Small Changes in Climate Can Profoundly Alter the Dynamics and Ecosystem Services of Tropical Crater Lakes

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Abstract

African tropical lakes provide vital ecosystem services including food and water to some of the fastest growing human populations, yet they are among the most understudied ecosystems in the world. The consequences of climate change and other stressors on the tropical lakes of Africa have been informed by long-term analyses, but these studies have largely focused on the massive Great Rift Valley lakes. Our objective was to evaluate how recent climate change has altered the functioning and services of smaller tropical lakes, which are far more abundant on the landscape. Based on a paired analysis of 20 years of high-resolution water column data and a paleolimnological record from a small crater lake in western Uganda, we present evidence that even a modest warming of the air (−0.9 °C increase over 20 years) and changes in the timing and intensity of rainfall can have significant consequences on the dynamics of this common tropical lake type. For example, we observed a significant nonlinear increase ($R^2_{adj} = 0.23$, $d.f. = 7$, $p<0.0001$) in thermal stability over the past 20 years. This resulted in the expansion of anoxic waters and consequent deterioration of fish habitat and appears to have abated primary production; processes that may impair ecosystem services for a vulnerable human population. This study on a system representative of small tropical crater lakes highlights the far-reaching effects of global climate change on tropical waters. Increased research efforts into tropical aquatic ecosystem health and the development of sound management practices are necessary in order to strengthen adaptive capabilities in tropical regions.

Citation: Saulnier-Talbot É, Gregory-Eaves I, Simpson KG, Efitre J, Nowlan TE, et al. (2014) Small Changes in Climate Can Profoundly Alter the Dynamics and Ecosystem Services of Tropical Crater Lakes. PLoS ONE 9(1): e86561. doi:10.1371/journal.pone.0086561

Editor: Judi Hewitt, University of Waikato (National Institute of Water and Atmospheric Research), New Zealand

Received: June 18, 2013; Accepted: December 12, 2013; Published: January 31, 2014

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Funding: This research was supported by grants from the National Science Foundation (NSF; http://www.nsf.gov/), the Wildlife Conservation Society (http://www.wcs.org/), the National Science and Engineering Research Council of Canada (NSERC; http://www.nserc-crsng.gc.ca/) and the Canada Research Chair in Respiratory Ecology to LJ.C, and by NSERC and the Canadian Foundation for Innovation (CFI) grants to IGE. EST and ZET benefited from postdoctoral and doctoral fellowships from Fonds québécois pour la Recherche sur la Nature et les Technologies (FQRNT; http://www.fqrnt.gouv.qc.ca/) and EST from a grant from the Percy Sladen Memorial Fund (http://www.linnean.org/The-Society/awards_and_grants/Awards+and+Grants). No individuals employed or contracted by the funders (other than the named authors) played any role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

The paucity of reliable long-term environmental and climatic data sets for the African continent is hindering progress in building capacity to adapt to global change [1], particularly in aquatic systems where potential impacts of climate change are not adequately documented and understood [2,3]. Given the range of uncertainty surrounding climate change scenarios and increasing pressures facing African inland waters [4] including a continent-wide shortage of potable water [5], the development of local scale data sets is critical for these systems [6]. Here, we address this problem by presenting an analysis of a 20-year high-resolution record of regular monitoring in a small but locally significant equatorial crater lake, Lake Nkuruba, located in a densely populated rural region of the East African highlands.

Crater lakes are a common lake type in the tropics [7]. About 90 crater lakes of varying sizes dot the landscape of western Uganda, one of the most densely populated rural areas in Sub-Saharan Africa [8]. Many of these lakes are relied upon for subsistence fishing and water supply for livestock and domestic use. Some, like Lake Nkuruba (Fig. 1), also provide additional sources of income for local populations (in this case, support for an orphanage in the form of a small-scale communal ecotourism venture; http://www.enfuzicommunitycampsite.com/). In this region, crater lakes have often experienced water quality degradation driven by watershed land-use changes [9]. However, our study lake’s catchment, which is limited to the surrounding crater walls up to the rim, has been the focus of an integrated conservation development program implemented in the early 1990s that resulted in the quick return and maintenance of the forest on the slopes to a near pre-disturbance state. As such, the basin’s forest has remained largely intact over the past 20 years. Consequently, cultural eutrophication threats are presently low in Lake Nkuruba, making it an ideal system for studying effects of recent climate change on small, warm tropical lakes, without the confounding effects of eutrophication.
Long-term studies of the much larger Lake Tanganyika show that 20th century climate warming, which is unprecedented in 1500 years [10], has modified water column dynamics, decreased ecosystem productivity and altered biotic assemblages [11,12]. Tanganyika is the largest African lake by volume and directly supports the livelihoods of millions of people [11]. However, small lakes are also of critical importance to humans throughout the tropics [13], and yet have received comparatively little attention from researchers. The present study provided a rare opportunity to both explore and assess impacts of recent climate warming on a smaller tropical lake ecosystem with high-resolution data that commence in 1992.

