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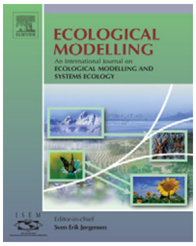

Examining the dynamics of phytoplankton biomass in Lake Tanganyika using Empirical Orthogonal Functions

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ABSTRACT

The spatial and seasonal variations in phytoplankton concentrations can be pronounced in large tropical lakes and can have a direct impact on the regional communities in developing nations. Given the complex hydrodynamics and ecology of the African Great Lakes, there is a clear need for spatial databases to address their inter-annual and seasonal variability. In the past, phytoplankton studies in these extensive ecosystems focused mostly on point stations or lake transects repeated over several years. In the present work, satellite based reflectances were used to determine anomalies in chlorophyll related reflectance bands over a 7-year period for the whole of Lake Tanganyika. Empirical Orthogonal Function analysis was used to define regions with similar temporal co-variation of phytoplankton biomass. Using AutoRegressive Integrated Moving Average modelling techniques, it was possible to determine differences in phytoplankton dynamics and link these to climate and lake basin characteristics. An important shift in the phytoplankton seasonality was observed at the end of 2000, in concomitance to changes in wind and air temperatures which favoured entrainment of nutrients present in the deeper lake waters. This shift confirms the high sensitivity of the lake to climate change. The combination of extensive satellite based measurements with modelling approaches that consider both spatial and temporal dynamics is an important contribution to the understanding of long term changes in this important freshwater ecosystem.

1. Introduction

Lake Tanganyika is located between $3^\circ 20'$ to $8^\circ 45'$ S and $29^\circ 05'$ to $31^\circ 15'$ E in the western branch of the East African Rift Valley. It contains about 9% of the Earth's freshwater (other than groundwater and ice) with an approximate surface area of $32{,}600\ \text{km}^2$ and volume of $18{,}880\ \text{km}^3$. While the large volume of Lake Tanganyika provides a temporary buffer against a deterioration in the water quality (Spigel and Coulter, 1996), the long residence time creates conditions in which human

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generated pollutants can accumulate, leading to negative effects on the lake's water quality, fish stocks and biodiversity (Duda, 2002; Verschuren, 2003).

The surface waters of Tanganyika are known to be nutrient poor (Edmond et al., 1993), whereas deep waters are relatively rich in nutrients and permanently stratified (Spigel and Coulter, 1996). About the 80% of the total water volume below the thermocline is anoxic. When wind-induced mixing occurs, anoxic waters upwell and sometimes cause fish kills, particularly in the southern part of the lake (Plisnier et al., 1999).

Seasonal and spatial variations in water quality can be particularly pronounced in large tropical lakes (Talling, 1986). Given their complex hydrodynamics and ecology, there is a clear need for spatio-temporal databases to address interannual and seasonal variability of ecosystem dynamics in the African Great Lakes (Ji et al., 2002). The assessment of phytoplankton variability is a prerequisite for the understanding of long term changes.

Due to the elongated and extensive nature of Lake Tanganyika, ecosystem dynamics are sensitive to meteorological and hydrological differences between the opposite ends of the lake. Using two sites located at the opposite extremes of the Lake Tanganyika, Langenberg et al. (2002) highlighted the differences in chlorophyll-a dynamics in these sites and their strong coupling to the annual climate cycle. A lag of 1 month between the upwelling near Mpulungu and Bujumbura was observed and associated to wind-induced water movement. A recent study suggested that nutrient availability in Lake Tanganyika is strongly controlled by the physical environment (water column stability, upwellings, currents, etc.) (Plisnier, 2002). Major steps forward have been made through extensive sampling (Descy et al., 2005), but long term full lake databases do not exist.

The aim of the present study is to determine variations in phytoplankton dynamics in Lake Tanganyika over spatial (horizontal) and temporal scales. To do so, satellite based reflectances were used to determine anomalies in chlorophyll related reflectance bands over a 7 years period. An Empirical Orthogonal Functions analysis was used to group areas of the lake with similar temporal dynamics into co-varying regions, subsections of the lake which show a similar behaviour over the 7-year period. A temporal decomposition modelling approach was then used to examine the seasonal patterns of each lake region and overall trends for the study period. The dynamics of each lake region were examined and compared to meterological and hydrological cycles as well as point measurements and transect data reported in the literature.

