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Écologie du phytoplancton du lac Kivu (Afrique de l'Est)



Dissertation présentée par
Hugo Sarmiento en vue de
l'obtention du grade de
Docteur en Sciences
2 0 0 6

Faculté des Sciences
Département de Biologie

Unité de Recherche en Biologie des Organismes



FUNDP Namur

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A Andreia

Abstract

With a volcanic origin, Lake Kivu is deep and meromictic, and shows a very particular limnology and some astonishing features. The data available on its limnology and phytoplanktic communities are limited, dispersed or outdated. This is the first deep, long term study (2002-2004) on limnology and phytoplankton ecology of Lake Kivu, combining different techniques: HPLC analysis of marker pigments, flow cytometry, light, epifluorescence and electron microscopy. Lake Kivu combines a relatively shallow euphotic layer (~18m) usually smaller than its mixed layer (20 – 60 m), and with a weak thermal gradient in the mixolimnion. With an annual average chlorophyll *a* in the mixed layer of 2.2 mg m⁻³ and low nutrient levels in the euphotic zone, the lake is clearly oligotrophic. Concerning its phytoplanktonic composition, the most common species were the pennate diatoms *Nitzschia bacata* Hust. and *Fragilaria danica* (Kütz.) Lange-Bert., and the cyanobacteria *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg and *Synechococcus* sp. Diatoms were the dominant group in the lake, particularly during the dry season episodes of deep mixing. During the rainy season, the stratified water column, with high light and lower nutrient availability, favoured dominance of cyanobacteria. Phycoerythrin-rich phototrophic picoplankton and heterotrophic bacteria cell numbers were constantly high, with relatively subtle spatial, seasonal and vertical variations. In open lake waters, where allochthonous carbon inputs are most probably inconsequential, HNA heterotrophic bacteria abundance is strongly correlated with chlorophyll *a*. Recent investigations revealed an increasing methane production in the deep waters during the past three decades, leading to an accumulation of gas and the subsequent lowering of the energy required to trigger a devastating release of gasses. The role of primary producers and the probable changes on the export ratio of the organic matter into deep waters after the introduction of the planktivorous sardine from Lake Tanganyika *Limnothrissa miodon*, is discussed. The actual primary production, 0.71 g C m⁻² d⁻¹ (~ 260 g C m⁻² y⁻¹), doesn't seem substantially different from some punctual measurements made in the past, which discards the hypothesis of anthropogenic eutrophication. We believe that the export ratio of organic matter into the deep waters was largely affected by biological changes that could explain part of the methane increase in the past 30 years in Lake Kivu.

Résumé

Le lac Kivu a une origine volcanique. C'est un lac profond et méromictique, avec des caractéristiques limnologiques très particulières. Les données disponibles sur sa limnologie et ses communautés phytoplanctoniques sont limitées, dispersées ou anciennes. Pour une première fois, une étude approfondie et à long terme (2002-2004) sur la limnologie et l'écologie de phytoplancton du lac Kivu a été menée, combinant différentes techniques: analyse en HPLC des pigments marqueurs, cytométrie de flux, microscopie optique, en épifluorescence et électronique à balayage. Le lac Kivu combine une zone euphotique relativement peu profonde (~18 m), habituellement inférieure à la zone de mélange (20 - 60 m), avec un gradient thermique faible dans le mixolimnion. Avec une moyenne annuelle de chlorophylle *a* dans la zone de mélange de 2.2 mg m⁻³ et des concentrations en nutriments dans la zone euphotique faibles, ce lac est clairement oligotrophe. En ce qui concerne sa composition phytoplanctonique, les espèces les plus communes rencontrées ont été les diatomées pennées *Nitzschia bacata* Hust. et *Fragilaria danica* (Kütz.) Lange-Bert., et les cyanobactéries *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg et *Synechococcus* sp. Les diatomées ont dominé le peuplement, en particulier pendant les épisodes de mélange profond durant la saison sèche. Pendant la saison des pluies, la colonne d'eau est stratifiée et les conditions de lumière sont plus favorables, mais la disponibilité nutritive est moindre, ce qui favorise la dominance de cyanobactéries. Les concentrations cellulaires de picoplancton phototrophe riche en phycoérythrine et de bactéries hétérotrophes ont été constamment élevées. Les variations spatiales, saisonnières et verticales ont été relativement légères. En zone pélagique, les apports allochtones de carbone sont probablement négligeables et l'abondance des bactéries hétérotrophes (HNA) est fortement corrélée à la chlorophylle *a*. Des investigations récentes ont indiqué une production croissante de méthane dans les eaux profondes au cours des trois dernières décennies, menant à une accumulation du gaz et à l'abaissement de l'énergie nécessaire pour déclencher un dégagement massif de gaz, qui serait dévastateur. Le rôle de la production primaire et des changements probables sur le flux d'exportation de matière organique vers les eaux profondes suite à l'introduction de la sardine planctivore du lac Tanganyika *Limnothrissa miodon*, sont discutés. La production primaire actuelle, de 0.71 g C m² j⁻¹ (~ 260 g C m² a⁻¹), ne semble pas spécialement différente des quelques mesures ponctuelles faites dans le passé, ce qui permet d'écarter l'hypothèse d'une eutrophisation d'origine anthropique. Le flux d'exportation de matière organique vers les eaux profondes a très probablement été affecté par des changements biologiques, qui seraient partiellement responsables de l'augmentation de méthane dans les eaux profondes du lac au cours des 30 dernières années.

