Spatio-temporal dynamics of phytoplankton and primary production in Lake Tanganyika using a MODIS based bio-optical time series

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1. Introduction

Knowledge of the spatial variations of primary production, nutrient concentration and community structure is fundamental to the understanding of ecosystem dynamics (Bootsma and Hecky, 1993). Lake Tanganyika is characterised by extensive patchiness in its water chemistry, plankton concentration and fish distribution (Plisnier et al., 1999; Salonen et al., 1999). Due to variations in incident light, mixing depth and nutrient availability, algal production is expected to be particularly variable in time and space.

The lack of extensive data on seasonal and local variations in large tropical lakes, such as Lake Tanganyika, limits the possibility to make reliable estimates of lake wide primary production. Indeed, estimates of phytoplankton biomass and primary production for Lake Tanganyika have been based on measurements made in a small number of offshore sites, often with different sampling design and estimation methods. This has led to significantly different estimates of primary production (Hecky and Fee, 1981; Sarvala et al., 1999; Descy et al., 2005; Stenuite et al., 2007). Accordingly, Descy et al. (2005) have stressed that apparent historical changes in primary production should be interpreted with care, as different methods of phytoplankton analysis could lead to different results.

To improve the assessment of primary production and its dynamics in Lake Tanganyika, it is necessary to extend information gained from spatially and temporally localised measurements to the entire lake. On the other hand, the synoptic perspective provided by satellite data provides valuable information regarding the surface spatio-temporal characteristics of extensive ecosystems. The use of backscattered solar radiation to model global distributions of phytoplankton primary production has provided valuable insights into ocean dynamics and global biogeochemistry (Bricaud et al., 2002; Tilstone et al., 2009). However, little has been done to develop approaches appropriate for lake ecosystems, in particular in the southern hemisphere.

In the present study, we used remotely sensed estimates of phytoplankton biomass (chlorophyll-a) and optical properties (K490) to perform a regionalisation of Lake Tanganyika according to geographic areas with similar temporal patterns. From these estimates, regional patterns of daily primary production were calculated, using photosynthesis parameters derived from in situ ¹³C incubations. Finally, we calculated the overall lake phytoplankton productivity and compared it with other studies.
2. Data and methods

Level 1B MODIS-AQUA images (1 km² resolution) were selected from July, 2002 to November, 2005. The parameters of interest, namely chlorophyll-a concentration (chl-a) and the diffuse attenuation coefficient at 490 nm (K490), were derived and optimized on the basis of *in situ* data and considering local atmospheric conditions (see Horion et al., 2010—this volume). The optimization utilised data from the CLIMLAKE cruises sampling series (Descy et al., 2006).

The missing values (pixels) in the daily data matrix were filled using a Data Interpolating method based on Empirical Orthogonal Functions (DINEOFs) described by Beckers and Rixen (2003) and Beckers et al. (2006). This approach allows for the detection of statistically significant Empirical Orthogonal Functions (EOFs) as well as the reconstruction of data gaps within a temporal/spatial matrix, without requiring *a priori* information. The process estimates missing data from an optimal number of EOFs determined by cross-validation methods (Brankart and Brasseur, 1996). This cross-validation also provides an estimate of the refilling error. EOF analysis aims to extract a limited number of significant degrees of freedom, from a large dataset. This reduced set of variables represents a large fraction of variability of the original dataset (Wilks, 1995). The dataset reconstruction was performed for pixels with valid data on more than 5% of the images. The original values were conserved during the refilling process.

### Table 1

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<th>EOF</th>
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Fig. 1. The regionalisation of Lake Tanganyika in 13 subregions (R1–R13) of co-varying chlorophyll-a concentrations with main rivers, Malagarasi (A), Rusizi (B) and Lukuga (C). Note that subregion 3 is a multi-patch region of coastal zones near the main river mouths and the Lake outlet. Likewise, subregion R5 (not shown) consists of isolated pixels near the coasts. Regions with similar temporal correlations (Table 2) were found to have a north–south gradient; north (6, 9, and 10), south (1, 4, 7, 12, and 13), and centre (2 and 11).
Correlations between the daily time series of chlorophyll-a concentration determined using the averages of each of the 13 regions. Bold figures are statistically significant for alpha<0.01.

