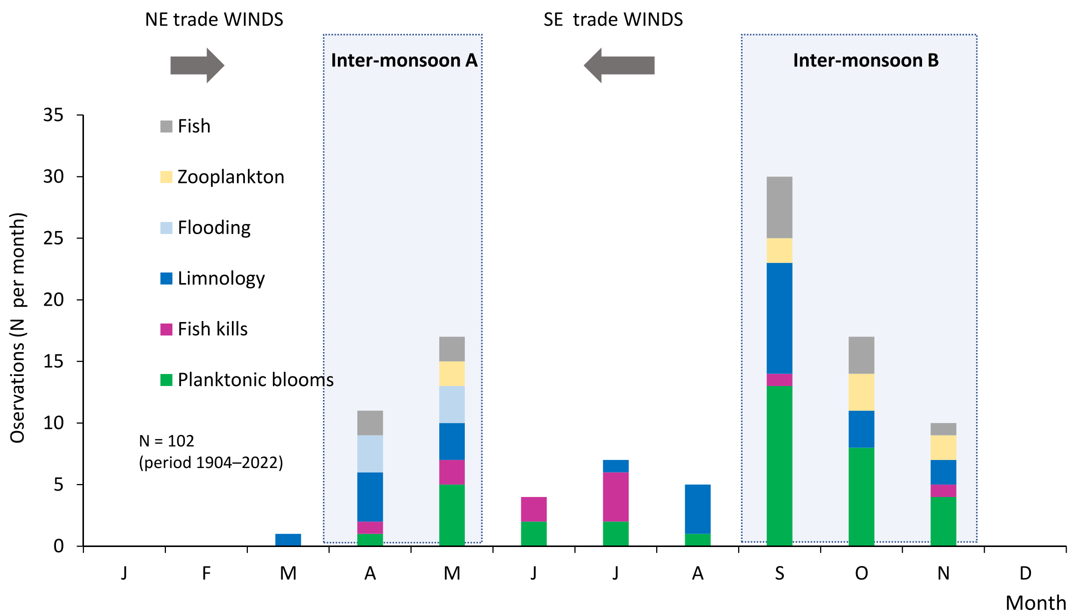

Fig. 6. Number per month of reported hydrodynamics mixing proxies events (plankton blooms, fish kills, limnological observations, flooding, zooplankton and fish abundance or reproduction related) showing increased frequency during inter-monsoons (A) in April-May (Table 1) and (B) from September to November (Table 2) in Lake Tanganyika for the period 1904–2022.

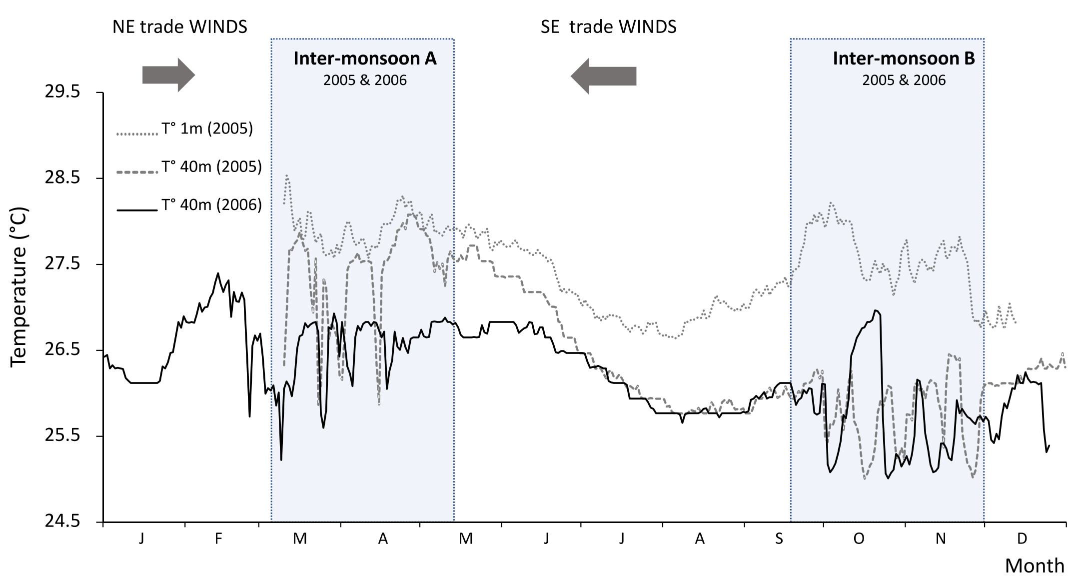

Fig. 7. Temperature at 1 m and 40 m depth near Bujumbura (Burundi) from March 2005 to December 2006. Running average of 48 h periods is shown. Four periods during an annual cycle may be identified: the SE and NE trade winds (or monsoon winds seasons) and two inter-monsoons (IM). Strong temperature oscillations observed during IM periods are indicative of increased hydrodynamic mixing.

3.4. High frequency temperature data in 2005–2006

Hourly temperature records at 1 m and 40 m in the north of the lake in 2005–2006 shows 4 periods during the year (Fig. 7). The NE trade winds season is followed by an inter-monsoonal period (A) which shows high fluctuations in water temperature at each depth. The SE trade winds season follows with cooling and fewer short-term variations in water temperature at 1 m and 40 m. This season is followed by a second inter-monsoon period (B) characterized again by increased variability in temperature resulting from oscillations of water layers. It is noted that in 2005 oscillations in temperature were stronger at inter-monsoon A period while in 2006 the oscillations had a higher amplitude during the inter-monsoon B period. Inter-annual change is expected in relation to meteorological conditions such as relative strength of NE and SE trade winds.

We note that the stronger oscillations of those temperature measurements in 2005–2006 are observed during the same inter-monsoon periods identified from local knowledge (Fig. 2B) and from increased occurrence of reported events as proxies of mixing (phytoplankton blooms, fish kills, etc.). (Fig. 6).

3.5. Remote sensing

Fig. 8 shows some quality metrics computed on the satellite estimate of chl a. The relative bias (Fig. 8B) and relative error dispersion (Fig. 8C) based on HPLC in situ reference show the imperfection of the tested

Table 3
Overview of events as proxies of type 3 mixing in July/August during the main southern upwelling in Lake Tanganyika. (L = limnology, FK = fish kill, B = phytoplankton bloom).

Year	Month	Site	Type	Observations	References
1960	7	Mpulungu (ZB)	L,FK, B	Upwelling of anoxic water near the shore. Fish kill close to shore (<30 m depth). Phytoplankton bloom.	Coulter, 1963; Game and Fisheries Dept. ,1965
1961	7	Mpulungu (ZB)	L,FK, B	Upwelling of anoxic water near the shore. Fish kill close to shore (<30 m depth).Phytoplankton bloom.	Coulter, 1963; Game and Fisheries Dept. ,1965
1962	7	Mpulungu (ZB)	FK	Fish kill.	Game and Fisheries Dept. ,1965
1963	7	Mpulungu (ZB)	FK	Fish kill.	Game and Fisheries Dept. ,1965
1993	7/8	Mpulungu (ZB)	L	The 23.75—24.00° C isopleth rises nearly to the surface.	Plisnier and Coenen, 2001
2002–2005	8	Southern Lake Tanganyika	L	Increase in net phytoplankton coincident with max. amplitude of internal waves.	Bergamino et al., 2010

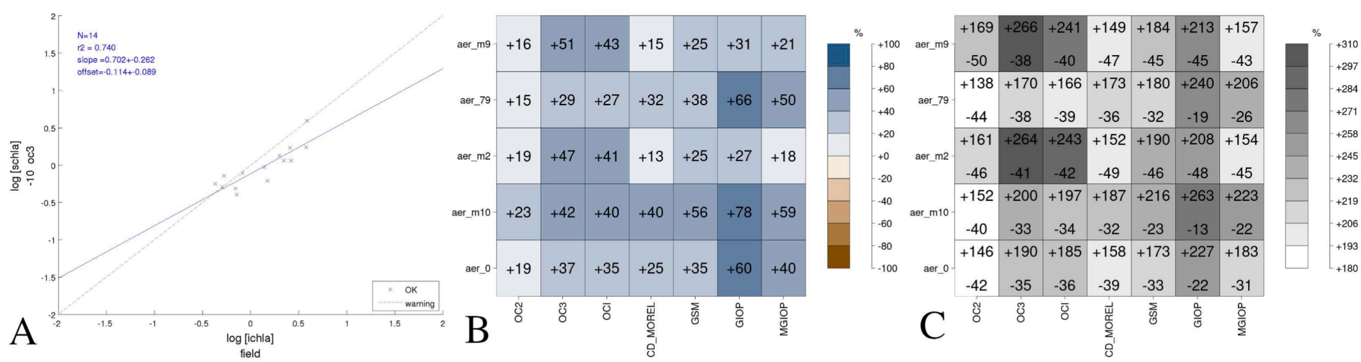

Fig. 8. A. Relationship between in situ chl a (field measurement method - N = 14) and remote sensing chl a computed with Aer_Opt-10/OC3 combination. B. Relative accuracy (%) of remote sensing chl a for different combinations of Aer_Opt (rows)/bioptical algorithms (columns) using in situ chl a (HPLC method - N = 77) as reference. C. Relative precision (%) of remote sensing chl a for different combinations of Aer_Opt (rows)/bioptical algorithms (columns) using in situ chl a (HPLC method - N = 77) as reference. Uncertainty metrics were computed using Campbell and O'Reilly (2006) protocol.

combinations of aerosol models and bio-optical algorithms. Only images showing physically realistic structures were used. For each illustrated case (year-season), the structures are visible on several images over a period of a few days.