Chapitre I

Introduction :

L'énigmatique lac Kivu

Il revint le 16 juin (1894), par un jour de chaleur brûlante. (...) Lorsque nous demandions où nous pourrions trouver de l'eau à boire, ils nous montraient le jus aqueux qu'ils pressaient des tiges spongieuses des bananes, ou bien ils nous montraient le sud et prononçaient le mot: Kivou. (...) Nous avons déjà eu le spectacle de deux merveilles de ces splendides pays: le Kigéri et le Kirounga. Nous avions devant nous la troisième: le lac Kivou.

"A travers l'Afrique de l'est à l'ouest"
M. le Comte de Götzen
1897

L'énigmatique lac Kivu

Un peu d'histoire...

L'histoire du lac Kivu, tout au moins aux yeux de l'homme blanc, remonte à la fin du XIX^e siècle. La première apparition du lac Kivu sur une carte date de la mission de l'illustre Henry Morton Stanley (1878, Fig.1), qui avait été envoyé par le rédacteur en chef du *New York Herald Tribune*, avec pour mission de retrouver David Livingstone, parti, lui, à la recherche de la source du Nil et porté disparu. Il lui faudra de longs mois pour découvrir le célèbre explorateur. Il y parviendra le 10 novembre 1871, sur les rives du lac Tanganyika, à Ujiji, prêt de Kigoma (Tanzanie). Le Roi Léopold II de Belgique avait également chargé Stanley d'explorer la région et d'établir une série de comptoirs commerciaux le long du Congo. Cependant, le premier Européen qui a visité le lac Kivu et qui en a réalisé une cartographie détaillée (Fig. 2), fut le Comte Adolf von Götzen (Fig. 1), un officier allemand qui, en 1894, entra au Rwanda à la tête d'une troupe de 620 soldats. Il fut également le premier européen à traverser le Rwanda.



M. DE GÖTZEN.
D'APRÈS UNE PHOTOGRAPHIE.

Figure 1: Portraits de Henry M. Stanley (gauche) et du Comte Adolf von Götzen (droite). Extrait de Helmolt (1902) et Götzen (1897).

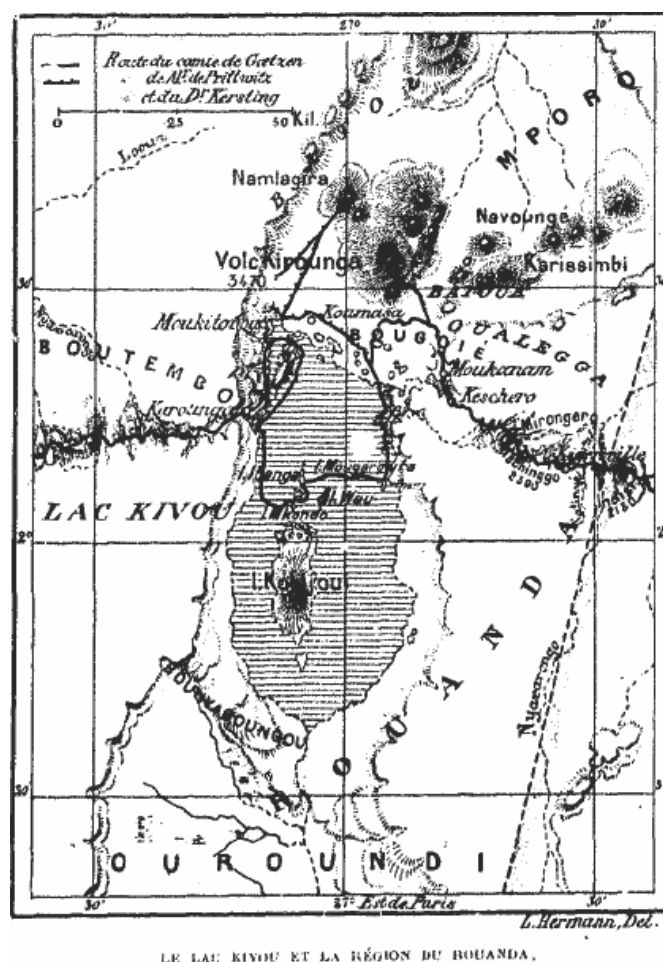


Figure 2: Première cartographie du lac Kivu par le Comte Adolf von Götzen (1897)