2. Methods

2.1. *Remote sensing analysis*

Monthly estimates of chlorophyll-a were obtained from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) from September 1997 to October 2004, building a database of 86 monthly images. Satellite imagery was acquired from the NASA Goddard Distribution Active Archive Center as Level 3 data. To cover the whole lake area, 350 pixels with a spatial resolution of 9 km × 9 km were used. Cloud obscured pixels in the spatio-temporal matrix were substituted using a Kriging interpolation technique. The chlorophyll-a concentration Level 3 data were computed using the OC4.V4 algorithm (O'Reilly et al., 2000). The OC4.V4 algorithm is based on an empirical maximum band ratio in the visible spectrum and it is designed to work between 0.01 and 64 μg/L of chlorophyll-a concentrations (Case I waters) and with a standard atmospheric correction. While the low phytoplankton biomass and low dissolved organic matter concentrations present in the pelagic zones of the lake (Descy et al., 2005) make the Case I approximation appropriate, atmospheric correction in this spectral region is quite problematic (Lidwine et al., 1999). To reduce atmospheric effects between images, the chlorophyll-a estimates were converted into anomalies for each image, creating a spatial distribution of relative biomass concentrations over the period of analysis.

After combining the 7-year dataset (86 samples), a temporal series of biomass anomalies for each pixel (9 km × 9 km) of the lake was assembled. The resulting analysis matrix (350 × 86) was then regionalised based on the temporal variation of each lake subsection (pixel) through the use of Empirical Orthogonal Function analysis.

2.2. *Empirical Orthogonal Function analysis*

Empirical Orthogonal Function analysis is widely used in oceanography and climate research (Raick et al., 2006) to extract structures from extensive data matrices in relation to spatial and temporal variability. We used this statistical approach to determine the principal modes of data variability of the lake dataset, focusing on the relative variability of phytoplankton biomass from 1997 to 2004. The eigenvectors of the correlation matrix (EOFs) represent independent modes of spatial or temporal variability, reducing the number of dimensions of the original dataset (Wilks, 1995). These EOFs represent a large part of the variability of the original data in a reduced variable space.

The monthly time-series of biomass anomalies for Lake Tanganyika were analysed using this approach to extract the EOFs which could explain the greatest variability, thereby determining the major spatial variance modes present in the dataset. Associated to each EOF is an eigenvalue, which describes the percent variance explained by each EOF. The first EOF accounts for the maximum amount of variance in the dataset. Successive EOFs explain the maximum variance not accounted for by preceding EOFs. After the EOFs are determined, those that represent physically relevant patterns are separated from those that represent only noise.

It is then possible to compare the most dominant EOFs with the temporal series of anomalies at each pixel, associating each pixel to a dominant variance mode (EOF) based on its degree of correlation (either positive or negative). Pixels which are assigned to the same mode are grouped together as co-varying (Cózar et al., 2005). By delimiting areas of co-varying pixels (pixels with a similar dominating EOF), regions with the same temporal characteristics are delimited. Outliers were replaced by geographical approximation.

2.3. *The extraction of temporal patterns using ARIMA*

Once co-varying regions have been identified, it is possible to examine season and inter-annual trends of each region. An important approach for the determination of temporal patterns of complex time series is the AutoRegressive Integrated Moving Average (ARIMA) model. This pattern analysis model allows for the decomposition of temporal modes into the seasonal patterns and overall trends. We explored two season pattern analysis models; the Demetra interface based on the X-12 ARIMA engine developed by the US Bureau of the Census (Findley et al., 1998), and the TRAMO-SEATS programme, developed by Gómez and Maravall (1996). The results of each were found to be similar. This similarly is expected as each differs only in their decomposition algorithms (Depoutot and Planas, 1998).