Many phytoplankton blooms were well marked on the sides of the lake (largely over 1 km from the coasts) although pelagic blooms were also observed (Fig. 9A and 9B). Those often resulted from the drifting of an initial coastal bloom.

-September-October coastal blooms

Coastal blooms in September-October were observed during this inter-monsoon period ending the SE trade winds in 2002, 2004, 2005, 2006, 2007, 2008 and 2013 (Fig. 9B). For the other years included in this study, cloudiness was too high to allow observations.

-April-May coastal blooms

Coastal blooms were prevalent mostly around the April-May inter-monsoon period (Fig. 9A) during the whole period of observation (2002–2014). This included a major coastal bloom mainly along the SE coast that was observed every year in this period excepted for 2008 when observation was made in June with clearer skies. This delayed event could result from a second oscillation after a first occurrence that was not visible earlier.

Each year, this major coastal bloom in April-May was particularly strong (>5 µg l^{-1}, possibly reaching values >30/40 µg l^{-1}) along the SE coast at about 100 km north of the southern lake end (Fig. 10). Some years, however, this major phytoplankton bloom seemed to be initiated in a more southern location (e.g., 2009). Those events took place during the inter-monsoon periods that followed the NE winds. An overview of the periods of blooms observed during clear sky days between 2003 and 2014 is provided in Table 4. The average observable bloom duration was 6 days (minimum of 2 days and maximum of 10 days). Often a second observation of those blooms could be made shortly afterwards (Table 4). In 2014, however this repeated event reached a duration of about 30 days and a strong bloom was also observed along the west coast before extending into the pelagic area. The longer period could be linked to an increased visibility that year that allowed to better observe the bloom duration. It could also result from higher solar radiation and lower winds which are known conditions favouring cyanobacteria blooms (Medrano et al., 2013; Paerl and Huisman, 2008). However local meteorological data were not available to check this hypothesis. This recurrent SE bloom event around April-May could be interpreted as resulting from the relaxation of tilted water layers (secondary upwelling) by previous NE trade winds toward the south soon followed by the onset of southerly winds. The Coriolis force inducing a stronger upwelling on its left side in the southern hemisphere could explain this location. The upwelling of nutrient-rich deeper water induces an increased primary production at the surface there. A repetition of this event is observed after a few weeks, as indicated in Table 4. Early eastern winds (data not available) might also have facilitated the upwelling there. Those blooms sometimes expanded into the pelagic area afterward. Those events should not be confused with the main southern upwelling happening later and often in a more southern location. The generally windy period from the end of June to August is less favorable to cyanobacteria blooms.

Alternatively, if the southerly winds begin in March or April, as they did in 1996 when continuous records were available (Huttula et al., 1997), the thermocline will begin to upwell in the southern portion of the basin. Due to the Coriolis force, larger upwelling could be expected to the southeast. Any wind event lasting one to three days could cause a local upwelling and downwelling of the now upwelling thermocline further impacting the flux of nutrients. This mechanism would also support many of the blooms as described above. It is probable that those SE coastal blooms of April-May result from the mixing of the "Yalafula waves" that are observed every year by fishermen in the south of the lake during this period (see above).

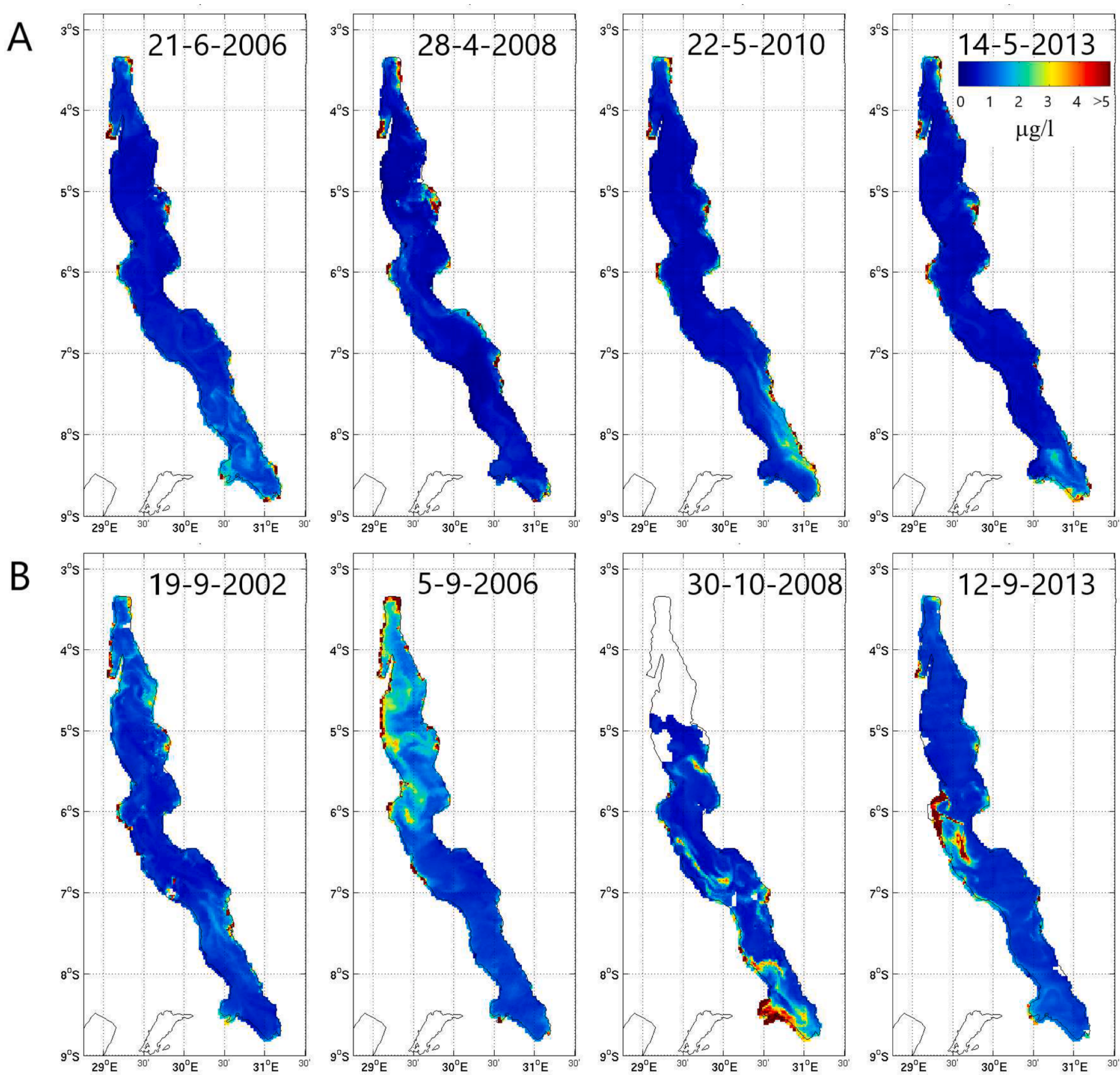

Fig. 9. Phytoplankton blooms (red color) during (A) the first inter-monsoon in 2006, 2008, 2010 and 2013 and (B) the second inter-monsoon in September 2002, 2006, 2013 and October 2008. Chl a (μg.l^{-1}) was derived from MODIS image processing. Areas not visible due to cloudiness are white. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