Il a fallu attendre 1935 pour voir arriver la première mission scientifique au lac Kivu, dirigée par H. Damas, de l'Université de Liège, dans le cadre de l'*Exploration du Parc National Albert* (Damas 1935-1936, 1937). Dans cette expédition, de nombreuses mesures des paramètres limnologiques de base ont été effectuées, et quelques échantillons ont été ramenés et confiés à différents spécialistes des différents groupes d'organismes. Plus de détails au sujet des résultats de ces recherches sont donnés dans l'introduction de

l'article "*Species diversity of pelagic algae of Lake Kivu (Eastern Africa)*", dans le Chapitre III.

En 1954, à l'initiative de l'ingénieur agronome Alphonse Collart, un événement marquait l'histoire du lac et des populations environnantes: l'introduction de la sardine endémique du Tanganyika, *Limnothrissa miodon* Boulenger. Après plusieurs tentatives infructueuses de transfert d'adultes à partir du lac Tanganyika, l'ingénieur a changé de stratégie et a essayé d'introduire des larves. Comme les larves de *Limnothrissa* et de *Stolothrissa* ne se distinguent pas à l'œil nu, les deux espèces ont probablement été introduites au lac Kivu. Ce n'est que quelques décennies plus tard que le monde scientifique apprend que l'introduction de *Limnothrissa* a réussi, et que cette petite sardine était à la base d'une pêche florissante (Spliethoff *et al.* 1983, de Jongh *et al.* 1983, Marshall 1991, 1995, Roest 1999).

Connaissances actuelles sur le lac Kivu

Le Kivu est un lac hors du commun relativement aux autres grands lacs de la vallée du rift africain. Si on peut dire que l'intérêt pour la limnologie des grands lacs est-africains s'est développé au cours des dernières décennies - ce dont témoignent les études réalisées sur les lacs Tanganyika (e. g. Hecky et Kling 1987, Descy *et al.* 2005), Malawi (e. g. Patterson et Kachinjika 1995) et Victoria (e. g. Talling 1957, 1987, Hecky 1993) - le lac Kivu reste encore assez peu connu, surtout en ce qui concerne sa composante biologique (Beadle 1981).

Haberyan et Hecky (1987) ont reconstitué l'histoire géologique de la région des grands lacs, et ont fait la liaison entre l'apparition du lac Kivu, il y a environ 15 000 ans, et l'élévation de toute la région des Virunga. Les laves de ces volcans, très actifs pendant le Pléistocène, auraient formé une barrière, et coupé la connexion au bassin du Nil (Beadle 1981). Désormais, le lac Kivu serait lié au lac Tanganyika par un seul exutoire, la Ruzizi, et ferait ainsi partie du bassin hydrographique du fleuve Congo. Le bassin versant du lac Kivu s'étend actuellement sur environ 7140 km² (Haberyan et Hecky 1987) et est drainé par d'innombrables petites rivières.

Une étude récente sur la génétique évolutive (Verheyen *et al.* 2003) a montré que les cichlidés des lacs situés au nord des Virunga (Edouard, Georges, Victoria...) seraient originaires d'un "proto-lac Kivu", bien plus ancien que l'intense activité volcanique (il y a 20 000 à 25 000 ans) qui a coupé cette connexion. L'élévation des montagnes à l'ouest du lac (où se situe actuellement le Parc National Kahuzi-Biega, une des plus importantes réserves de gorilles de montagne au monde), allié à l'élévation du rift de l'est (situé à l'est du Rwanda) seraient responsables par un drainage des eaux

du centre du Rwanda dans la région du lac Kivu actuel. Ce concept de "proto-lac Kivu" est et assez contesté par manque de preuves géologiques consistantes (Stager *et al.* 2004), même si l'horloge moléculaire des cichlidés semble montrer l'existence d'un lac bien plus ancien que les 15 000 ans cités couramment.

La littérature disponible à l'heure actuelle sur le lac Kivu est surtout orientée vers les concentrations considérables de gaz carbonique (CO₂) et de méthane (CH₄) dans les eaux profondes. Cette réserve de méthane, de dimensions uniques au monde (Tietze 1980, 1991, Tietze *et al.* 1980, Jannasch 1975, Schmid *et al.* 2005), représente une ressource économique potentiellement importante. Cependant, un risque pour la population de la région, en cas d'éruption gazeuse, n'est pas négligeable: de telles éruptions se sont produites dans les lacs Nyos et Monoun (au Cameroun), provoquant la mort par asphyxie (au CO₂) de 1700 et 37 personnes, respectivement (Kling *et al.* 1987, Sigurdsson 1989, Sigurdsson *et al.* 1987).