A set of statistical diagnostics was performed on each temporal pattern to evaluate the robustness of each decomposition. Ljung-Box statistic on 2 years of autocorrelations and Kurtosis test were conducted at 0.1% level of significance. In order to evaluate the decomposition quality, two additional statistical indices were performed: the combined Q statistic value and the SA quality index (Eurostat, 2002).

2.4. *Climate data*

An appropriate average seasonal series of surface meteorology was constructed to determine the influence of climate on the seasonal cycle. Mean wind speed data were available from the NOAA NCDC DAILY GLOBALSOD database at the Kigoma station. Mean monthly precipitation and air temperature are taken from CRU data of 1991–2002. We used the CRU Global Climate Dataset available through the IPCC DDC with a 0.5° resolution (Mitchell et al., 2004).

3. Results

3.1. *Spatial analysis*

The EOFs analysis of the Lake Tanganyika dataset (350 lake sections × 86 months) showed that only the first two EOFs showed eigenvalues above the noise threshold (North et al., 1982). These two modes explained, respectively, 17.1 and the 12.3% of the total variance. We compared the temporal series of each pixel to the two EOFs, assigning each lake section (pixel) to a specific EOF according to its correlation coefficient. By grouping pixel clusters which were correlated to the same EOF, it was possible to regionalise the lake into three co-varying regions: north, central and south (Fig. 1). The south region is positively correlated to the first EOF, while the north is negatively correlated. The central region is mainly defined by a positive correlation with the second mode. The north region covers 39% of the lake's surface, followed by the south region with 33% and the central one with 28%.

3.2. *Temporal analysis*

The temporal patterns of the three macro-regions were analysed and decomposed to determine seasonal and trend factors. Diagnostic tests were used to choose the best ARIMA model and to check for the presence of a significative autocorrelation in the residuals (Table 1).

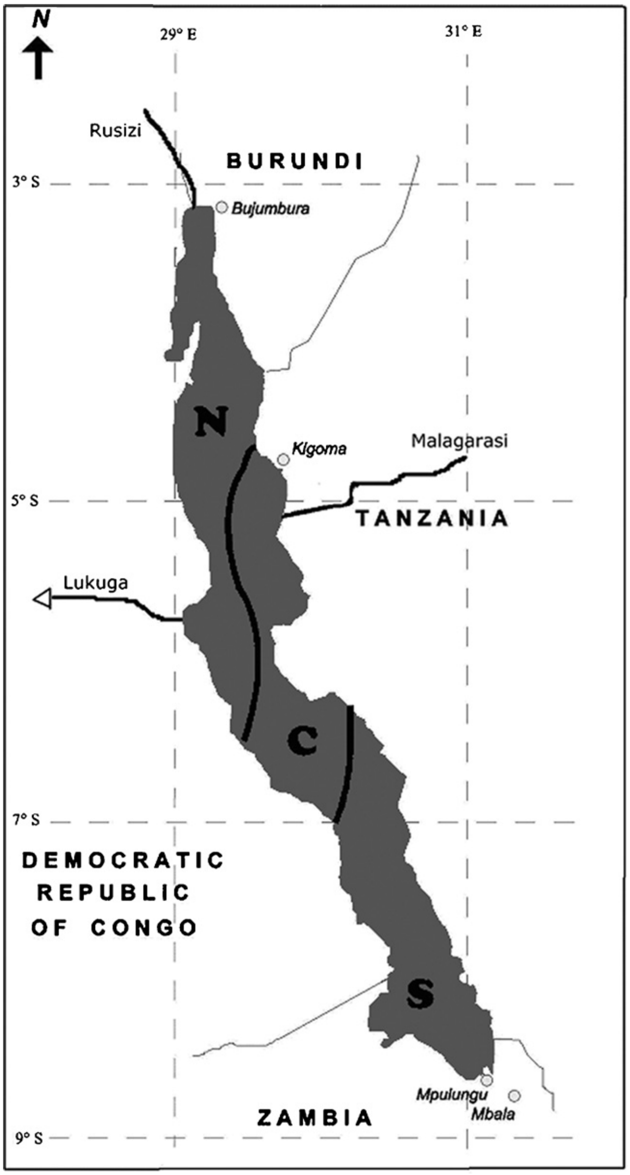

Fig. 1 – Results from the regionalisation of Lake Tanganyika showing three regions: north (N), central (C) and south (S). Also indicated are the major rivers (Rusizi, Malagarasi and Lukuga) and population centres.