<table>
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<tr>
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Fig. 2. Daily time series of chlorophyll-a concentrations (mg m⁻³) for each subregion in the year 2003. Regional patterns (R1–13) are grouped in: north basin (A), central basin (B), south basin (C and D) and coastal areas (E).
2.1. Spatio-temporal analysis

To identify lake regions which have similar temporal dynamics, the dominant EOF modes of the chlorophyll-a dataset were used to perform a pre-classification based upon the Ward hierarchical classification algorithm (Statistica 7.1, StatSoft, Inc.). This iterative method uses an analysis of variance approach to evaluate the distances between clusters, minimizing the sum of squares of any two (hypothetical) clusters that can be formed at each step (Ward, 1963). The distance between clusters globally increased during the classification process. The final number of clusters was then set as the number of clusters corresponding to the sharp change in the linkage distance.

Using the chl-a filled matrix and the final number of clusters as input, each pixel of the Lake was assigned to a specific cluster according to the K-means classification method (Statistica 7.1), which minimized the intra-class variability and maximized of the inter-class variability. The Euclidean distance was used to determine aggregation distances. Each cluster represents a lake region with similar temporal dynamics of phytoplankton concentration.

Daily chl-a means were calculated for each region using the dataset prior to the refilling process, to avoid possible errors associated with the refilling process. Using the larger regional unfilled dataset, it was possible to construct a temporal dataset of variations that was not influenced by missing data.

2.2. Primary production

Although photosynthesis is a key component of the global carbon cycle, its spatial and temporal variabilities are poorly understood (Carr et al., 2006).

Talling (1957) derived a depth-integrated model using in situ vertical distributions of phytoplankton biomass, available solar irradiance and
the photosynthesis-irradiance relationship (Eq. (1)). The model is robust and has given reliable estimates of the amount of daily phytoplankton photosynthesis per unit area in various types of lakes (Kirk, 1983).

$$\text{Daily PP per unit area} = 0.9 N \cdot \text{chl-a} \cdot P_{\text{max}} \cdot \ln \left( \frac{I_o}{0.5 \cdot I_o} \right) \cdot K^{-1}_{\theta}$$  \[1\]

Where \( N \) is daylight hours (h), \( K_{\theta} \) is the vertical attenuation coefficient (m\(^{-1}\)), \( P_{\text{max}} \) is the maximum specific photosynthetic rate at light saturation or the assimilation number (mg C/mg(chl-a)\(^{-1}\) h\(^{-1}\)), chl-a\(_{eu}\) is the chlorophyll-a concentration in the euphotic layer expressed as \( \mu g \) l\(^{-1}\), \( I_o \) is the mean downward irradiance of Photosynthetic Active Radiation (PAR) just below the surface (\( \mu E \) m\(^{-2}\) s\(^{-1}\)), \( K_{\theta} \) is the irradiance value defining the onset of light saturation of photosynthesis (\( \mu E \) m\(^{-2}\) s\(^{-1}\)) and 0.9 is an empirical correction factor.

The values of \( P_{\text{max}} \) and \( I_o \) were taken from in situ measurements from Lake Tanganyika (Stenuite et al., 2007) for the dry (May–September) and wet seasons (October–April). The database consisted of 52 primary production measurements made in both wet and dry seasons between 2002 and 2005 in two lake transects and in permanent stations off Kigoma and Mpuulugu. \( P_{\text{max}} \) for the dry season was estimated to average 5.29 ± 1.96 mg C/mg(chl-a)\(^{-1}\) h\(^{-1}\) while \( P_{\text{max}} \) for the wet season was estimated to average 3.67 ± 1.38 mg C/mg(chl-a)\(^{-1}\) h\(^{-1}\). These seasonal values fall in the range reported by Hecky and Fee (1981). \( I_o \) was estimated to average 386 ± 84 \( \mu E \) m\(^{-2}\) s\(^{-1}\) and 315 ± 36 \( \mu E \) m\(^{-2}\) s\(^{-1}\) respectively for the dry and wet seasons.

Using the regional clusters, the average daily surface chl-a concentration was calculated for each region (chl-a\(_{0}\)). To extend this surface concentration throughout the euphotic layer (chl-a\(_{eu}\)), we used the vertical profile of chlorophyll-a determined in permanent stations by HPLC (Descy et al., 2005). The resulting regression equation (chl-a\(_{eu}\) = (0.802 ± 0.031) * chl-a\(_{0}\) + (0.228 ± 0.034), \( R^2 = 0.81, n = 149 \)) was then applied to satellite estimated surface concentration. The vertical attenuation coefficient within the water column was estimated based upon MODIS derived K490 product. K490 data were validated against in situ measurements of vertical attenuation of PAR (Horion et al., 2010-this volume).

\( I_o \) was determined for the central point of the lake (08°5′ S) using a model based on zenith angles and considering cloudless conditions. Reflection from the water surface was determined considering the change in solar declination in 15-minute intervals. The reduction in \( I_o \) due to clouds and the increase in \( I_o \) due to lake surface roughness (wave state) were not considered to have a significant impact on the estimated PP.