En réalité, les eaux du lac Kivu sont un mélange de deux eaux de nature très différente: les eaux superficielles (provenant du bassin versant et des eaux de pluie) et les sources géothermiques (majoritairement situés dans les zones profondes du lac). Ceci a été démontré par les résultats d'analyses isotopiques de deutérium et d'¹⁸O, qui se superposent parfaitement avec les profils de conductivité et température (Tietze 1978). Ce phénomène extrêmement rare à une aussi grande échelle, expliquerait le fort gradient de salinité, qui maintient la stratification. Cette stratification est formée de plusieurs chimioclines, dont une particulièrement marquée à 260 m (Schmid *et al.* 2005).

Les eaux de surface sont ainsi complètement isolées des eaux profondes. Deux facteurs contribuent à la stabilité de la stratification: le gradient de salinité et la concentration de CO₂ (croissantes avec la profondeur), qui augmentent la densité de l'eau. Ces deux facteurs de stabilisation surpassent largement les autres facteurs déstabilisants, à savoir, la température et la concentration de CH₄, également croissantes avec la profondeur (Schmid *et al.* 2005). Moins soluble que le CO₂, le CH₄ a une contribution plus importante à la pression totale, même s'il est présent en moindre quantité. Si les concentrations en CH₄ venaient à atteindre la saturation (prévisible pour la fin de ce siècle si la tendance à l'augmentation se confirme, voir ci-dessous), une éruption gazeuse aurait lieu, et le CO₂ serait le principal élément libéré par des bulles gazeuses. A haute concentration, cette masse de gaz plus dense que l'air, pourrait rester ou se déplacer par l'effet des vents vers des zones habitées et avoir des conséquences catastrophiques. Les travaux sur la stratigraphie des sédiments (Haberyan et Hecky 1987) suggèrent que des telles éruptions ont, en fait, déjà eu lieu par le passé au lac Kivu.

Il existe environ 60 km³ de CH₄ dissous (à 0°C et 1 atm) dans les eaux profondes du lac Kivu, ce qui correspond à cinq fois moins que la quantité de CO₂. Les valeurs de $\delta^{13}\text{C}$, typiques du CO₂ magmatique, montrent que le CO₂ situé dans les eaux profondes est d'origine géothermique. Par contre, le CH₄ est généré de deux manières: la réduction du CO₂ magmatique et la décomposition de la matière organique. L'hypothèse d'une origine magmatique du CH₄ a été exclue par l'étude des isotopes. Ainsi, 67% du CH₄ proviendrait de la réduction du CO₂, alors que la fermentation de la matière organique serait à l'origine de 33% du CH₄, selon les estimations de Schoell *et al.* (1988). Ce modèle a été soutenu par les observations de Bochem *et al.* (1982), qui ont trouvé des souches de bactéries méthanogènes (*Methanosarcina* et *Methanococcus*) dans un inoculum de sédiments du lac Kivu.

Des travaux récents indiquent une augmentation significative de la concentration en CH₄ des eaux profondes du lac Kivu (Schmid *et al.* 2005). De plus, cette tendance serait probablement liée aux changements des flux de carbone entre la zone oxique et anoxique, puisque l'augmentation de CH₄ (significative, entre 15 et 20 %) et de CO₂ (non significative, <10%) ne sont pas du même ordre de grandeur. Un autre argument qui fait le lien entre l'augmentation du CH₄ et des hypothétiques changements biologiques de la zone oxique (avec des conséquences dans les flux de matière), est l'augmentation des concentrations de phosphates (d'un facteur 3), de silice (de 30-35 %) et de calcium (25-30 %) dans les eaux profondes, et la diminution de ces éléments dans les eaux superficielles, durant ces 30 dernières années. Le rôle du phytoplancton et de la production primaire dans cette dynamique est abordé dans le Chapitre V.

La faune ichtyologique relativement pauvre (28 espèces, selon Snoeks *et al.* 1997) et, outre des études sur plusieurs espèces endémiques d'*Haplochromis* (cichlidés), on relève plusieurs travaux sur le petit clupéidé *Limnothrissa miodon* (Kaningini 1995, Marshall 1995, Spliethoff *et al.* 1983, Isumbisho *et al.* 2004). Son stock exploitable a été estimé à 2000 - 4000 tonnes/an, mais présente des variations saisonnières et interannuelles importantes (Marshall 1995, Spliethoff *et al.* 1983, Lamboeuf 1989, 1991, Lamboeuf *et al.* 1989).