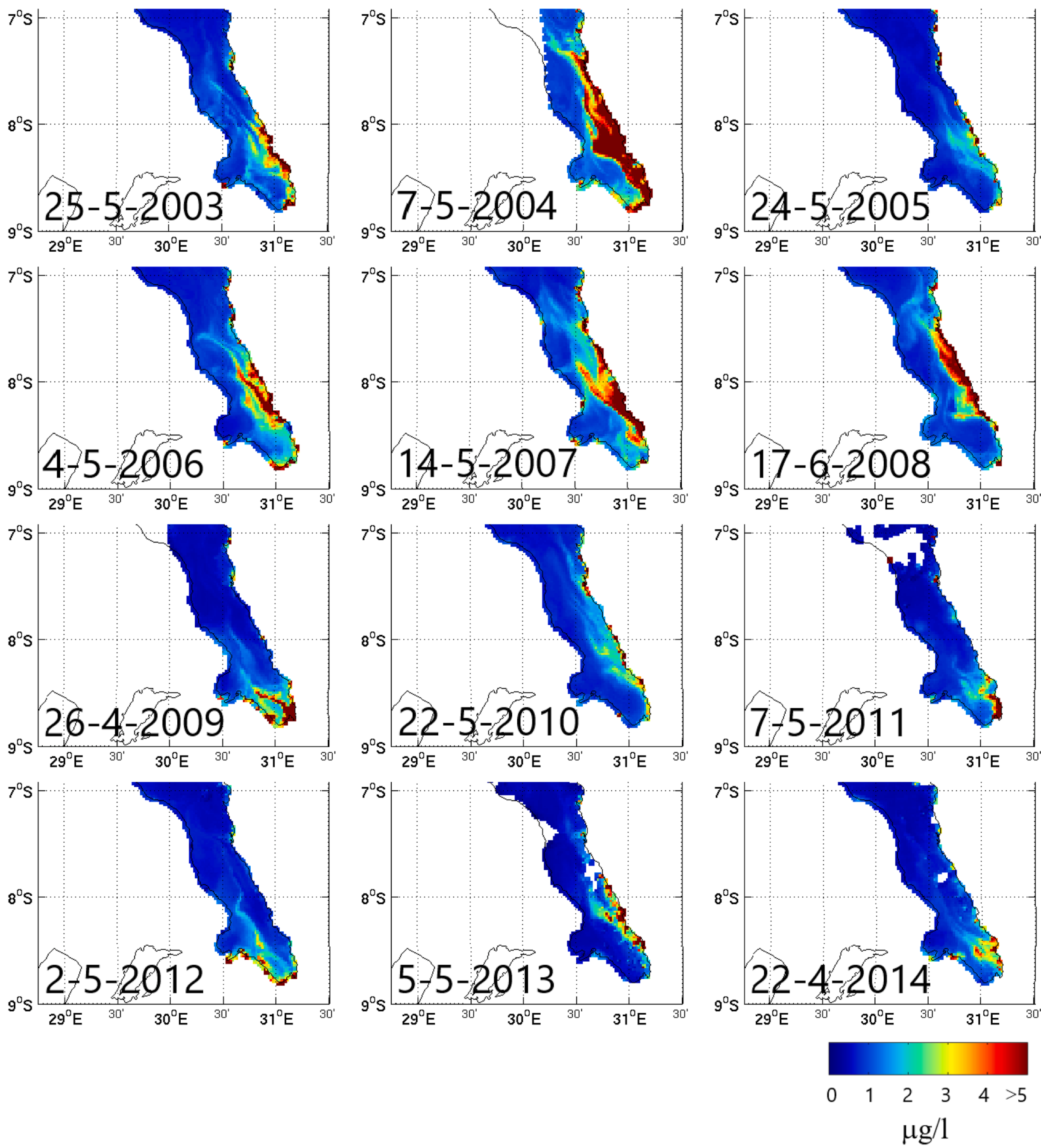

Fig. 10. Southern part of Lake Tanganyika showing phytoplanktonic bloom in April-May/June each year between 2003 and 2014. Chl a ($\mu g.l^{-1}$) derived from MODIS image processing. Area not visible due to cloudiness and other image processing constraints are white.

Table 4
Duration (days) of phytoplankton blooms (chl a ≥5 μg l^{-1}) observed during cloudless periods from MODIS image processing (2003 to 2014) at the SE of Lake Tanganyika during the inter-monsoon period (April-May). * The second period of bloom observations in 2014 was exceptionally long (30 days) and not included for the average.

	Southern plankton blooms starting during the April-May intermonsoon					
	First observation			Second observation		
Year	Start	End	Days	Start	End	Days
2003	05-24-03	05–26-03	3	Clouds		
2004	05-03-04	05–07-04	5	05-29-04	05-30-04	2
2005	05-21-05	05–26-05	6	07-02-05	07-04-05	3
2006	05-03-06	05–07-06	5	06-08-06	06-14-06	7
2007	05-07-07	05–16-07	10	06-20-07	06-29-07	10
2008	05-23-08	05–25-08	3	06-14-08	06-17-08	4
2009	04-19-09	04–26-09	7	05-16-09	05-17-09	2
2010	05-20-10	05–27-10	8	06-07-10	06-08-10	2
2011	05-06-11	05–11-11	6	Clouds		
2012	04-30-12	05–02-12	3	Clouds		
2013	05-05-13	05–14-13	10	06-23-13	06–27-13	5
2014	04-22-14	04–24-14	3	(05-13-2014)*	(06-11-2014)*	(30)*
Average			6			4
Range			3 to 10			2 to 10

4. Discussion

4.1. Annual limnological cycle

Observations presented above from recent observations (Fig. 2a), local knowledge (Fig. 2b), historical observations (Figs. 4, 5 and 6), time series of temperature (Fig. 7) and remote sensing images (Figs. 9 and 10) enable an updated summary of the Lake Tanganyika limnological cycle (Fig. 11) from that developed in Plisnier et al. (1999). It now includes the impact of both trade winds and support for the hypothesis of the occurrence of clockwise Kelvin waves moving along the shores of Lake Tanganyika. The following sequence is identified:

A. May to September: **SE TRADE WINDS** (Fig. 11; step 1).

The strong SE trade winds induce considerable upwelling to the south and downwelling of epilimnetic waters toward the north. In consequence, the thermocline tilts toward the north. During this period, coastal upwelling is observed, particularly in the southern half of the lake (Plisnier et al., 2015). Calculations of the Wedderburn number indicate that it drops to less than 0.5 to 0.08 for winds of 5.6 to 11 m.s^{-1} as the southeast trade winds begin to increase. These values indicate full upwelling will occur and that the upwelled water will extend some distance from south to north (Coulter and Spigel, 1991).

B. September-October: Inter-monsoon (Fig. 11; steps 2a and 2b alternating).

The end or just a decrease (particularly if abrupt) of the SE winds allows the gravitational relaxation of the tilted epilimnion. At the northern end, the upwelling of deep nutrient-rich waters (secondary upwelling) induces a subsurface plankton bloom near the thermocline. Some years, however, after a windy season, this bloom may develop at the surface such as in September 2018 (Cocquyt et al., 2021). At the same time, water from the now upwelling upper mixed layer flows towards the south and, based on the timing of the observations of surges, these non-linear waves flow toward the south along the thermocline. We hypothesize that this progressive wave is impacted by the rotation of the earth (Coriolis effect) resulting in it progressing clockwise along the shoreline although it may also propagate across the full width of the lake. It causes upwelling of sub-surface waters with higher nutrient concentrations, but poorly oxygenated or anoxic water. Mixing is likely to be severe (Horn et al., 2001). We infer that the fluxes from this type of internal wave can induce plankton blooms and fish kills along the coasts (Table 2). Oscillations between the lake ends dampen but may remain strong until November/December as observed from recurrent "Chimbanfula" waves in the south. It is also possible that "Chimbanfula" waves are associated with large amplitude internal waves, which if influenced by rotation would be Kelvin waves. Further investigations are needed to confirm that Kelvin waves occur. Such evidence requires deployment of thermistor arrays in both inshore and offshore waters. This period corresponds to the north to south migration of the ITCZ over Lake Tanganyika.

C. October/November to April: **NE TRADE WINDS** (Fig. 11; step 3).

The cumulative impact of NE trade winds induces a downward tilting of the epilimnion toward the south in some years although it might remain more level in others (Coulter and Spigel, 1991; Huttula, 1997; Kufferath, 1952; Van Meel, 1954). This tilting is difficult to identify because of seasonal heating and a more diffuse thermocline. Coastal upwellings are frequently observed in the northern half of the lake during this period (Plisnier et al., 2015). With lower average wind speeds than in the SE monsoon, the Wedderburn number, when calculated using temperatures and mixed layer depths as in Huttula (1997) and wind speeds of 5 m.s^{-1}, drops to values of 0.5. The thermocline and nutricline in the north are now closer to the surface, (Plisnier et al., 2015, 1996).

D. April-May: Inter-monsoon (Fig. 11; steps 4a and 4b).

The end or decrease of the NE winds is linked to a gravitational relaxation of the southward tilted epilimnion water. A strong coastal bloom is observed in the SE end of the lake (Fig. 10) possibly corresponding to a secondary upwelling resulting from relaxation of the tilted waters layers toward the south. The basin scale modes generated by these and earlier winds cause up and downwelling within the rising thermocline, and if, influenced by rotation, the expected Kelvin waves would progress clockwise along the coasts. In the south, their first strong occurrence could correspond to the "Yalafula" waves . Strong coastal upwelling during the inter-monsoon period of April-May is deduced from plankton blooms and sometimes also observations of fish kills (Table 1). This period corresponds to the south to north migration of the ITCZ over Lake Tanganyika.

This hypothesized limnological cycle of Lake Tanganyika will certainly need to be improved and completed in the future as more advanced technology is used on the lake and when continuous observations from long-term monitoring will be available. However, the proposed sequence of events is coherent with the multidisciplinary observations presented above. It could enable modelling to include processes during both trade winds for example as they appear to be important drivers in the limnological cycle of Lake Tanganyika.

Why are trade winds so important for the hydrodynamics of Lake Tanganyika compared to local winds? Although trade winds are estimated to represent only 25 % of winds stress at Lake Tanganyika compared to orographic and lake/land thermal winds (Docquier et al., 2016; Savijärvi, 1997), they appear to have a main impact on the