Results and Discussion

On a global scale, mid- and high-latitude northern hemisphere lakes are exhibiting much more pronounced warming than tropical lakes [14]. However, because the rate of change in water density is greater at higher temperatures [13], warm equatorial lakes are more sensitive than temperate lakes to small increases in temperature. Since the early 21st century, Lake Nkuruba has been subject to warmer than average temperatures. Indeed, nonlinear modeling indicates that between 2002 and 2010 surface water temperatures consistently showed a positive anomaly from the 1992–2012 mean ($R^2_{adj} = 0.22$, e.d.f. = 8.6, $p<0.0001$; Fig. 2). Likewise, we detected increased stratification of the water column over time, indicated by higher than average values of the Schmidt Stability Index post 2006 (SSI; Fig. 3a; $n = 478$, $R^2_{adj} = 0.23$, e.d.f. = 7, $p<0.001$). The strong positive correlation of thermal stability and surface water temperature in Nkuruba ($r = 0.93$, $p<0.001$ [15]; and $n = 478$, $r = 0.55$, $p = 0.0001$, this study) explains in part this increase. The relationship between SSI and surface temperature was found to be non-linear (sigmoidal: $R^2_{adj} = 0.29$, e.d.f. = 3.7, $p<0.0001$). Bottom temperatures also increased significantly (about 0.5°C) and became more stable between 2002 and 2010 ($R^2_{adj} = 0.24$, e.d.f. = 8.7, $p<0.0001$; Fig. 3b), consistent with late 20th century observations in Lake Malawi [16]. Ensuing these changes in thermal structure, with a lag of several years, we detected a transition to less transparent waters (Secchi and photic depth: $R^2_{adj} = 0.33$, e.d.f. = 8.1, $p<0.0001$; Fig. 3c) and shallower depth to anoxia post 2006 (defined as $z_{DO} <1$ mg L$^{-1}$) ($R^2_{adj} = 0.32$, e.d.f. = 8.6, $p<0.0001$; Fig. 3d). Since late 2006, Secchi (transparency) readings have consistently been below the 20-year mean value (2 m), signifying a reduction in the depth of the underwater photic zone (Fig. 2c). Annual thermocline depth and depth to anoxia were correlated to Secchi depth ($n = 20$ annual means, $r = 0.51$, $p = 0.02$ and $r = 0.68$, $p<0.001$, respectively) and to each other ($n = 20$ annual means; $r = 0.69$, $p<0.001$). These variables show a trend of shallower and more stable values for this period (Fig. 3).

Because hydrographic features, particularly water column structure and circulation, affect nutrient cycling and can dominate annual patterns of phytoplankton seasonality in the tropical belt...
changes to the vertical structure of the water column triggered by sustained warmer temperatures will almost certainly have an impact on the lake’s biota. Over the entire monitoring period, we observed only four episodes of thermal and/or oxic homogenization, defined as sampling days with either <0.2°C amplitude in the water column and/or ≤1 mg L⁻¹ DO at the lake’s surface (Table 1). These observations provide clear evidence of oligomixis, which had previously been presumed [17,18], but rarely recorded in this lake type. More commonly detected in Lake Nkuruba were large increases in the thickness of the mixed layer, indicated by variability in the depths of the thermocline (Fig. 3c).