Le lac Kivu est profond (max. 489 m). A cause de son altitude relativement élevée (1463 m), ses eaux de surface sont 2 à 4°C moins chaudes que celles des autres grands lacs de la région: 23 à 24.5 °C, par rapport aux 26 à 29°C des lacs Tanganyika, Mobutu et Edouard (Spigel et Coulter 1996). L'étude des sédiments (Haberyan et Hecky 1987) indique que le lac Kivu actuel est assez récent, du fait qu'il a été profondément modifié par l'intense activité volcanique et tectonique de cette région, il y a environ 5000 ans. Ces phénomènes auraient provoqué, via un réchauffement excessif, une anoxie et

l'extinction massive de la faune et de la flore. Ces phénomènes sont sans doute l'explication la plus plausible de la pauvreté de la faune ichthyologique du lac Kivu, relativement aux autres grands lacs du rift oriental.

C'est sans doute cette faible biodiversité du lac Kivu qui explique le peu d'attrait du lac pour les biologistes, alors que les lacs Malawi et Tanganyika ont fait l'objet d'études relativement nombreuses pour la région, avec des moyens techniques et scientifiques importants. Ainsi, la dynamique du plancton et de la chaîne trophique n'ont fait l'objet d'aucune étude approfondie, à suffisamment long terme, alors que l'exploitation durable de la ressource en poissons pélagiques est à l'évidence étroitement dépendante de la production planctonique. Au moment où débute notre étude, le fonctionnement écologique du lac est peu connu et forcément non intégré dans la gestion des ressources halieutiques. On est pourtant en droit de s'inquiéter: bien que les données sur le plancton soient fragmentaires, il semble bien que l'introduction de la sardine ait eu un impact majeur sur la composition et la biomasse du zooplancton (Dumont 1986). Avant l'introduction de *Limnothrissa*, le zooplancton était dominé par des copépodes et des cladocères de grande taille, dont *Daphnia curvirostris* (Verbeke 1957). Cette espèce n'a plus été retrouvée par la suite (Dumont 1986), ce qui suggère un impact majeur des sardines sur le zooplancton (e. g. Gliwicz 1984, 1991) et très probablement sur le reste de la chaîne trophique. Aujourd'hui, le zooplancton du lac Kivu est dominé par trois espèces de copépodes: *Thermocyclops consimilis* Kiefer, *Mesocyclops aequatorialis* Kiefer et *Tropocyclops confinis* Kiefer (Isumbisho et al. sous presse).

En ce qui concerne le phytoplancton, la référence la plus récente date de 1990 (Descy 1990) suite à une étude de courte durée réalisée dans le cadre d'un projet PNUD/FAO (RWA/87/012). Déjà dans ce rapport, la dispersion et le manque d'une série suffisamment longue de données ont été mis en évidence, de même que la nécessité d'une étude continue et approfondie des peuplements phyto et zooplanctoniques. En effet, la composition phytoplanctonique est pratiquement inconnue. La seule information fiable provient d'une campagne d'échantillonnage d'eau de surface réalisée au mois de mars de 1972 en différents points du lac (Fig. 3). Une dizaine d'espèces sont citées par Hecky et Kling (1987), notamment des cyanophytes filamenteuses (*Lyngbya circumcreta*, *L. bipunctata*, *Cylindrospermopsis*, *Anabaenopsis* et *Raphidiopsis*), des chlorophytes (*Cosmarium laeve*, *Tetraedron minimum*, *Oocystis lacustris* et *Gloeotila* sp.) et quelques péridiniens (*Peridinium inconspicuum*, *Gymnodinium pulvisculus* et *Glenodinium* sp.). Curieusement, les diatomées (*Nitzschia* et *Synedra*) ne sont signalées que dans une des baies isolées. Dans le Chapitre III, dédié à la diversité des algues pélagiques du lac Kivu, la composition floristique a été actualisée et complétée par des descriptions

morphologiques, des photos et des dessins. Ce chapitre fait l'objet d'un article, actuellement sous presse, dans *Cryptogamie-Algologie*.

Dans l'étude de Hecky et Kling (1987), la biomasse algale moyenne au lac Kivu (en poids frais) était de 1100 mg.m^{-3} (Fig. 3) soit plus de dix fois supérieure à celle estimée pour le lac Tanganyika dans la même étude (90 mg.m^{-3}), ce qui est quand-même surprenant. La méthode de prélèvement (uniquement en surface où par filet à plancton) et la durée probable de stockage des échantillons (prélèvement effectués en 1972 et résultats publiés en 1987) sont sans doute à l'origine de possibles sources d'erreur. L'absence de mesure de chlorophylle *a* rend impossible toute comparaison. Ces aspects sont discutés en profondeur dans le Chapitre IV.