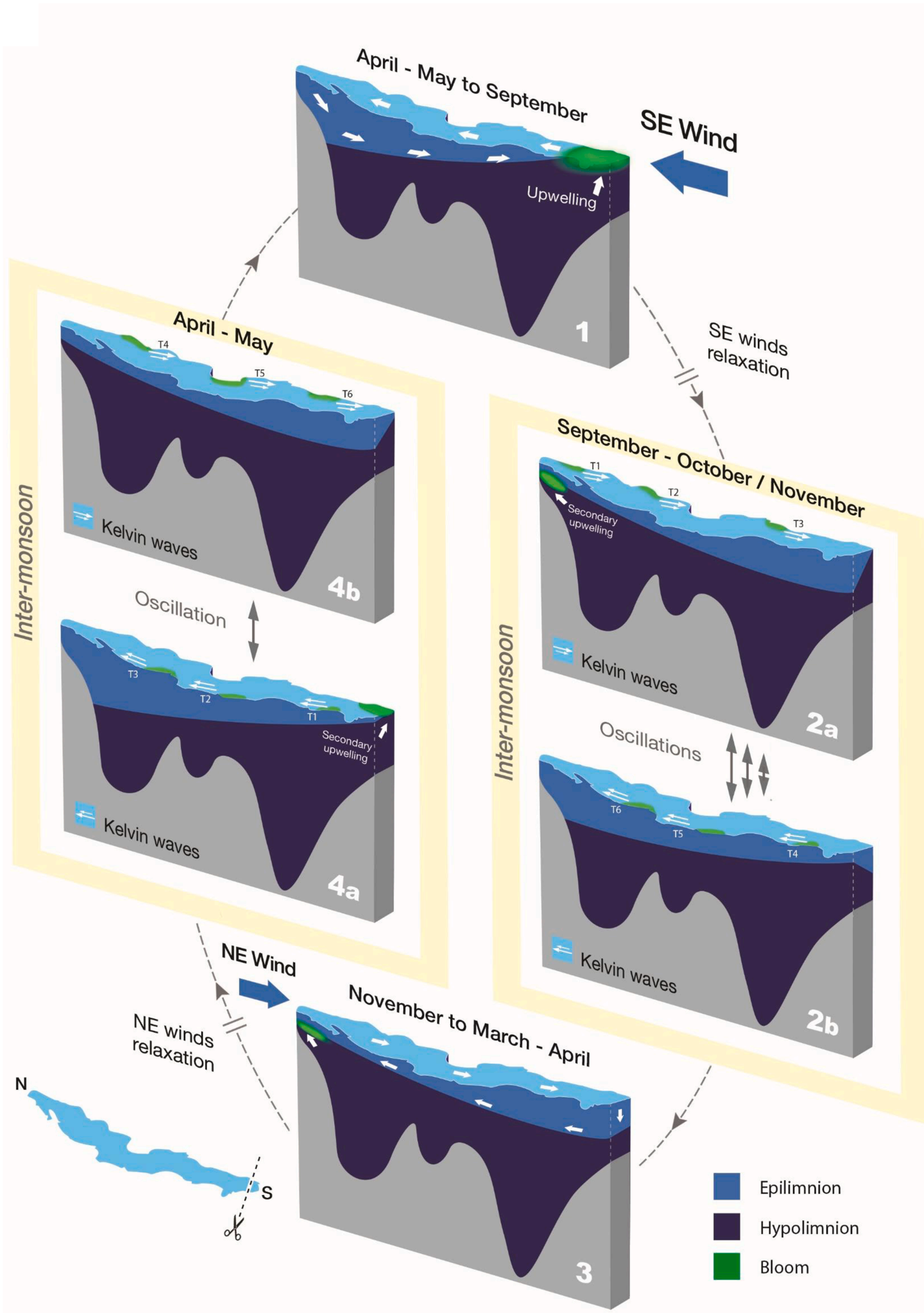

Fig. 11. Schematic profile of hydrodynamic events during an annual cycle at Lake Tanganyika. Four periods are identified: (1) SE trade winds (2) Inter-monsoon (3) NE trade winds (4) Inter-monsoon. During inter-monsoons, strong oscillations of water layers are driven by gravity between the lake ends. Probable Kelvin waves are indicated. Those would progress clockwise around the lake, inducing plankton blooms, possibly fish kills and other events considered as proxies of strong hydrodynamic mixing. The indicated months may vary by ± 1 month interannually. Figures are shown as a cut profile near the southern end to represent transversal tilting. T1, T2, T3 represent the chronological progression of the suggested Kelvin waves along the shores. The tilting extent is exaggerated for didactic reasons.

limnological cycle of Lake Tanganyika. Their quasi-unidirectional stress during several months has a cumulative impact on water layers tilting and the piling up of epilimnetic water at the lee end of the lake. Additionally, velocities stay elevated throughout the day with periods of increased activities. The persistent basin scale modes (Naithani et al., 2002) indicates that once these waves are generated, they do not readily decay. Hence, they modulate the amplitude of the seasonal thermocline even as it is rising or falling in periods with more sustained winds. Inversely, orographic and lake/land breezes revert direction on a daily basis and are generally opposed to similar winds on the other side of the lake. That said, Naithani et al.'s (2002) analysis indicates winds with periodicities shorter than that of the basin scale modes computed by Coulter and Spigel (1991) and often with duration of 4 to 8 days. If these winds are offshore and occur when the basin scale modes are upwelling, the results would be to cause tilting of the basin scale wave such that upwelling occurred nearshore. Thus, while this linkage between wind and upwelling has not yet documented for L. Tanganyika, the persistent local winds may contribute to the upwellings and blooms described in this paper.

Although NE wind velocities are generally lower than SE winds with more intermittent and calm spells (Coulter, 1991), their cumulative impact appears to be significant. Occasional violent storms occur during the NE trade wind season (winds speed > 25 $m.s^{-1}$) and a strong waterspout may progress across the main axis (Capart, 1952).

The observations in this paper could explain the two large blooms in September and October 1975 in the north of Lake Tanganyika (Hecky and Kling, 1981). One was the result of the secondary upwelling in response to the end of the southeast monsoon and the other would have been a result of the abrupt upwelling and Kelvin waves that subsequently formed.

4.2. Kelvin waves

Kelvin waves inferred on the basis of the calculated Burger numbers are supported by the lines of evidence below:

- Local knowledge (3.1) (Fig. 2b)
- Phytoplanktonic blooms and fish kill propagating in a clockwise direction in coastal sites around the lake in September 2018 (Fig. 2a)
- Coastal mixing events during inter-monsoon periods using proxies as phytoplankton blooms and fish kills or in situ measurements reported in publications or observed during past projects (Fig. 6; Tables 1 and 2).
- Coastal phytoplankton blooms during inter-monsoons periods observed from remote sensing images (Figs. 9 and 10)
- It is also noted that a cross-lake transect at the southern end of the lake in April 1997 showed downwelling to the west and a slight upwelling to the east (Huttula et al., 1997, Fig. 2.4 2/3).

A latitudinal pattern in phytoplankton productivity of Lake Tanganyika was identified by Bergamino et al. (2010). Thirteen sub-regions based on co-varying chl a concentration are identified in their Fig. 1. Wide subregions including eastern and western sides are observed in the north while in the south, subregions are smaller with a marked east/west separation. It is suggested that this latitudinal difference could be related to a stronger Coriolis impact in the south than in the north of the lake. A better understanding of probable Kelvin waves at Lake Tanganyika is important to understand their impacts on the coastal ecosystem in general and to possibly anticipate some events such as coastal flooding.

The high chl *a* concentration observed from remote sensing indicates punctual eutrophic and even hyper-eutrophic short and local events (>40 $\mu g\ l^{-1}$) in the coastal area at Lake Tanganyika, possibly mainly induced by Kelvin waves. Previously, values of 30 $\mu g\ l^{-1}$ were indicated by Bergamino et al. (2010). A recent remote sensing study found a few chl *a* values between 20 and 70 $\mu g\ l^{-1}$ (Vinel, 2022). Intense phytoplankton blooms seem more frequent along some shores (fishermen, pers. com.) which could depend on site characteristics and bathymetry.

The regular occurrence of anoxic waters along the shores of Lake Tanganyika could explain the absence of deepwater (>100 m) fish species in this lake as suggested by Eccles (1986). The fluctuating environmental conditions induced by Kelvin waves could induce specialization/segregation between local abundance of fish species such as observed in the pelagic area between *Stolothrissa tanganicae* and *Lates stappersii* (Plisnier et al., 2009).

Another possible consequence of the hypothesized Kelvin waves is their probable impact on the precipitation of carbonates along the shores (whiting events). A wide variety of carbonate facies, dominated by high-magnesian calcite, occurs along the littoral and shallow sublittoral zones (<50 m) of Lake Tanganyika (Cohen and Thouin, 1987; Coulter, 1991). The precipitation process is often linked to phytoplankton activity and increased pH (Dittrich and Obst, 2004). In Lake Kivu, the sudden onset of carbonates is believed to have been induced by higher primary productivity (Pasche et al., 2010).

Could the episodic algal bloom events occur due to nutrient loading from other external sources such as from the rivers and precipitations? The volumes of inflowing rivers during a year (18 km^3) and precipitation (35 km^3) are negligible compared to the lake total volume (18,000 km^3) (Spigel and Coulter, 1996) or even to the average mixolimnion volume (1,500 km^3). The main rivers are not situated near the sites where we do observe major phytoplankton blooms and those are also not observed during the rainy season. The additional nutrient input of rivers is also not significant with respect to the nutrient storage in the monimolimnion. A putative nutrient loading to the mixolimnion of Lake Tanganyika indicated percentage input by rivers of only 0.1 % for N, 1 % for P and 0.16 % for Si compared to an estimated 97.4 % for N (mainly from fixation), 90.9 % and 97.6 % for P and Si respectively from internal loading (Hecky et al., 1991). The river waters are generally colder than the lake and their elevated density causes the incoming water to rapidly sink below the thermocline (Capart, 1952; Dubois, 1958b; Kufferath, 1952). The exceptional accumulation of nutrients in the deep water of Lake Tanganyika results from its old age (>10 million years) and its huge size. The hydrodynamics allow from time to time the access of those deep waters toward the surface of the lake. Hecky and Kling (1981) observed that planktonic peaks can develop rapidly at Lake Tanganyika. ln the course of a single day (October 10, 1975), the biomass rose and fell dramatically owing to a rapid increase in *Dolichospermum* (previously named *Anabaena*). Hecky and Kling (1981) had observed a greater relative range in maximum and minimum chl a concentration, 20x, at Lake Tanganyika than at any of the Laurentian Great Lakes. Upwelling and mixing of nutrient rich deep water within the lake is without doubt the main source of nutrients explaining the major phytoplankton blooms observed at Lake Tanganyika. It is observed that these events take places mainly after the relaxation of both trade winds seasons during inter-monsoon periods.