The seasonal patterns extracted from ARIMA analysis show the periodicity of the phytoplankton bloom (Fig. 2). In the south region, the maximum net production occurs from March to September, with an annual maximum between September and October. From October to March, there is a constant decrease in phytoplankton biomass, especially in November.

The north region shows a significantly different seasonal pattern, with a 1-month delay in the biomass maximum (October–November) with respect to the south. A secondary lower peak occurs in August, while the minimum occurs in

Table 1 – Diagnostic test outputs. Ljung-Box and Kurtosis tests are in the range of $\alpha = 0.1\%$

Regions	ARIMA model	Test Ljung-Box	Test Kurtosis	Q combined statistic [0,1]	SA quality index [0,10]
North	(1,0,0) (0,0,1)	36.85	3.47	0.89	7.57
South	(0,1,1) (0,1,1)	16.81	3.13	0.45	5.58
Central	(2,0,0) (0,1,1)	32.54	2.97	0.84	6.35

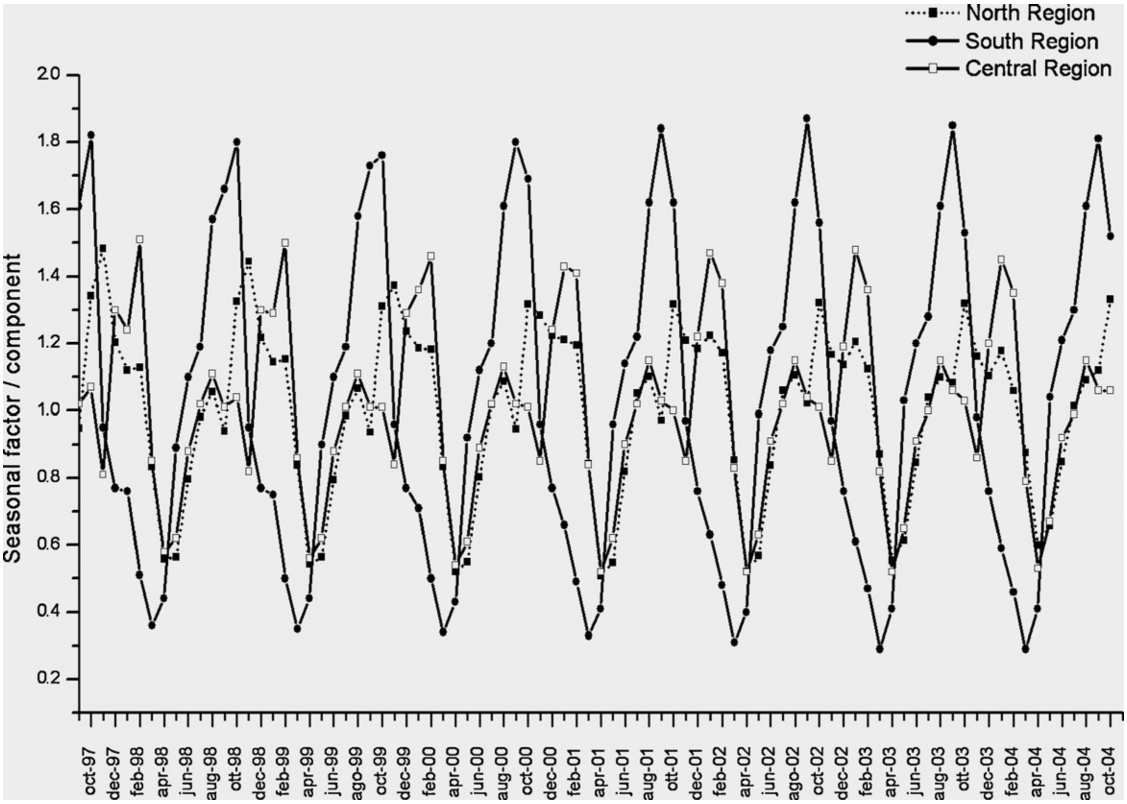

Fig. 2 – Seasonal components of the phytoplankton dynamics for the three regions of Lake Tanganyika. The components were extracted from temporal series of SeaWiFS-derived chlorophyll-a through an X-12 ARIMA analysis.