The regional daily primary production (PP) was estimated using monthly averages of \( K_{\theta} \) and chl-a\(_{eu}\) for each separate region (Eq. (1)). The daily PP for the whole lake was estimated by using the monthly means for each separate region after weighting each mean according to its relative area (in pixels) to the whole lake.

3. Results

3.1. Spatial analysis

The EOF analysis of the extensive satellite dataset showed a variance dominated by the first 11 modes for the chlorophyll-a and by the first 6 for the light attenuation coefficient. The proportion of the spatio-temporal variance explained by these EOFs is larger than 94% (Table 1).

The spatial regionalisation of the Lake Tanganyika, based on EOFs modes, showed a similar spatial structure for both chl-a and K490, with a higher variability present in the time series of chl-a images. In particular, chl-a based clusters allowed us to separate the lake in 13 co-varying regions (Fig. 1). Each cluster, in fact, represents a region with a characteristic temporal variation in phytoplankton concentration. Pixels that were found to pertain to each of the 13 regions (R1–13) were generally found to be spatially coherent (connected), with the exception of the pixels pertaining to R3 and R5 which were found to be delocalised along the coastline. Co-varying pixels assigned to R3 were found to be present near the major rivers outlets: Malagarasi river, the main tributary, in the eastern part of the lake and Rusizi river in the northern part. The Lukuga river, the lake’s only river outlet in the west was also assigned to R3.

Correlation coefficients between regions show that the traditional division of the Lake Tanganyika in three main basins is basically correct (Hecky and Kling, 1981; Bergamino et al., 2007): the northern regions (R6, R9, R10) are well correlated to each other and poorly correlated to the southern ones. The central regions (R2 and R11) are more correlated with those found in the north (Table 2). The southern part of Lake Tanganyika is characterised by more regions with smaller
dimensions (R1, R4, R7, R12, R13, and R8). The northern and central areas of the lake were segmented in geographically larger regions.

3.2. Temporal analysis

Temporal dynamics of chl-a showed significant differences between regions (Fig. 2). During 2003, the northern basin of the lake showed phytoplankton surface blooms between the end of the dry season and the beginning of the wet season (Fig. 2A). Chlorophyll-a concentrations were consistently lower in the northern regions (R6, R9, and R10) with respect to south and centre. The maximum peak in the north (R10) occurred during the second week of January. In the same period, higher concentrations also occurred in the central basin regions (Fig. 2B), after which there were no significant phytoplankton surface blooms. The southern basin showed higher oscillations in space and time (Fig. 2C and D). At the extreme south, phytoplankton concentrations increased at the beginning of the dry season and reached a maximum concentration in May. In the coastal R3, phytoplankton concentrations were consistently high throughout the wet season (Fig. 2E).

In general, minimum chlorophyll-a concentrations occurred at the end of the wet season, when the amplitude of internal waves is lowest.

3.3. Primary production

We determined the temporal variation of primary production in each lake region for 2003 (using Eq. (1)). The mean daily primary production showed an evident north–south gradient (Fig. 3), with a higher average productivity present in the south (Descy et al., 2006; Stenuit et al., 2007). To determine whole-lake primary production, we averaged the monthly chl-a and $K_d$ values weighted by the area (in pixels) of each separate region (Fig. 4).

These results indicate that the dry season is more productive than the wet season in all regions with few exceptions. The southern part was characterised by two main peaks during the dry season while the northern and central parts showed one smaller peak in August–September. Secondary peaks occurred contemporaneously throughout the Lake in January/February. In R3 (coastal areas), primary production reached a maximum during the wet season, probably due to the more intensive discharge of nutrients from the surrounding catchments. The minimum PP value occurred in March and December simultaneously throughout the lake. The only exception is the southernmost coastal region (R1) that showed a peak of PP in December.

The monthly averaged daily primary production ranged from 382 to 1653 mg C m$^{-2}$ d$^{-1}$ with a minimum in December in R7 and a maximum in May in R4.

Fig. 3. Daily primary production (PP) averaged in the year 2003 for each subregion.
4. Discussion

An extensive dataset of satellite images provides an opportunity to track dynamics in ecosystems with high spatial and temporal variabilities (Alvera-Azcárate et al., 2005). For Lake Tanganyika, a filled spatio-temporal matrix for chlorophyll-a and K490 was built at a spatial resolution of 1 km² (lake area = 31,745 pixels) for an average of 394 days, extending from 5/7/2002 to 30/11/2005. The analysis of this extensive dataset confirmed the patterns observed in the field studies and allowed us to gain a better picture of spatial and temporal heterogeneities of phytoplankton production in Lake Tanganyika. Actually, spatio-temporal variation in this lake is even greater than previously described, as 13 different co-varying regions were identified.