5. Conclusions

We identify four periods in the limnological cycle of Lake Tanganyika using observations from remote sensing, in situ measurements, local knowledge, historical observations and published data. These include two seasons with trade winds when momentum from the trade winds induces tilting of the upper water layers and two inter-monsoons periods when this energy is released and internal waves form causing periodic up and downwelling around the lake. An annual sequence is proposed that completes a previous hypothesis (Plisnier et al., 1999). SE winds from May to August/September (phase 1) are followed by relaxation of downwelled epilimnetic water in the north and basin scale internal waves, likely influenced by rotation (hence, Kelvin waves). If so, these waves would cause coastal upwellings which rotate in a clockwise direction around the lake between September and October/November (phase 2) allowing deeper nutrient rich water, sometimes anoxic to reach the photic layers inducing phytoplankton blooms and possible fish kills These internal waves and resulting phytoplankton blooms lead to changes in abundance and reproduction peaks of various upper food web organisms (zooplankton, jellyfish, shrimp, fish). NE trade winds start in October/November and persist until March/April (phase 3). Their influence appears to be more muted than that of the SE trade winds with epilimetic water moving southward . The basin scale modes energized by the SE monsoon persist through to the following SE monsoon (Huttula 1997, Fig. 2.4.1/13, 2.4.1/14), hence the NE trades may serve to moderate their frequency or amplitude. Those winds generally relax around April-May to the north (phase 4) before winds from the south and southeast increase at the south of the lake. In fact, in some years winds from the south begin in February. The cessation of NE trade winds followed by a calm period before the onset of SE trade winds, causes the relaxation and the seasonal thermocline to upwell with the basin scale waves still maintained (Huttula, 1997). Periods of enhanced winds for several days at a time could further enhance upwelling leading to phytoplankton blooms and fish kills.

Here we show the influence of the hydrodynamics of Lake Tanganyika in other periods than during the SE trade winds. The mainly unidirectional trade winds pile up lighter upper water layers at the lake ends for several months. The strong thermocline deflection at Lake Tanganyika is clearly evident as a result of its north/south orientation being close to the trade winds direction. The potential energy accumulated, particularly during the higher winds of the SE monsoon, is released during calmer inter-monsoon periods. A strong inter-annual variability in upwelling and any associated mixing is expected particularly in relation to fluctuating trade winds intensities and probably also their ending (gradual or abrupt).

Although Lake Tanganyika is situated relatively close to the equator and is relatively narrow, the earth's rotation's effect is not negligible and has an impact on the water circulation in this lake. The existence of Kelvin waves had been deduced from hydrodynamic models (Delandmeter et al., 2018; Naithani and Deleersnijder, 2004). The coastal location, timing and propagation of mixing events that are presented in this paper support a clockwise coastal wave circulation as expected for Kelvin waves in the southern hemisphere although detailed analysis is needed to confirm their existence unequivocally.

Episodic upwelling of water from 70 m and below leads to diverse ecosystem consequences and maintenance of Lake Tanganyika's productive fishery. Upwelling may explain the precipitation of carbonates observed along the shores of Lake Tanganyika (Cohen and Thouin, 1987). Upwelling of anoxic waters induces temporary fish kills. Most importantly, upwelling of nutrient-rich water leads to plankton blooms which sometimes reach for a short period a eutrophic or hyper-eutrophic level. These upwelling events, over the annual cycle, are critical drivers of the abundance and reproduction of many organisms (phyto- and zooplankton, fish) and support the productive fishery on which so many lives depend.

In Lake Tanganyika, many assumptions about the ecosystem functioning are based on inadequate temporal and spatial coverage (Coulter, 1991). Here we have illustrated the value of combining local knowledge, historical observations, in situ sampling and remote sensing. However, long-term monitoring at various sites around the lake is needed to further illustrate the hydrodynamics as a key driver of Lake Tanganyika's ecosystem and variability in fish stocks (Plisnier et al., 2023). For Lake Tanganyika and other lakes, in addition to instrument monitoring and satellite observation, systematically recording events such as phytoplankton blooms and fish kills provides useful proxies of hydrodynamic events. This combination enables improved description of limnological cycles and ecosystem functioning to better address local ecosystem threats but also to better understand the lake's response to global scale climate drivers.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Remote sensing data were collected in the framework of the CHOLTIC (Cholera outbreaks at Lake Tanganyika induced by climate change?) project (SD/AR/04A) funded by the Belgian Science Policy. REGIDESO at Bujumbura, Burundi is thanked for assistance in setting up thermistors in 2005-2006. Physico-chemistry data from vertical profiles were collected during the FAO-FINNIDA project in 1993-1994. We thank various persons or institutions who provided observations: P. Petit (fisheries expert), L. Tack (senior researcher), P. Nielsen (farmer in Zambia), M. Deladerrière (MSF staff in Kalemie, D.R. Congo), A. Denayer (Belgian Development Agency), Lake Tanganyika Research Unit in Zambia, W. Akilimali, staff of the Maman Benita boat, M. Mupape (Research Cruise Organizer) and various fishermen. We have appreciated the helpful comments from J. Melack. Many thanks also to N. D'Hoedt for its graphic design skills.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2023.102247.

References

Abila, R., Akoll, P., Albertson, C., Antunes, D., Banda, T., Bills, R., Bulirani, A., Manda, A., Cohen, A., Cunha-Saraiva, F., Derycke, S., Donohue, I., Du, M., Dudu, A., Egger, B., Fritzsche, K., Frommen, J., Gante, H., Genner, M., Härer, A., Hata, H., Irvine, K., Isumbisho, P., Janssens de Bisthoven, L., Jungwirth, A., Kaleme, P., Katongo, C., Kéver, L., Koblmüller, S., Konings, A., Lamboj, A., Lemmel-Schaedelin, F., Schiaffino, G., Martens, K., Masilya, P., Meyer, A., More, H., Musilova, Z., Bukinga, F., Muzumani, D., Ntakimazi, G., Okello, W., Phiri, H., Pialek, L., Plisnier, P.-D., Raeymaekers, J., Rajkov, J., Rican, O., Roberts, R., Salzburger, W., Schoen, I., Sefc, K., Singh, P., Skelton, P., Schneider, K., Snoeks, J., Sturmbauer, C., Svardal, H., Svensson, O., Dowdall, J., Turner, G., Tyers, A., van Rijssel, J., van Steenberge, M., Vanhove, M., Verheyen, E., Weber, A., Weyl, O., Ziegelbecker, A., Zimmermann, H., 2016. Oil extraction imperils Africa's Great Lakes. Science. 354 (6312), 561–562. https://doi.org/10.1126/science.aal17.

Actualite.cd, 2020. https://actualite.cd/2020/07/27/sud-kivu-plusieurs-poissons-porteurs-des-lesions-meurent-sur-le-lac-tanganyika-la. Accessed on March 7, 2023.

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A., Winder, M., 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. 54, 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Allafrica.com. https://allafrica.com/stories/201209260457.html. Accessed on September 10, 2021.

Antenucci, J.P., 2005. Comment on "Are there internal Kelvin waves in Lake Tanganyika ?" by Jaya Naithani and Eric Deleersnijder. Geoph. Res. Lett. 32, L22601. https://doi.org/10.1029/2005GL024403.

Bailey-Watts, A., 2000. Pollution Control and other measures to protect biodiversity in Lake Tanganyika. UNDP/GEF/RAF/92/G32. Global Environment Facility, United Nations Development Programme.

G.P. Bazigos Biological sample survey at Lake Tanganyika (Burundi). Statistical analysis of purse-seine fishery catches Fishery survey and development project, working paper FAO UNDP/SF/BDI/70/508 1973 FAO, Rome.

Beauchamp, R.S.A., 1939. Hydrology of Lake Tanganyika. Int. Revue Ges. Hydrobiol. 39, 316–353. https://doi.org/10.1002/iroh.19390390303.

Bergamino, N., Horion, S., Stenuite, S., Cornet, Y., Loiselle, S., Plisnier, P.-D., Descy, J.-P., 2010. Spatio-temporal dynamics of phytoplankton and primary production in Lake Tanganyika using a MODIS based bio-optical time series. Remote Sens. Environ. 114, 772–780. https://doi.org/10.1016/j.rse.2009.11.013.

Bergonzini, L., Richard, Y., Petit, L., Camberlin, P., 2004. Zonal circulations over the Indian and Pacific Oceans and the level of lakes Victoria and Tanganyika. Int. J. Climatol. 24, 1613–1624. https://doi.org/10.1002/joc.1089.

Bose, A.P.H., Zimmermann, H., Sefc, K.M., 2019. Freshwater hydrozoan blooms alter activity and behaviour of territorial cichlids in Lake Tanganyika. R. Soc. Open Sci. 6, 191053 https://doi.org/10.1098/rsos.191053.

Caljon, A., 1991. Sedimentary diatom assemblages in the northern part of Lake Tanganyika. Hydrobiologia 226, 179–191. https://doi/10.1007/BF00006859.

Campbell, J.W., O'Reilly, J.E., 2006. Metrics for quantifying the uncertainty in a chlorophyll algorithm: Explicit equations and examples using the OC4. v4 algorithm and NOMAD data, in: Proceedings of the Ocean Color Bio-Optical Algorithm Mini

(OCBAM) Workshop, New England Center, Southborough, MA, USA, 27–29 September 2005; 1–15.

Capart, A., 1952. Exploration hydrobiologique du lac Tanganika, 1946–1947: résultats scientifiques. Le milieu géographique et géophysique, Institut royal des sciences naturelles de Belgique, Bruxelles.

Chale, F.M.M., 2004. Inorganic nutrient concentrations and chlorophyll in the euphotic zone of Lake Tanganyika. Hydrobiologia. 523, 189–197. https://doi/B:HYDR.0000033125.87313.53.

Chapman, D.W., Bayona, J.D.R., Ellis, C., 1974. Preliminary analysis of test fishing and limnological sampling in Tanzanian waters of Lake Tanganyika in October 1974. FAO/URT/71/012, Working Paper 12. Bujumbura; Burundi.