April. The period of high phytoplankton concentrations covers more months in the north section but the maximum concentrations are lower.

The central region shows a greater delay with respect to the south, occurring usually in January–February. A secondary peak also occurs in the same period as the maximum peak in the south (June–October). Absolute minimums occur in coincidence with the north basin.

Examining the inter-annual variability, a clear and important shift in the annual maximums was observed in the middle of the study period. A delay of 1 month in the seasonal maxima occurs for the main biomass maxima in each lake region in 2000. In the central region, the shift in the seasonal cycle occurs at the beginning of 2001 as the biomass maximum occurs in later this region. This shift does not return after the year 2000 but becomes more evident after 2001 (Table 2).

Table 2 – Seasonal maximum peaks of biomass anomalies for the three regions defined in Lake Tanganyika (the bold line highlights a 1-month shift in bloom seasonality which occurred in 2000–2001)

Region	1997	1998	1999	2000	2001	2002	2003	2004
South	OCT	OCT	OCT	SEP	SEP	SEP	SEP	SEP
North	NOV	NOV	NOV	OCT	OCT	OCT	OCT	OCT
Central		FEB	FEB	FEB	JAN	JAN	JAN	JAN

3.3. Climate data

The region of Lake Tanganyika has two main weather seasons: the wet season, usually from November to April, and the cool windy season, usually from May to September. The annual mean of air temperature, wind speed and precipitation have significant inter-annual changes. The years 1997–1998 were very dry (monthly mean 22 mm). The year 2000 was particularly wet (monthly mean 159 mm) and characterised by a lower annual temperature. Compared to the 7-year average from 1997 to 2004, the mean decrease in air temperature in 2000 was about 0.7 °C in the north and 1.4 °C in the south region. The wind speed was also highest in the same year, reaching an annual maximum of 3.5 m/s.

4. Discussion

The identification of three co-varying regions confirms information from transect (Descy et al., 2005) and fixed station studies (Langenberg et al., 2002) related to difference between the north and the south sections of Lake Tanganyika. The present analysis allows for a geographical definition of these areas and indicates that the central area of the lake acts as a transitional area with specific dynamics of its own. In many studies, the central region (near Kigoma) is often grouped together with the north region in a single subsection.

Different timing of the phytoplankton maxima has been hypothesized by Hecky (Hecky and Kling, 1981) and others based transect data through the whole lake and fixed sites in the north and south. The close ties between the temporal dynamics of the phytoplankton biomass and physical limits of the two deep water basins of the lake tend to confirm that phytoplankton dynamics are strongly influenced by hydrodynamics. The position of these two regions with respect to the dominant wind direction determines different mixing depth cycles influencing the entrainment of nutrients from the deep water layers. During the cool windy season (from May to September), the vertical temperature gradient is weaker as result of the cooling of the surface waters with respect to the deep nutrient rich waters. Persistent southerly winds during this season tilt the thermocline to induce a seiche activity (Coulter, 1991; Plisnier et al., 1999). This seiche movement supplies the kinetic energy necessary to favour the mixing of the water column, permitting nutrient entrainment to the surface waters. However, this thermocline oscillation along the South–North axis leads to a separation in upwelling events between the lake basins.

Initially, the southerly trade winds push the warm surface waters north, allowing for deeper waters to be brought to the surface in the south region. Nutrient inputs enter the euphotic zone of the south basin, leading to an increase in net phytoplankton production, with a maximum in October. When the trade winds cease, light availability and the column stability govern phytoplankton growth until the nutrient supply is exhausted in November. The 3-month mean of wind speed shows a significative correlation with the phytoplankton seasonal component of the south region ($R = 0.67$, $n = 29$, $p < 0.001$).