In Nkuruba, deeper thermoclines are significantly more likely to occur during the dry seasons (i.e. between early December through to late February and between approximately late May through to early September) than during the wet seasons (i.e. early March through late May and September to November; \( t = 1.36, p = 0.05 \)), despite muted seasonality in these equatorial waters. Termed “atelomixis”, this partial mixing is thought to be very important in nutrient recycling in the photic zone and negatively affects primary production. Data for other pigments representing the major algal and bacterial groups present in the lake (Fig. 4b) generally follow a similar trend, showing an overall coherent response to the physical changes in the lake over the sampling period. Therefore, within the timeframe of the 20 year monitoring period, the few data points available for the period subsequent to 2006 highlight the importance of tracking primary productivity to evaluate whether it continues to decrease in the context of prolonged warmer conditions.

The decline in water transparency that accompanies the observed decrease in primary production to date (Fig. 4a) is perhaps counter-intuitive. One might expect that reduced productivity in the lake would equate to higher transparency, as it does in Lake Tanganjika [12]. However, the Nkuruba region has experienced a recent increase in days with heavy rainfall (i.e. days receiving ≥50 mm of rain, as measured in nearby Kibale National Park, \( R_{50}^{adj} = 0.41 \), \( t.d.f. = 5.1, p = 0.05 \)). As such, greater sediment loads that negatively affect water transparency is a viable hypothesis to explain the decline in water transparency in this small lake without any surface inflow other than rainfall. Enhanced sediment loading is supported by higher sedimentation rates detected in the core in the mid-2000s, relative to the previous 80 years (Fig. 5). The significant relationship between years with extreme rainfall events and proportion of minerogenic input in the core (\( n = 10, r = 0.68, p = 0.03 \)) is also concordant with this hypothesis (Fig. 5). A shift in the vertical distribution of the lake’s planktonic assemblage could also explain the recent decline in transparency. Studies of Nkuruba’s phytoplankton indicate that there is an important peak in the abundance of the cyanobacteria that dominate the assemblage (>70·10⁶ L⁻¹ cells), situated in the lower epilimnion at the limit of the oxic zone [21]. A shallower epilimnion is likely causing an upward migration of this peak, thus potentially contributing to reduced water transparency. This mechanism may be common in tropical crater lakes as suggested by the strong correlation between mixing depth and water column transparency observed previously in the tropical crater lakes of Cameroon [18]. The effects of the recent changes in the water column structure of our study lake on the specific composition of its phytoplankton assemblage are still unknown; however, from the sedimentary pigment data (Fig. 4b), it does not appear that a recent change in the composition of planktonic assemblages has occurred (at the group level).

The longer temporal context provided by the entire sediment core shows that productivity in the lake has undergone major fluctuations over the past 100 years (Fig. 6a). Given the substantial history of anthropogenic disturbances in the lake’s catchment pre-

| Date of observation | Surface temperature | Adj Temp surface-bottom | Surface DO (mg L⁻¹) | Adj DO surface-bottom (mg L⁻¹) |
|---------------------|---------------------|------------------------|---------------------|-------------------------------|
| 1994-12-03          | 21.9                | 0.15                   | 0.4                 | 0.3                           |
| 1999-08-30          | 22                  | 0                      | 1.5                 | 1.3                           |
| 2006-08-10          | 23                  | 1.0                    | 0.6                 | 0.5                           |
| 2006-10-05          | 23.2                | 1.55                   | 1.0                 | 0.9                           |

Table 1. Observed mixing events in Lake Nkuruba 1992–2012.

Mixing events are defined as sampling days with either <0.2°C amplitude in water column and/or ≤1 mg L⁻¹ DO at surface. All temperatures are in °C.

doi:10.1371/journal.pone.0086561.t001
1990, it is not possible to directly attribute earlier variations in sedimentary pigments to climatic mechanisms. Many of the Ugandan crater lakes, including Lake Nkuruba, host populations of non-native tilapias introduced into the lakes in the 1940s and later to boost protein availability for the local communities [21,22]. The timing of the fish introductions seems to correspond to the most pronounced increase in primary productivity over the last century (however, this did not lead to a major increase in the sedimentation rate at the time). This suggests that changes in algal abundance in the last 20 years could in part be due to changes in fish community structure. Several of the lakes are currently producing “stunted” tilapia populations [9,22]. Some also suffer periodic fish kills due at least in part, to severe short-lived hypoxia events triggered by mixing of the anoxic hypolimnion with the surface water or the expansion of the anoxic zone, such as the one recently observed in our study lake. Furthermore, in Lake Nkuruba, herbivores are mostly consumed by invertebrate predators that are favoured by anoxia [21], which could ultimately lead to lowered fish yield per unit of primary production. Environmental predictors of fish condition in the Ugandan crater lakes are not straightforward [22], but a prolonged period of warmer than average temperatures will affect fish habitat availability and quality. Detrimental conditions for tilapias in Nkuruba, and possibly in other nearby lakes would further reduce reliability of the regional protein supply for local human populations and would require managers to rethink the viability of some of the ecosystem services that have been provided until recently by the Ugandan crater lakes. In lakes such as Nkuruba, with long water residence times and where internal recycling is a major process, human use and management of the lake and its catchment can have a lasting impact on present functioning, which may only recently have been affected by climate change.