Cocquyt, C., Plisnier, P.-D., Mulimbwa, N.T., Nshombo, M.V., 2021. Unusual massive phytoplankton bloom in the oligotrophic Lake Tanganyika. Plant Ecol. Evol. 154, 351–361. https://doi.org/10.5091/plecevo.2021.1890.

Cocquyt, C., Vyverman, W., 2005. Phytoplankton in Lake Tanganyika: a comparison of community composition and biomass off Kigoma with previous studies 27 years ago. J. Great Lakes Res. 31, 535–546. https://doi.org/10.1016/S0380-1330(05)70282-3.

Cohen, A.S., Bills, R., Cocquyt, C., Caljon, A., 1993. The impact of sediment pollution on biodiversity in Lake Tanganyika. Conserv. Biol. 7, 667–677. https://doi/10.1046/j.1523-1739.1993.07030667.x.

Cohen, A.S., Gergurich, E.L., Kraemer, B.M., McGlue, M.M., McIntyre, P.B., Russell, J.M., Simmons, J.D., Swarzenski, P.W., 2016. Climate warming reduces fish production and benthic habitat in Lake Tanganyika, one of the most biodiverse freshwater ecosystems. Proc. Natl. Acad. Sci. 113 (34), 9563–9568. https://doi.org/10.1073/pnas.16032371.

Cohen, A., Thouin, C., 1987. Nearshore carbonate deposits in Lake Tanganyika. Geology. 15, 414–418. https://doi.org/10.1130/0091-7613(1987)15<414:NCDILT>2.0.CO;2.

Coulter, G.W., 1963. Hydrological changes in relation to biological production in southern Lake Tanganyika. Limnol. Oceanogr. 8, 463–477. https://doi.org/10.4319/lo.1963.8.4.0463.

Coulter, G.W., 1966a. Hydrological processes in Lake Tanganyika. Fish. Res. Bull. Zambia. 1965–1966, 53–56.

Coulter, G.W., 1966b. Changes in the pelagic fish population in the Southeast arm of Lake Tanganyika between 1962–1966. Fish. Res. Bull. Zambia. 4, 29–32.

Coulter, G.W., 1968. Hydrological processes and primary production in Lake Tanganyika. Proceedings 11th Conference. Great Lakes Research. 11, 609–626.

Coulter, G.W., 1970. Population changes within a group of fish species in Lake Tanganyika following their exploitation. J. Fish Biol. 2, 329–353. https://doi.org/10.1111/j.1095-8649.1970.tb03292.x.

Coulter, G.W., 1977. Approaches to estimating fish biomass and potential yield in Lake Tanganyika. J. Fish. Biol. 11, 393–408. https://doi.org/10.1111/j.1095-8649.1977.tb04134.x.

Coulter, G.W., 1992. Vulnerability of Lake Tanganyika to pollution, with comments on social aspects. Mitt. Internat. Verein. Limnol. 23, 65–70. https://doi.org/10.1080/05384680.1992.11904009.

G.W. Coulter R.H. Spigel Hydrodynamics G.W. Coulter Lake Tanganyika and its life 1991 Oxford University Press London 49 75.

G.W. Coulter (Ed.), Lake Tanganyika and its life 1991 Oxford University Press London 10.1007/BF00042885.

De Vis, P., Mélin, F., Hunt, S.E., Morrone, R., Sinclair, M., Bell, B., 2022. Ancillary data uncertainties within the SeaDAS Uncertainty Budget for Ocean Colour Retrievals. Remote Sens. 14 (3), 497. https://doi.org/10.3390/rs14030497.

Delandmeter, P., Lambrechts, J., Legat, V., Vallaeys, V., Naithani, J., Thiery, W., Remacke, J.F., Deleersnijder, E., 2018. A fully consistent and conservative vertically adaptive coordinate system for SLIM 3D v0. 4, a DG finite element hydrodynamic model, with an application to the thermocline oscillations of Lake Tanganyika. Geosci. Model Dev. 11, 1161–1179. https://doi.org/10.5194/gmd-11-1161-2018, 2018.

Descy, J.-P., Hardy, M.-A., Stenuite, S., Pirlot, S., Leporcq, B., Kimirei, I., Sekadende, B., Mwaitega, S.R., Sinyenza, D., 2005. Phytoplankton pigments and community composition in Lake Tanganyika. Freshw. Biol. 50, 668–684. https://doi.org/10.1111/j.1365-2427.2005.01358.x.

Descy, J.-P., Plisnier, P.-D., Leporcq, B., Stenuite, S., Pirlot, S., Stimart, J., Gosselain, V., André, L., Alleman, L., Vyverman, W., Cocquyt, C., De Wever, A., Stoyneva, M., Deleersnijder, E., Naithani, J., Chitamwebwa, D., Kimirei, I., Sekadende, B., Mwaitega, S., Muhoza, S., Sinyenza, D., Makasa, L., Lukwessa, C., Zulu, I., Phiri, H., 2006. Climate variability as recorded in Lake Tanganyika (CLIMLAKE). EV/02 Final Report. Belgian Science Policy, Brussels.

Descy, J.P., Tarbe, A.-L., Stenuite, S., Pirlot, S., Stimart, J., Vanderheyden, J., Leporcq, B., Stoyneva, M.P., Kimirei, I., Sinyinza, D., Plisnier, P.-D., 2010. Drivers of phytoplankton diversity in Lake Tanganyika. Hydrobiologia. 653 (1), 29–44. https://doi.org/10.1007/978-90-481-9908-2_4.

Dittrich, M., Obst, M., 2004. Are picoplankton responsible for calcite precipitation in lakes? Ambio. 33, 559–564. https://doi.org/10.1579/0044-7447-33.8.559.

Docquier, D., Thiery, W., Lhermitte, S., van Lipzig, N., 2016. Multi-year wind dynamics around Lake Tanganyika. Clim. Dyn. 47, 3191–3202. https://doi.org/10.1007/s00382-016-3020-z.

Dorostkar, A., Boegman, L., 2013. Internal hydraulic jumps in a long narrow lake. Limnol. Oceanogr. 58 (1), 153–172. https://doi.org/10.4319/lo.2013.58.1.0153.

Dubois, J., 1958a. Evolution de la temperature de l' oxygène dissous et de la transperance dans la baie nord du Lac Tanganika. Hydrobiologia. 10, 215–240. https://doi.org/10.1007/BF00142188.

Dubois, J., 1958b. Les concrétions déposées par les eaux du Lac Tanganyika sur ses rives rocheuses. Bull. CEBEDEAU. 96, 2–4.

Eccles, D.H., 1986. Is speciation of demersal fishes in Lake Tanganyika restrained by physical limnological conditions? Biol. J. Linn. Soc. 29, 115–122. https://doi.org/10.1111/j.1095-8312.1986.tb01826.x.

Edmond, J.M., Stallard, R.F., Craig, H., Craig, V., Weiss, R.F., Coulter, G.W., 1993. Nutrient chemistry of the water column of Lake Tanganyika. Limnol. Oceanogr. 38, 725–738. https://doi.org/10.4319/LO.1993.38.4.0725.

Ferro, W., Coulter, G.W., 1974. Etude limnologique de la partie nord du lac Tanganika. DP/BD1/73/020/7 Report. United Nations Food and Agriculture Organisation, Bujumbura, Rome.

Franz, B.A., Kwiatkowska, E.J., Meister, G., McClain, C.R., 2007. Utility of MODIS-Terra for ocean color applications. Earth Observing Systems XII. 6677, 1–14. https://doi.org/10.1117/12.732082.

Game and Fisheries Department, 1965. Fisheries research Bulletin 1963–1964. Zambia.

Gourgue, O., Deleersnijder, E., White, L., 2007. Toward a generic method for studying water renewal, with application to the epilimnion of Lake Tanganyika. Estuar. Coast. Shelf Sci. 74, 628–640. https://doi.org/10.1016/j.ecss.2007.05.009.

Gourgue, O., Deleersnijder, E., Legat, V., Marchal, E., White, L., 2011. Free and forced thermocline oscillations in Lake Tanganyika. In: Alpert, P., Sholokhman, T. (Eds.), Factor Separation in the Atmosphere: Applications and Future Prospects. Cambridge University Press, Cambridge, pp. 146–162.

R.E. Hecky R.H. Spigel G.W. Coulter The nutrient regime G.W. Coulter Lake Tanganyika and its life 1991 Oxford University Press London 76 89.

Hecky, R.E., Kling, H.J., 1981. The phytoplankton and protozooplankton of the euphotic zone of Lake Tanganyika: species composition, biomass, chlorophyll content, and spatio-temporal distribution. Limnol. Oceanogr. 26, 548–564. https://doi.org/10.4319/lo.1981.26.3.0548.

Hopkins, J.E., Palmer, M.R., Poulton, A.J., Hickman, A.E., Sharples, J., 2021. Control of a phytoplankton bloom by wind-driven vertical mixing and light availability. Limnol. Oceanogr. 66, 1926–1949. https://doi.org/10.1002/lno.11734.

Horion, S., Bergamino, N., Stenuite, S., Descy, J.-P., Plisnier, P.-D., Loiselle, S.A., Cornet, Y., 2010. Optimized extraction of daily bio-optical time series derived from MODIS/Aqua imagery for Lake Tanganyika, Africa, Remote Sens. Environ. 114, 781–791. https://doi.org/10.1016/j.rse.2009.11.012.

Horn, D.A., Imberger, J., Ivey, G.N., 2001. The degeneration of large-scale interfacial gravity waves in lakes. J. Fluid Mech. 434, 181–207. https://doi.org/10.1017/S0022112001003536.