The northward-driven surface waters accumulate at the downwind end (north basin) of the lake. As the water mass oscillates towards an equilibrium, the elongated and narrow shape of the basin induces an internal seiche along the South–North axis (Spigel and Coulter, 1996; Plisnier et al., 1999) with an oscillation period of 3–4 weeks (Naithani et al., 2003). The resulting upwelling in the north basin occurs after the first oscillation of the internal seiche. This results in the 1-month delay in the seasonal phytoplankton bloom in the north (October–November) with respect to the south.

Relative differences in maxima between regions may also be related to this internal oscillation of the lake surface water mass. As the epilimnion tilting is less intense in the north following oscillation, a lower degree of nutrient upwelling occurs, perhaps leading to lower biomass concentrations (maximum and integrated) in the north. This is also confirmed in the data from Descy et al. (2005), where soluble reactive phosphorus and dissolved inorganic nitrogen are higher in the south with respect to the north.

The central part of the lake is characterised by a shallow shoal area, and represents a transition zone. In a standing wave, the water oscillates around a central node. No vertical movement occurs at the nodal point, whereas maximum vertical movement takes place at the ends (Wetzel, 1983). The seasonal oscillation along the North–South axis and a central node could help to explain why the vertical physical structures towards the lake centre show less overall response to hydrodynamical structure (Allanson, 1990). The phytoplankton bloom in the central region (January, February) coincides with the rainy season that provides nutrients and with a less intensive nutrient upwelling event registered during December–January (Langenberg et al., 2003). Diffusive transfer from the south to the north basin (Coulter, 1977) may also contribute to primary production in the north and central waters.

The shift in the seasonal phytoplankton cycle observed in 2000 was found to occur in a year characterised by higher winds and cooler air temperatures, which would favour a deeper mixing and the entrainment of nutrients present in the deep water layer. The continued shift in the seasonal maxima in the years following (2001–2004) indicates that the lake is highly sensitive to changes regional climate patterns. It is interesting to note that these changes occurred also in the central part of the lake, where hydrodynamics may play a lesser role in nutrient dynamics.

5. Conclusions

In the present work, spatial and temporal variations of surface phytoplankton biomass concentrations for the whole of Lake Tanganyika were analysed over a 7-year period using EOF analysis and an ARIMA approach. The identification of three co-varying regions, each with a different seasonality, provides important information for the understanding of the relationship between climate and productivity, mediated by hydrodynamic conditions. The sensitivity of the ecosystem dynamics of Lake Tanganyika to changes in climate is linked to its tropical location and extreme depth (1470 metres) (Verschuren, 2003). As mixing in tropical lakes is strongly linked to evaporative cooling of the surface waters, changes in climate variables have a major influence on the productivity of each lake region. Links between climate, ecosystem dynamics and fish yields further show how heat accumulation in this deep lake, modified by climate warming, may be linked to reductions in fish yields (Verburg et al., 2003; O'Reilly et al., 2003). Such modifications have direct impacts on the developing economies of the four countries which share the Tanganyika coasts. Fish resources of the lake supply the 25–40% of the protein for the local population living in the riparian countries: Burundi, Democratic Republic of Congo, Tanzania and Zambia (Mölsä et al., 1999). More investigations are needed to understand how such a long lasting shift in seasonality could have occurred and its persistence in time. The further exploration of spatio-temporal relationships between phytoplankton and fish abundance should be a priority in the sustainable management of Lake Tanganyika.

The present approach to examine mediated satellite data through EOF and ARIMA techniques represents an important tool to unravel the short term modifications in the dynamics of Lake Tanganyika. However, as such data is based on a 7-year set (less than one solar period) of largely surface water data, some caution must be exercised in extending these results to a long term analysis. It should also be noted that the present analysis was focused on relative differences in phytoplankton biomass rather than absolute concentrations, therefore, there was no consideration of changes in community characteristics. We determined relative trends and differences between lake regions over a 7-year period. In situ three-dimensional limnological data are clearly needed, as is the development of new approaches to climate modelling to study of the impacts of long term wind and temperature trends on one of the world's most important freshwater ecosystems.

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