Figure 4. Water column dynamics in Lake Nkuruba 1992–2010. a) annual means of depth to anoxia (squares) and transparency (diamonds), and inferred primary production (circles) expressed as sedimentary concentrations of β-carotene. b) 1992–2007 variations in the concentrations of four sedimentary pigments associated with diatoms (diamonds), cryptophytes (triangles), chlorophytes (squares *concentration values for sedimentary lutein were an order of magnitude higher than the others, and were divided by 10 to fit the graph) and cyanobacteria (circles). doi:10.1371/journal.pone.0086561.g004

Conclusions

Our long-term observations show that small changes in climate, in the form of sustained warmer-than-average annual temperatures and more heavy rainfall days, are a major driver of change in Lake Nkuruba. We provide evidence that small, deep tropical crater lakes can show effects arising from climate warming that are comparable to those described for the African Great Lakes, namely abated production due to reduced mixing, hinting towards widespread concern for the general health of aquatic ecosystems in East Africa. We still know very little about the resilience of tropical lakes to global change, and it is difficult to predict if Lake Nkuruba has crossed over into a kind of alternative steady state, or if the present conditions could easily be reversed with the onset of a sustained cooler period. For now, it appears that one cooler than average year (2011) did not alter the depth to anoxia or thermocline depth. Clearly, African crater lakes should be better monitored so that hypotheses about the future impacts of climate change can be tested. In tropical regions of Africa, such as western Uganda and Cameroon where crater lakes are prevalent and provide local populations with ecosystem services, problems of food, water and energy security due to rapid population increases could be exacerbated by the effects of climate change on the dynamics of these ecosystems.

Materials and Methods

Nkuruba (Fig. 1) is a small (3 ha), moderately deep (max $z = 38$ m, mean $z = 16$ m), slightly alkaline (pH = 8); freshwater (mean surface salinity = 360 μS cm$^{-1}$) maar lake. It is surrounded by high forested walls averaging 48 m above the water surface which shelter the lake from wind action. It has no apparent inflow or outflow, and water level changes are relatively small but were observed to fluctuate considerably (falling over 3 m) following an
earthquake in February 1994 [15]. Permission and all necessary permits were obtained for the described study, which complied with all relevant regulations, from the appropriate Uganda government authorities (Uganda National Council for Science and Technology).

We measured water temperature, dissolved oxygen, and transparency in the water column of Lake Nkuruba roughly bi-monthly between March 1992 and February 2012, with a period of reduced sampling frequency (monthly) between August 1998 and June 2001, for a total of 489 sampling days. In general, duplicate profiles of dissolved oxygen and water temperature were taken with a YSI Model 50 or 51B meter, calibrated on each sampling day. Values presented are averages of the two profiles measured at each depth. Transparency was measured with a 22 cm Secchi disk by two different people, and then averaged. Measurements were generally taken before local noon at a station in the middle of the lake, where maximum depth reaches 30 m to 38 m. Sampling efforts were occasionally hindered by the presence of wildlife (hippopotamus) and the location of the profile was moved slightly, though it remained in the deeper zone. Previous sampling protocols of 6 sites across the lake during a continuous period of 24 months (between July 1992 and July 1994) indicated significant but very low variation in dissolved oxygen across sites (<0.5 mg L⁻¹). Therefore, we used only the one central lake profile throughout the 20 year period. Air temperatures and rainfall were measured at the Makerere University Biological Field Station (MUBFS), located in nearby Kibale National Park.

A 28 cm-long sediment core was retrieved from the deepest part of the lake using a gravity corer in January 2008. The core was extracted vertically on site into 1-cm increments using a portable extruder. At all times during sediment processing care was taken not to expose the sediments to direct sunlight. Samples were kept in the dark and frozen until analyses were performed at McGill University’s Department of Biology.