Huttula, T., Kotilainen, P., Podsetchine, V., Peltonen, A., 1997. Inter-agency activity report in hydrodynamics during January-June 1997. Research for the Management of Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/76 Report. Food and Agriculture Organisation of the United Nations/Finnish International Development Agency, Bujumbura.

Huttula, T. (Ed.), 1997: Flow, thermal, regime and sediment transport studies in Lake Tanganyika. Kuopio University Publications C., Natural and environmental Sciences 73. Kuopio University Printing Office, Kuopio.

Imberger, J., Patterson, J., 1989. Physical limnology. Adv. Appl. Mech. 27, 303–475. https://doi.org/10.1016/S0065-2156(08)70199-6.

Iwacu, 2016. http://www.iwacu-burundi.org/les-eaux-du-lac-tanganyika-menacent-une-partie-de-la-plaine-de-limbo/. Accessed on March 7, 2023.

Jfro, 1962. Annual report 1960. Northern Rhodesia Joint Fisheries Research Organisation, Lusaka.

Kufferath, J., 1952. Le milieu biochimique. Résultats scientifiques de l' exploration hydrobiologique du lac Tanganika (1946–1947). 1, 29–47. Institut Royal des Sciences Naturelles de Belgique, Bruxelles.

Kurki, H., Vuorinen, I., Bosma, E., Bwebwa, D., 1999. Spatial and temporal changes in copepod zooplankton communities of Lake Tanganyika. Hydrobiologia. 407, 105–114. https://doi.org/10.1023/A:1003793532168.

Kutser, T., 2009. Passive optical remote sensing of cyanobacteria and other intense phytoplankton blooms in coastal and inland waters. Int. J. Remote Sens. 30, 4401–4425. https://doi.org/10.1080/01431160802562305.

Langenberg, V., Mwape, L.W., Tschibangu, K., Tumba, J.-M., Koelmans, A.-A., Roijackers, R., Salonen, K., Sarvala, J., Mölsä, H., 2002. Comparison of thermal stratification, light attenuation and chlorophyll-a dynamics between the ends of Lake Tanganyika. Aquat. Ecosyst. Health Manag. 5, 255–265. https://doi.org/10.1080/14634980290031956.

Loiselle, S.A., Bracchini, L., Dattilo, A.M., Ricci, M., Tognazzi, A., Cózar, A., Rossi, C., 2009. The optical characterization of chromophoric dissolved organic matter using wavelength distribution of absorption spectral slopes. Limnol. Oceanogr. 54 (2), 590–597. https://doi.org/10.4319/lo.2009.54.2.0590.

LTBP, 2000. Lake Tanganyika. The transboundary diagnostic analysis. Pollution control and other measures to protect biodiversity in Lake Tanganyika, UNDP/GEF/RAF/92/G32.

MacIntyre, S., 2013. Climatic variability, mixing dynamics, and ecological consequences in the African Great Lakes. In: Goldman, C.R., Kumagai, M., Robarts, R.D. (Eds.), Climatic Change and Global Warming of Inland Waters: Impacts and Mitigation for Ecosystems and Societies. Wiley-Blackwell, Hoboken, New Jersey, United States, pp. 311–336. https://doi.org/10.1002/9781118470596.ch18.

MacIntyre, S., Flynn, K.M., Jellison, R., Romero, J.R., 1999. Boundary mixing and nutrient fluxes in Mono Lake. California. Limnology and Oceanography 44 (3), 512–529. https://doi.org/10.4319/lo.1999.44.3.0512.

MacIntyre, S., Romero, J.R., Kling, G.W., 2002. Spatial-temporal variability in surface layer deepening and lateral advection in an embayment of Lake Victoria. East Africa. Limnol. Oceanogr. 47 (3), 656–671. https://doi.org/10.4319/lo.2002.47.3.0656.

MacIntyre, S., Romero, J.R., Silsbe, G.M., Emery, B.M., 2014. Stratification and horizontal exchange in Lake Victoria. East Africa. Limnol. Oceanogr. 59 (6), 1805–1838. https://doi.org/10.4319/lo.2014.59.6.1805.

Mackey, M.D., Mackey, D.J., Higgins, H.W., Wright, S.W., 1996. CHEMTAX – a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. Mar. Ecol. Prog. Ser. 144, 265–283. https://doi.org/10.3354/meps144265.

Matthes, H., 1967. Preliminary investigations into the biology of the Lake Tanganyika Clupeidae. Fish. Res. Bull. Zambia. 4, 39–46.

Medrano, E.A., Uittenbogaard, R.E., Pires, L.D., Van de Wiel, B.J.H., Clercx, H.J.H., 2013. Coupling hydrodynamics and buoyancy regulation in *Microcystis aeruginosa* for its vertical distribution in lakes. Ecol. Modell. 248, 41–56. https://doi.org/10.1016/j.ecolmodel.2012.08.029.

Mölsä, H., Reynolds, J.E., Coenen, E.J., Lindqvist, O.V., 1999. Fisheries research towards resource management on Lake Tanganyika. Hydrobiologia. 407, 1–24. https://doi.org/10.1023/A:1003712708969.

Mortimer, C.H., 1974. Lake hydrodynamics. Mitt. Internat. Verein. Limnol. 20, 124–197. https://doi.org/10.1080/05384680.1974.11923886.

Mortimer, C.H., 1952. Water movements in lakes during summer stratification; evidence from the distribution of temperature in Windermere. Philos. Trans. R. Soc. Lond., B: Biol. Sci. 236(635), 355–398. Doi: 10.1098/rstb.1952.0005.

Nahimana, D., Brion, N., Nzeyimana, E., Baeyens, W., Ntakimazi, G., 2008. General nutrient distribution in the water column of Northern Lake Tanganyika. Aquat. Ecosyst. Health Manag. 11 (1), 8–15. https://doi.org/10.1080/14634980701878116.

Naithani, J., Deleersnijder, E., Plisnier, P.-D., 2002. Origin of intraseasonal variability in Lake Tanganyika. Geophys. Res. Lett. 29, 2093. https://doi.org/10.1029/2002GL015843.

Naithani, J., Deleersnijder, E., Plisnier, P.-D., 2003. Analysis of wind-induced thermocline oscillations of Lake Tanganyika. Environ. Fluid Mech. 3, 23–39. https://doi.org/10.1023/A:1021116727232.

Naithani, J., Deleersnijder, E., 2004. Are there internal Kelvin waves in Lake Tanganyika? Geophys. Res. Lett. 31, L06303. https://doi.org/10.1029/2003GL019156.

Naithani, J., Plisnier, P.-D., Deleersnijder, E., 2007. A simple model of the eco-hydrodynamics of the epilimnion of Lake Tanganyika. Freshw. Biol. 52, 2087–2100. https://doi.org/10.1111/j.1365-2427.2007.01831.x.

Narita, T., Mulimbwa, N., Mizuno, T., 1986. Vertical distribution and seasonal abundance of zooplankters in Lake Tanganyika. Afr. Stud. Monogr. 6, 1–16. https://doi.org/10.14989/68016.

Nicholson, S.E., 2000. The nature of rainfall variability over Africa on time scales of decades to millenia. Glob. Planet. Change. 26, 137–158. https://doi.org/10.1016/S0921-8181(00)00040-0.

O'Reilly, C.M., Alin, S.R., Plisnier, P.-D., Cohen, A.S., McKee, B.A., 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika. Africa. Nature. 424, 766–768. https://doi.org/10.1038/nature01833.

Ocha, 2021. Burundi : désastres naturels. Flash Update Gatumba N°9.

Radio Okapi, 2021. https://www.radiookapi.net/2021/05/25/actualite/societe/uvira-plusieurs-quartiers-inondes-la-suite-de-la-montee-des-eaux-du-lac. Accessed on March 7, 2023.

Paerl, H.W., Huisman, J., 2008. Blooms like it hot. Science. 320 (5872), 57–58. https://doi.org/10.1126/science.1155398.

Pasche, N., Alunga, G., Mills, K., Muvundja, A.F., Ryves, D.B., Schurter, M., Wehrli, B., Schmid, M., 2010. Abrupt onset of carbonate deposition in Lake Kivu during the 1960s: response to recent environmental changes. J. Paleolimnol. 44, 931–946. https://doi.org/10.1007/s10933-010-9465-x.

Petit, P., 1995. Les pêcheries du secteur burundais du lac Tanganyika: évolution durant les années 80 et situation actuelle. Institut National Polytechnique de Toulouse, Toulouse, France. Ph.D. thesis.

Plisnier, P.-D., Chitamwebwa, D., Mwape, L., Tshibangu, K., Langenberg, V., Coenen, E., 1999. Limnological annual cycle inferred from physical-chemical fluctuations at three stations of Lake Tanganyika. Hydrobiologia. 407, 45–58. https://doi.org/10.1023/A:1003762119873.

Plisnier, P.-D., Coenen, E.C., 2001. Pulsed and dampened annual limnological fluctuations in Lake Tanganyika. In: Munawar, M., Hecky, R. (Eds.), The Great Lakes of the World (GLOW): Food-Web, Health and Integrity. Backhuys Publishers, Leiden, The Netherlands, pp. 83–96.