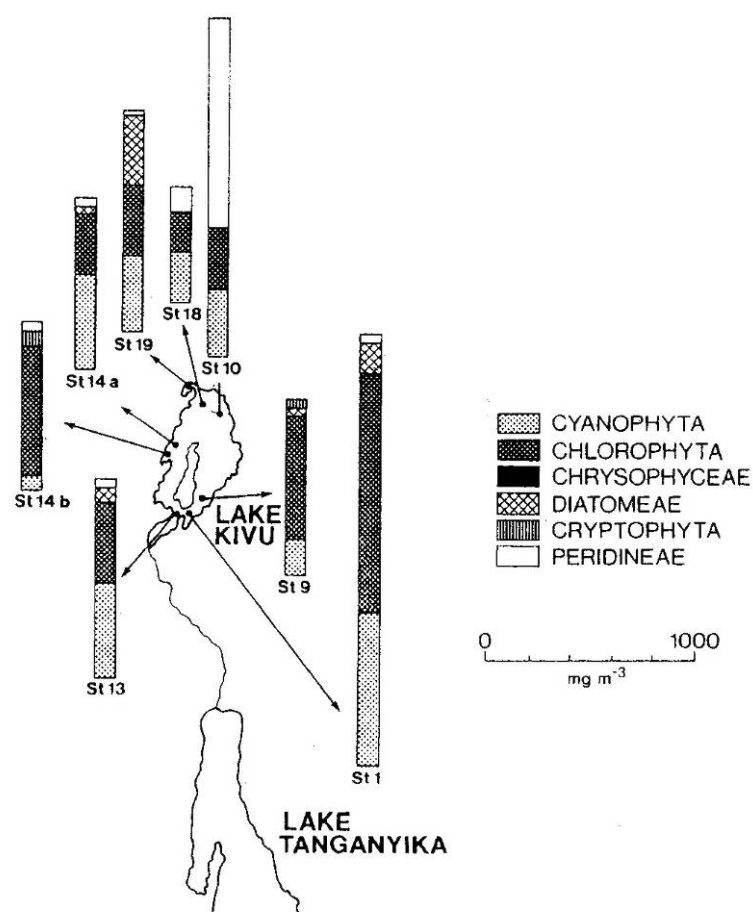


Figure 3: Biomasse (en poids frais) et composition algales au lac Kivu en mars 1972, selon Hecky et Kling (1987).

Des travaux sur d'autres grands lacs africains ont montré l'importance de la connaissance de la composition quantitative du phytoplancton pour la compréhension de son écologie (e. g. Hecky et Kling 1987, Kilham *et al.* 1986, Lewis 1996). Pourtant, le lac Kivu a été d'une certaine façon oublié, peut-être par ses caractéristiques uniques qui ne sont pas représentatives de la majorité des lacs est-africains. Une approche maintenant couramment utilisée pour interpréter l'écologie des communautés phytoplanctoniques présentes dans un système lacustre est celle des groupes fonctionnels, établie par Reynolds *et al.* (2002). Ce système, basé sur la définition d'assemblages de taxons dominants et sur la connaissance des conditions favorables et défavorables à leur développement, permet d'identifier des caractéristiques environnementales qui ont permis l'apparition de ces assemblages: conditions de lumière, disponibilité des nutriments, profondeur de mélange, pression de grazing, etc. (Appendice I du Chapitre IV). L'article dédié à l'écologie du phytoplancton du lac Kivu (Chapitre IV, publié dans *Journal of Plankton Research*) établit une analyse comparative des groupes fonctionnels qui se succèdent au cours des différentes saisons, dans les grands lacs de l'Afrique de l'est.

Comme tous les grands lacs africains, le lac Kivu semble présenter une production primaire importante contrastant avec des valeurs de biomasse algale relativement faibles (Hecky et Kling 1981). L'ensemble des mesures, malgré leur caractère nécessairement ponctuel vu les techniques utilisées, est cohérent et pointe vers une production primaire journalière légèrement supérieure à $1 \text{ g C.m}^{-2}.\text{j}^{-1}$ en zone pélagique. Malgré le nombre limité de données disponibles et leur caractère ponctuel, on peut avancer l'hypothèse qu'une des raisons expliquant le contraste entre forte production primaire et faible biomasse algale serait une forte limitation par le phosphore (suggéré par les quelques mesures effectués par Descy 1990). Cette limitation pourrait restreindre la biosynthèse et réduire la croissance algale, ce qui expliquerait la biomasse peu élevée. Il est aussi possible que l'assimilation brute de carbone par les cellules algales soit très importante vu les forts éclaircissements et la transparence de l'eau élevée, mais que leur excrétion et leur respiration réduisent leur photosynthèse nette, donc leur croissance. A ce sujet, Harris (1986) a bien résumé l'effet du métabolisme algal sur la production de biomasse dans la phrase suivante: "*Growth is not just photosynthesis and photosynthesis is not just C-fixation or O₂ release*".