Sedimentary pigments were analyzed in September 2008. A known pre-weighed amount of roughly 0.3 g (±0.0127 g) of freeze-dried sediment per subsample was treated. Pigments were isolated/extracted into 5 ml (final volume) of 100% acetone, and
pre-processed by sonication in an ice bath for heat dissipation. Sample vials were purged of oxygen/air and placed in an atmosphere of argon. The extraction was allowed to continue for 24 h at −20°C. Sediments were separated from the supernatant by centrifugation in a refrigerated unit and filtration through 2 μm PTFE filters. Aliquots were analyzed using high performance liquid chromatography [23] (Waters HPLC, model no 600/626 with a Waters Photodiode Array 2996, a Waters 2475 Multi λ Fluorescence detector and a refrigerated waters autosampler 717). Individual pigments were identified and quantified using external standards purchased from DHI (Denmark). Sedimentary pigment concentrations were calibrated relative to organic matter content. Organic matter and minerogenic content was measured by loss on ignition [24].

Sediment core chronology was based on the measurement of 210Pb, 214Pb, and 214Bi from a known mass and volume of freeze-dried sediment from 16 downcore intervals. All radiometric measurements were made using a Canberra well-detector gamma spectrometer over a 24 hr period. Given that there was approximately a one-year error associated with sediment ages for the past 20 years, the correlation between monitoring and paleolimnological time series were improved when we accounted for this error. We considered linear and non-linear relationships between variables of interest. In particular we ran generalized additive models (GAMs) to test for the significance of a smoother term using the mgcv package for R [26]. Akaike Information Criterion (AIC) with a Chi-square test on model deviance was used to evaluate whether linear or nonlinear relationships had stronger statistical support. The effective degrees of freedom (e.d.f.; also known as the effective number of parameters of the cubic spline smoother) presented here indicate the amount of smoothing, such that an e.d.f. value very close to 1 suggests that the relationship is linear. We also ran an Analysis of Variance and post-hoc Tukey test to determine whether there was a significant difference in thermocline depth between the wet and dry seasons.

Acknowledgments

We thank members of the Kibale Fish and Monkey Project for data collection and Colin A. Chapman for sharing rainfall and temperature data. Jovan Abwooli and the participants in the East African Ecology course, Canadian Field Studies in Africa program class of 2008, helped with the coring and Stéphane Boudreau assisted with drawing the figures. Jean Guillard commented on an earlier version. The comments and suggestions of two anonymous reviewers improved the manuscript.

Author Contributions

Conceived and designed the experiments: EST IGE LJC. Performed the experiments: EST KGS. Analyzed the data: EST IGE KGS JE TEN ZET LJC. Contributed reagents/materials/analysis tools: IGE LJC. Wrote the paper: EST IGE KGS JE TEN ZET LJC. Collected field data and samples: EST JE LJC.

References

1. Washington R, Harrison M, Conway D, Black E, Challinor A, et al. (2006) African Climate Change: Taking the shorter route. B. Am. Meteorol. Soc. 87: 1355–1366.
2. Kundzewicz ZW, Mata LJ, Arnell NW, Doll P, Jimenez B, et al. (2008) The implications of projected climate change for freshwater resources and their management. Hydrolog. Sci. J. 53: 3–10.
3. Sarmento H, Amado AM, Desy JP (2013) Climate change in tropical fresh waters (comment on the paper “Plankton dynamics under different climatic conditions in space and time” by Senerpont domis et al. 2013). Freshwater Biol. doi: 10.1111/fwb.12140.
4. Arnell NW (1999) Climate change and global water resources. Glob. Environ. Change 9: 831–849.
5. Chapman LJ, Chapman CA, Crisman TL, Kaufman L (2003) The conservation and management of African inland waters: A synthesis. In Crisman TL, Chapman LJ, Chapman CA & Kaufman L, editors. Conservation, ecology, and management of African freshwaters. Gainesville, Florida, University Press of Florida. 474–488.
6. Pachauri RK, Reisinger A, editors (2007) Climate Change 2007: Synthesis Report. Cambridge, UK, Intergovernmental Panel on Climate Change.
7. Lewis WM Jr (1996) Tropical lakes: how latitude makes a difference. In Schiemer F & Boland KT, editors. Perspectives in tropical limnology. Amsterdam, SPB Academic Publishing. 43–64.