Plisnier, P.-D., Kayanda, R., MacIntyre, S., Obiero, K., Okello, W., Vodacek, A., Cocquyt, C., Abegaz, H., Achieng, A., Akonkwa, B., Albrecht, C., Balagizi, C., Barasa, J., Bashonga, R.A., Bishobibiri A.B., Bootsma, H., Borges, A.V., Chavula, G., Dadi, T., De Keyzer, E.L.R., Doran, P.J., Gabagambi, N., Gatare, R., Gemmell, A., Getahun, A., Haambiya, L.H., Higgins, S.N., Hyangya, B.L., Irvine, K., Isumbisho, M., Jonasse, C., Katongo, C., Katsev, S., Keyombe, J., Kimirei, I., Kisekelwa, T., Kishe, M., Koding, S. O.A., Kolding, J., Kraemer, B.M., Limbu, P., Lomodei, E., Mahongo, S.B., Malala, J., Mbabazi, S., Masilya, P.M., McCandless, M., Medard, M., Ajode, Z.M., Mrosso, H.D., Mudakikwa, E.R., Mulimbwa, N., Mushagalusa, D., Muvundja, F.A., Nankabirwa, A., Nahimana, D., Ngatunga, B.P., Ngochera, M., Nicholson, S., Nshombo, M., Ntakimazi, G., Nyamweya, C., Nyeko, J.I., Olago, D., Olbamo, T., O'Reilly, C.M., Pasche, N., Phiri, H., Raasakka, N., Salyani, A., Sibomana, C., Silsbe, G.M., Smith, S., Sterner, R.W., Thiery, W., Tuyisenge, J., Van der Knaap, M., Van Steenberge, M., van Zwieten, P.A.M., Verheyen, E., Wakjira, M., Walakira, J., Wembo, O.N., Lawrence, T., 2023. Need for harmonized long-term multi-lake monitoring of African Great Lakes. J. Great Lakes Res. 49, 101988 https://doi.org/10.1016/j.jglr.2022.01.016.

Plisnier, P.-D., Langenberg, V., Mwape, L. Chitamwebwa, D. Tshibangu, K., Coenen, E.C., 1996. Limnological sampling during an annual cycle at three stations on Lake Tanganyika (1993-1994). GCP/RAF/271/FIN-TD/46. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika.

Plisnier, P.-D., Poncelet, N., Cocquyt, C., De Boeck, H., Bompangue, D., Naithani, J., Jacobs, J., Piarroux, R., Moore, S., Giraudoux P., Batumbo, D., Mushagalusa, D., Makasa, L., Deleersnijder, E., Tomazic, I., Cornet, Y., 2015. Cholera outbreaks at Lake Tanganyika induced by Climate Change? (CHOLTIC). SD/AR/04A, Final Report. Belgian Science Policy, Brussels. https://www.belspo.be/belspo/SSD/science/Reports/CHOLTIC_FinRep.pdf.

Plisnier, P.-D., Mgana, H., Kimirei, I., Chande, A., Makasa, L., Chimanga, J., Zulu, F., Cocquyt, C., Horion, S., Bergamino, N., Naithani, J., Deleersnijder, E., André, L., Descy, J.-P., Cornet, Y., 2009. Limnological variability and pelagic fish abundance (Stolothrissa tanganicae and Lates stappersii) in Lake Tanganyika. Hydrobiologia. 625, 117–134. https://doi.org/10.1007/s10750-009-9701-4.

Plisnier, P.-D., Nshombo, M., Mgana, H., Ntakimazi, G., 2018. Monitoring climate change and anthropogenic pressure at Lake Tanganyika. J. Great Lakes Res. 44, 1194–1208. https://doi.org/10.1016/j.jglr.2018.05.01.

Plisnier, P.-D., 1996. Limnological sampling during a second annual cycle (1994-1995) and some comparisons with year one on Lake Tanganyika. GCP/RAF/271/FIN-TD/56. FAO/FINNIDA Research for the Management of Fisheries on Lake Tanganyika.

Plisnier, P.-D. 1998. Lake Tanganyika: Recent climate changes and teleconnections with ENSO, in: Demarée, G., Alexandre, J., De Dapper, M. (Eds), Tropical climatology, meteorology and hydrology. In memoriam F. Bultot (1924–1995). Proceedings of the International Conference, Brussels, 22–24 May 1996. Royal Meteorological Institute of Belgium & Royal Academy of Overseas Sciences, 228–250. http://hdl.handle.net/1854/LU-279068.

Podsetchine, V., Huttula,T., 1996. Hydrological modelling. Activity report for the periods of 01.04–31.05.1995 and 01.09–30.09.1995. FAO/FINNIDA Research for the Management of the Fisheries on Lake Tanganyika. GCP/RAF/271/FIN-TD/45.

Podsetchine, V., Huttula, T., Savijärvi, H., 1999. A three dimensional-circulation model of Lake Tanganyika. Hydrobiologia. 407, 25–35. https://doi.org/10.1023/A:1003758003034.

Reynolds, C.S., 2006. The ecology of phytoplankton. Cambridge University Press.

Richardson, K., 1997. Harmful or exceptional phytoplankton blooms in the marine ecosystem. Adv. Mar. Biol. 31, 301–385. https://doi.org/10.1016/S0065-2881(08)60225-4.

Ruddick, K.G., Ovidio, F., Rijkeboer, M., 2000. Atmospheric correction of SeaWiFS imagery for turbid coastal and inland waters. Appl. Opt. 39 (6), 897–912. https://doi.org/10.1364/AO.39.000897.

Salonen, K., Sarvala, J., Järvinen, M., Langenberg, V., Nuottajärvi, M., Vuorio, K., Chitamwebwa, D.B.R., 1999. Phytoplankton in Lake Tanganyika – vertical and horizontal distribution of in vivo fluorescence. Hydrobiologia. 407, 89–103. https://doi.org/10.1023/A:1003764825808.

Salonen, K., Högmander, P., Langenberg, V., Mölsä, H., Sarvala, J., Tarvainen, A., Tiirola, M., 2012. Limnocnida tanganyicae medusae (Cnidaria: Hydrozoa): a semiautonomous microcosm in the food web of Lake Tanganyika. Hydrobiologia. 690, 97–112. https://doi.org/10.1007/978-94-007-5316-7_8.

Sarvala, J., Langenberg, V.T., Salonen, K., Chitamwebwa, D., Coulter, G.W., Huttula, T., Kanyaru, R., Kotilainen, P., Makasa, L., Mulimbwa, N., Mölsä, H., 2006. Fish catches from Lake Tanganyika mainly reflect changes in fishery practices, not climate. Verh. Internat. Verein. Limnol. 29, 1182–1188. https://doi.org/10.1080/03680770.2005.11902871.

Savijärvi, H., 1997. Diurnal winds around Lake Tanganyika. Q. J. r. Meteorol. Soc. 123, 901–918. https://doi.org/10.1002/qj.49712354006.

Spigel, R.H., Coulter, G.W., 1996. Comparison of hydrology and physical limnology of the East African great lakes: Tanganyika, Malawi, Victoria, Kivu and Turkana (with reference to some North American Great Lakes). In: Johnson, T.C., Odada, E.O., Whittaker, K.T. (Eds.), The Limnology, Climatology and Paleoclimatology of the East African Lakes. Gordon and Breach Science Publishers, Amsterdam, pp. 103–139.

Stanley, H.M., 1889. Through the dark continent: or, the sources of the Nile, around the great lakes of equatorial Africa and down the Livingstone River to the Atlantic Ocean. Sampson Low, Marston, Searle, Rivington, London.

Symoens, J.-J., 1955. Sur le maximum planctonique observé en fin de saison sèche dans le bassin nord du Lac Tanganika. Folia Scientifica Africae Centralis. 1 (4), 12.

Symoens, J.-J., 1956. Sur la formation de "fleurs d'eau" à Cyanophycées (Anabaena flos-aquae) dans le bassin nord du lac Tanganika. Bull. Acad. Roy. Sciences Coloniales Belge. 2, 414–419.

Talling, J.F., 1965. The photosynthetic activity of phytoplankton in East African lakes. Int. Revue Ges. Hydrobiol. 50 (1), 1–32. https://doi.org/10.1002/iroh.19650500102.

Talling, J.F., 1966. The annual cycle of statification and phytoplankton growth in Lake Victoria (East Africa). Int. Revue Ges. Hydrobiol. 51 (4), 545–621. https://doi.org/10.1002/iroh.19660510402.

Tierney, J.E., Mayes, M.T., Meyer, N., Johnson, C., Swarzenski, P.W., Cohen, A.S., Russell, J.M., 2010. Late-twentieth-century warming in Lake Tanganyika unprecedented since AD 500. Nat. Geosci. 3, 422–425. https://doi.org/10.1038/ngeo865.

Van Meel, L., 1954. Le phytoplankton. Résultats scientifiques de l'exploration hydrobiologique du lac Tanganika (1946-1947) 4(1). Institut royal des Sciences naturelles de Belgique, Bruxelles.

Verburg, P., Hecky, R.E., Kling, H., 2003. Ecological consequences of a century of warming in Lake Tanganyika. Science. 301, 505–507. https://doi.org/10.1126/science.108484.

Vinel, A., 2022. Caractérisation de la variabilité spatiale et temporelle de la chlorophylle a des eaux du lac Tanganyika (Ms thesis). Université catholique de Louvain, Louvain-la-Neuve, Belgium.

Wekesa, C.W., 2001. An integrated survey of local knowledge in resource utilization and management in relation to climatic and land use changes in Kigoma area. Lake Tanganyika, Nyanza Project report.

West, G.S., 1907. Report on the freshwater algae, including phytoplankton, of the third Tanganyika expedition conducted by Dr. W.A. Cunnington, 1904–1905. Bot. J. Linn. Soc. 38(264), 81–197. Doi: 10.1111/j.1095-8339.1907.tb00848.x.

Williamson, C.E., Dodds, W., Kratz, T.K., Palmern, M., 2008. Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. Front. Ecol. Environ. 6, 247–254. https://doi.org/10.1890/070140.