Il est à noter qu'une production dissoute importante et les températures élevées toute au long de l'année pourraient favoriser le développement du bactérioplancton. Les travaux de Hecky et Kling (1981) ont déjà permis de souligner le rôle trophique probable des bactéries et du protozooplancton dans la zone pélagique du lac Tanganyika. Les résultats de Pirlot *et al.* (2005) sur ce lac vont dans le même sens, en démontrant qu'une proportion

élevée du carbone organique particulaire se trouvait dans des compartiments du réseau trophique microbien. Plusieurs campagnes de mesure en différents points du lac Kivu nous ont permis d'établir une évaluation de la production primaire journalière moyenne du lac, de la confronter aux mesures antérieures et de discuter les hypothèses expliquant l'augmentation de la concentration en méthane dans les eaux profondes (Schmid *et al.* 2005). Le chapitre V de notre travail traite de cet aspect, sous forme d'un manuscrit prêt à soumettre à une revue.

Enfin, une autre explication possible du "décalage" carbone assimilé/chlorophylle est la proportion significative de phytoplancton de très petite taille (picophytoplancton), dont les études précédentes ne font pas mention. Au lac Tanganyika, l'abondance de picoplancton est extrêmement élevée (Vuorio *et al.* 2003, Descy *et al.* 2005, Pirlot *et al.*, *soumis*), ce qui pose le problème du devenir trophique d'une bonne partie de la production primaire. Sur des lacs en zone tempérée (e.g. Lavalée et Pick 2002, Stockner *et al.* 2000), de nombreuses études ont bien démontré que la prise en compte du picophytoplancton peut être essentielle dans un bilan de biomasse ou de production primaire. Dans notre chapitre VI, grâce à une application de la cytométrie de flux (une "première" dans un lac tropical), nous évaluons l'importance du bactérioplancton et du picophytoplancton dans la colonne d'eau du lac Kivu, ainsi que leurs variations saisonnières et spatiales. Ces résultats sont discutés et comparés avec d'autres environnements aquatiques (océanique, estuarien et lacustre, à différentes latitudes).

Le principal objectif de ce travail fut de contribuer à l'acquisition d'une solide base de connaissances sur le phytoplancton (micro, nano et picophytoplancton) du lac Kivu et de son écologie, en termes qualitatif et quantitatif (composition, biomasse et production). Ces données, mises en relation avec les données limnologiques et météorologiques et en articulation avec l'étude du zooplancton mené par M. Isumbisho dans la même période, permettront une meilleure compréhension du fonctionnement écologique du lac Kivu.

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Chapitre II

Le phytoplancton tropical

Toute écologie est incomplète, parfois irrémédiablement incomplète, si on ne tient pas en considération les régions tropicales. Dans le cas de la limnologie, aucune typologie développée en région tempérée ne peut prétendre être universelle.

Traduit de "*Limnologia*"
R. Margalef
1983

Le phytoplancton tropical

Dans des nombreux ouvrages de référence sur la limnologie générale, une ligne imaginaire fait la distinction entre les zones dites tempérées et tropicales (ou pantropicales, entre les deux tropiques). Si bien que les gammes de température et radiation solaire y sont clairement supérieures, si l'on regarde strictement le phytoplancton (en diversité, production ou biomasse), les écarts ne sont pas aussi contrastés qu'en milieu terrestre. Souvent, en ce qui concerne le phytoplancton, le simple constat immédiat de: "*faible latitude*" égale à "*eaux plus chaudes et plus de luminosité incidente*", n'est pas suffisant pour surmonter une série de paramètres physiques ou environnementaux (comme par exemple la profondeur et étendue de la masse d'eau, l'altitude, les nutriments, la prédation, la structure de la chaîne trophique, les matières en suspension, etc., ...), ce qui rend une classification basée uniquement sur la latitude pratiquement impossible. L'idée que la plupart des espèces phytoplanctoniques ont une distribution subcosmopolite est souvent citée, surtout quand il s'agit d'une analyse écologique, que souvent ne tient compte que des espèces dominantes (Padisák 2004, Reynolds 1984).

Toutefois, il y a un certain nombre de considérations à grande échelle qui peuvent être émises, même si les études approfondies dans des zones tropicales sont considérablement moins nombreuses qu'en zones tempérées. Ce chapitre couvre quelques généralisations sur le plan de la distribution géographique de quelques espèces de phytoplancton et de son articulation avec l'ensemble des paramètres environnementaux, soit son écologie, tout d'abord dans les régions tropicales, puis, plus particulièrement dans les grands lacs anciens. Comme les seuls grands lacs anciens situés en zone tropicale sont les grands lacs d'Afrique de l'est (Margalef 1983), nous y prêterons une attention particulière.