8. Hartter J, Stampone MD, Ryan SJ, Kirner K, Chapman CA, et al. (2012) Patterns and perceptions of climate change in a biodiversity conservation hotspot. *PLoS ONE* 7: e32408. Available: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0032408 Accessed 17 June 2013.

9. Efite J (2007) Life history variation in tilapia populations within the Crater Lakes of Western Uganda: The role of size-selective predation. PhD Thesis, University of Florida.

10. Tierney JE, Mayes MT, Meyer N, Johnson C, Swarzenski PW, et al. (2010) Late-twentieth-century warming in Lake Tanganyika unprecedented since AD 500. *Nature Geosci.* 3: 422–425.

11. O'Reilly CM, Alin SR, Plisnier P-D, Cohen AS, McKee BA (2003) Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature* 424: 766–768.

12. Verburg P, Hecky RE, Kling H (2003) Ecological consequences of a century of warming in Lake Tanganyika. *Science* 301: 505–507.

13. Lewis WM Jr (2000) Basis for the protection and management of tropical lakes. *Lakes and Reservoirs: Research and Management* 5: 35–48.

14. Schneider P, Hook SJ (2010) Space observations of inland water bodies show rapid surface warming since 1985. *Geophys. Res. Lett.* 37: L22405. Available: http://onlinelibrary.wiley.com/doi/10.1029/2010GL045059/abstract Accessed 17 June 2013.

15. Chapman LJ, Chapman CA, Crisman TL, Nordlie FG (1998) Dissolved oxygen and thermal regimes of a Ugandan crater lake. *Hydrobiologia* 385: 201–211.

16. Vollmer MK, Bootsma HA, Hecky RE, Patterson G, Halfman JD, et al. (2005) Deep-Water Warming Trend in Lake Malawi, East Africa. *Limnol. Oceanogr.* 50: 727–732.

17. Melack JM (1978) Morphometric, physical and chemical features of the volcanic crater lakes of western Uganda. *Arch. Hydrobiol.* 84: 430–453.

18. Kling GW (1988) Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West Africa. *Limnol. Oceanogr.* 33: 27–40.

19. Lewis WM Jr (1973) The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. *Limnol. Oceanogr.* 18: 209–217.

20. Leavitt PR, Hodgson DA (2001) Sedimentary pigments. In: Smol JP, Birks HJB, Last WM (eds) Developments in paleoenvironmental research, Vol 3. Tracking environmental changes using lake sediments: terrestrial algal and siliceous indicators. Kluwer Academic Publishers, Dordrecht. 295–325.

21. Kiisto Y, Naarvariek A, Chapman LC, Koste W (1995) A limnological survey of some western Uganda crater lakes. *Limnologica* 25: 335–347.

22. Efite J, Chapman LJ, Murie D (2009) Predictors of fish condition in introduced tilapias of Uganda crater lakes in relation to fishing pressure and deforestation. *Environ. Biol. Fish.* 85: 63–75.

23. Zapata M, Rodriguez F, Garrido JL (2000) Separation of chlorophylls and carotenoids from marine phytoplankton: a new HPLC method using a reversed phase C8 column and pyridine containing mobile phases. *Mar. Ecol-Prog Ser.* 195: 29–45.

24. Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *J. Paleolimnol.* 25: 101–110.

25. Appleby PG (2008) Three decades of dating recent sediments by fallout radionuclides: a review. *Holocene* 18: 83–93.

26. Wood SN (2006) Generalized Additive Models: an introduction with R. Boca Raton, Florida, CRC/Chapman & Hall.

27. Taranu ZE, Zurrwail RW, Pick F, Gregory-Eaves I (2012) Predicting cyanobacterial dynamics in the face of global change: the importance of scale and environmental context. *Glob. Change Biol.* 18: 3477–3490.

28. Margalef R (1983) *Limbnotogia*. Barcelona, Ediciones Omega. 1010 p.

29. Guillizzoni P, Lami A (2002) Paleolimnology: use of algal pigments as indicators. In Bitton G, editor. The *Encyclopedia of Environmental Microbiology*. Chichester, John Wiley & Sons. 2306–2317.