The results demonstrate that remote sensing can be a sensitive tool for monitoring the temporal and spatial variations in phytoplankton productivity. Primary production has been correlated to fisheries yield (Ware and Thomson, 2005), hence the present work should provide useful information for fisheries management in relation to spatial and temporal (e.g. climate) changes in this important tropical lake.

Our analysis of satellite data confirms several classic features of Lake Tanganyika (Coulter 1991): (i) the division of the lake into three main basins, north, central and south, with clearly different behaviours characterising the southern basin; (ii) the occurrence of surface phytoplankton blooms during the transition between the dry and the wet seasons; (iii) lower phytoplankton production in the northern basin, and higher production in the coastal areas; and (iv) the lowest

Table 3
Phytoplankton production in Lake Tanganyika: comparison of four research results.

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<tr>
<th>References</th>
<th>PP range (year)</th>
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<td></td>
<td>mgC m⁻² day⁻¹</td>
<td>gC m⁻² day⁻¹</td>
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<td>Hecky and Fee (1981)</td>
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phytoplankton biomass at the end of the wet season, and (v) a higher production in the dry season when compared to the rainy season.

This study has provided a more detailed analysis of the differences in the timing of chlorophyll-a peaks across the lake and within each region. It is clear that the heterogeneity in Lake Tanganyika is greater than previously thought, making it necessary to consider whole-lake dynamics when conclusions about primary production and fish production are desired. Spatial considerations are fundamental to improving the understanding of the main drivers of the lake productivity. Lake Tanganyika is fed by two major rivers, the Rusizi river which receives waters from Lake Kivu to the north, and the Malagarasi drains western Tanzania south of the Victoria Basin. These rivers create lake areas (R3) which have very different behaviours with respect to the rest of the Lake, including frequent blooms and a high mean chlorophyll-a concentration (2.7 mg m$^{-3}$). These differences are particularly evident in the rainy season.

Chlorophyll-a concentrations at the lake surface reach a maximum during the dry–wet seasons transition (Fig. 4). At that time, the water column begins to re-stratify (Pilsnier et al., 1999) and Anabaena blooms are observed on the surface (Salonen et al., 1999). They have the advantage of N$_2$ fixation in their heterocytes, but have high P requirements. They are more successful during lake transition periods when P is more available (following a deep mixing event), storing P as polyphosphate in their cells. In stratified conditions, Anabaena becomes more competitive, due to P storage, N$_2$ fixation and vertical migratory capacity to optimise light conditions. Anabaena surface blooms may have been responsible for high extreme values in chlorophyll-a concentrations detected by MODIS sensors on several occasions (Horion et al., 2010-this volume). In the south and central regions, the maximum was reached in the first half of January, a period of limited upwelling (Langenberg et al., 2003), but where mixing of upper layers is possible due to the colder temperatures. Throughout the lake, phytoplankton concentrations begin to increase with the onset of the dry season winds (May). Dry season peaks consist mostly of picophytoplankton or diatoms (Descy et al., 2005), which do not form surface blooms. The highest chlorophyll-a estimations were observed at the windward side of the lake (R1, R4 and R12) and appear to be linked to mixing. Trade winds favour the mixing of deep nutrient-rich water into the surface layer where light and temperature are optimal for phytoplankton growth.

The spatial distribution of chlorophyll-a is consistent with in situ measurements made in previous studies (Descy et al., 2005) and remote sensing anomalies (Bergamino et al., 2007). Although the lake lies just south of the equator, an evident latitudinal pattern in phytoplankton productivity was confirmed in this study, apparently driven by seasonal hydrodynamic changes. This pattern is related to internal waves, which favour nutrient transport through the thermocline with respect to wind induced mixing and greater nutrient availability (Coulter, 1991; Pilsnier et al., 1999). From the present analysis, the major difference between regions is mostly due to bloom intensity and only secondarily linked to the timing of the bloom.

Thickness of the upper mixed layer fluctuates strongly in tropical lakes (Talling, 1969; Lewis, 1984) and this variability has major implications for productivity and phytoplankton biomass (Hecky and Fee, 1981). Large-scale upwelling events, which characterise the south basin of Lake Tanganyika, lead to greater primary productivity. Seasonal upwelling is not as intensive in the north (Coulter, 1991), and thus it might be expected that average productivity values are lower. Nutrient inputs that enter the euphotic zone of the south basin lead to an increase in net phytoplankton production in April–May with another peak in August. The April-May peak could be associated to a strong mixing event which may be driven by a change in the direction of the trade winds. The August peak is coincident with maximum amplitude of the internal wave which has a stronger effect on surface conditions during the southern main upwelling period when there is no permanent thermocline. In the north, the increase in primary productivity is more gradual and leads to a less intensive maximum around August–September.

The annual water temperature gradient in the northern part of the lake is more marked than that of the south (Descy et al., 2006). This leads to differences in stability and depth of the mixed layer, a key variable determining nutrient availability and phytoplankton production, which is the sole source of organic carbon for the pelagic food web (Pirrot, 2006).

Primary production oscillations may be due to the trade-off between the availability of nutrients and light (Hecky and Kling, 1987). Although deep mixing might enhance productivity by increasing nutrient input from the hypolimnion, it simultaneously decreases primary production as light becomes limiting within a significantly deeper mixed layer. However, the effect of light limitation may be attenuated by low light acclimation or low light adapted phytoplankton: an increase of the Zm/Zeu ratio (Zm = mixed layer depth; Zeu = euphotic layer depth) typically favours the development of diatoms in lakes (Reynolds, 1984).

The daily primary productivity calculated on an annual basis (2003) was $646 ± 142$ mg C m$^{-2}$ day$^{-1}$. The deviation is dominated by the spatial and temporal heterogeneities of the lake dataset. This average value falls into the range determined by in situ estimates measured in the last five years ($110–1410$ mg C m$^{-2}$ day$^{-1}$), although it is larger than the annual average provided by Stenuite et al. (2007). Differences are expected between this estimate and in situ measurements, as the latter were based on calculation of PP at specific sites (2), with a time interval of two weeks. The present PP is derived from the MODIS based dataset which considers a wide range of conditions, based on whole-lake chlorophyll-a and vertical attenuation trends over the yearly cycle, including high biomass events which were not captured by the in situ sampling. Temporal variation is significant, whole-lake PP is $524 ± 67$ mg C m$^{-2}$ day$^{-1}$ in the wet season and $815 ± 157$ mg C m$^{-2}$ day$^{-1}$ in the dry season. It should also be noted that the present average PP (and its variance) is influenced by the estimates of chl-a and $K_{d}$ in the dataset as well as the in situ estimates of (P$_{max}$ and $K_{d}$). Validation of the MODIS based dataset shows a high consistency between measured and estimated values, even considering differences in the vertical profile of phytoplankton (Horion et al., 2010-this volume). The present estimate of daily primary productivity is also consistent with the eco-hydrodynamic model of Lake Tanganyika epilimnion (Naithani et al., 2007) which estimated an average net primary production of $750$ mg C m$^{-2}$ day$^{-1}$ for 2003.

Comparing our estimation to previous studies (made using different measurement approaches), a decrease in the photosynthetic production in Lake Tanganyika over the last 20 years does appear probable (15% lower with respect to Hecky and Fee, 1981), considering north–south transects during periods of high and low algal biomass (Table 3). This potential decrease in lake productivity has also been reported using different approaches by Verburg et al. (2003, 2006) and O’reilly et al. (2003), who estimated a 20% PP decrease based on a decrease of phytoplankton biovolume over three decades and changes of 6°C in the lake sediments. They associated this reduction to climate change impact on lake dynamics. It is also important to stress that our recent primary production measurements have shown the lowest minima ever reported, and that the present maxima are about half that reported three decades ago. These large differences in range estimates of primary production may be more indicative of a substantial decrease than use of yearly averages, which are greatly influenced by location, timing and number of measurements. However, caution should be taken when different estimation methods are used. Our estimates contrast with the high primary production averages ($1168–1813$ mg C m$^{-2}$ day$^{-1}$) published by Sarvala et al. (1999). The discrepancy may have several causes, including interannual variability, estimation methods and different time scales (Cohen et al., 2006).

5. Conclusions

Large lakes may be a good metric for global processes: large enough to damp out localised phenomena, yet small enough (compared to
oceans) to generate observable responses. The African Great Lakes are sensitive to climate change and therefore serve as important long-term indicators. Previous research has established that Lake Tanganyika may be affected by global change through a decrease in primary production. The present study demonstrates that satellite-based measurements can provide valuable information for understanding primary production and provide a basis for the development of quantitative and cost-effective monitoring methodologies. By exploring seasonal and interannual variabilities, it is possible to detect and characterise both long-term changes and short-term events at local scales.

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