Sans être exhaustifs, nous pouvons citer quelques espèces de phytoplancton à distribution typiquement pantropicale (selon Padisák 2004): toutes les espèces du genre *Cylindrospermopsis* (à l'exception de *C. raciborskii* et de *C. sinuosa*), *Anabaena fuellebornii*, *A. iyengarii*, *A. leonardii*, *A. oblonga*, *A. recta*, *Anabaenopsis tanganyikae*, *Aulacoseira agassizii*, *A. ikapoensis*, *Schoederia indica*, *Mallomonas bangladeshica*, *M. bronchartiana*, *M. tropica*, *Synura australiensis*, *Ceratium bracyceros* et *Peridinium gutwinskii*. On pourrait aussi citer des nombreux cas d'endémisme ou de distribution régionale, comme par exemple: *Aphanizomenon manguinii*, *Trichodesmus subtropicus* (dans la région des Caraïbes), *Cyclotella tasmanica*, *Tessellaria volvocina*, *Dinobryon gentariforme*, *Chrysonephele palustris*... (en Tasmanie). Dans la région des grands lacs, en Afrique de l'est, les cas d'endémisme régional sont assez communs, surtout en ce qui concerne les

diatomées des genres *Aulacoseira* (*A. ambigua*, *A. agassizii*, *A. nyassensis*), *Nitzschia* et *Surirella* (voir le Chapitre III pour plus de détail sur la distribution géographique des taxons présents au lac Kivu).

Sur le point de vue fonctionnement du système, les lacs situés à faible latitude se comportent de façon similaire à ceux des zones tempérées puisque les communautés phytoplanctoniques répondent exactement aux mêmes contraintes (Reynolds 1984). Les deux grandes différences sont l'intensité de lumière incidente et les températures des couches superficielles plus élevées. Ainsi, les lacs exposés au vent ou bien mélangés, ou encore l'épilimnion de ceux très profonds, sont typiquement dominés par des diatomées, desmidiées ou des grandes Chlorococcales (par exemple *Pediastrum*); Les cyanobactéries et dinoflagellés sont souvent dominants dans des milieux plus stables dans lesquels la zone euphotique est fréquemment plus profonde que la zone de mélange.

Malgré ce mode de fonctionnement similaire en termes de grands groupes d'algues, il existe des différences évidentes en ce qui concerne les taxons les plus représentés au sein de chaque groupe taxonomique en milieu tropical et tempéré, et ces différences ne sont pas nécessairement attribuables uniquement à la température. Les diatomées centriques (particulièrement *Aulacoseira* et *Cyclotella*) sont fréquemment plus abondantes que les formes pennées en zone tropicale. Au sein des dinoflagellés, *Peridinium* tend à remplacer *Ceratium*, et *Staurastrum* à 8, 12 ou 20 bras tendent à remplacer les formes à 4 ou 6 bras, plus communes en zone tempérée. Les cyanobactéries sont généralement plus présentes (en abondance relative ou absolue) dans des lacs tropicaux. Quelques espèces à occurrence sporadique dans des latitudes plus élevées sont très régulièrement observées dans les assemblages phytoplanctoniques tropicaux (*Anabaena*, *Planktolyngbya*). *Arthrospira* (ex-*Spirulina*) est un autre genre très commun dans des lacs peu profonds et riches en nutriments (souvent salins). L'écologie de ce taxon trouve en quelque sorte un parallèle avec certaines *Oscillatoria* en zone tempérée (Reynolds, 1984).

Evidemment, l'amplitude des variations des facteurs environnementaux dans les régions tropicales est beaucoup plus faible que celle observée en milieu tempéré. Un exemple très parlant c'est l'amplitude thermique annuelle des couches de surface: souvent plus que 20°C en zone tempérée, contre un maximum de 5°C en région tropicale. Kilham & Kilham (1990) résument magistralement ces différences et ses conséquences sur le fonctionnement des systèmes aquatiques dans un papier intitulé "*Endless summer: internal loading processes dominate nutrient cycling in tropical lakes*". Une de leurs principales conclusions est que les taux de régénération de nutriments dans les lacs tropicaux est largement supérieur aux taux de pertes, surtout dans des lacs avec des zones de mélange de plus de 50 m. Ainsi, les processus

biologiques domineraient les cycles de nutriments dans les lacs tropicaux, au contraire des lacs tempérés, où les processus physiques seraient prédominants, au moins pendant une bonne partie de l'année.

Logiquement, ces conditions "*éternellement constantes*" (surtout sur les grands lacs anciens proches de l'équateur) pourraient, d'une part, conduire à une considérable réduction du nombre d'espèces présentes puisque celles-ci doivent être extrêmement bien adaptées, et d'autre part, entretenir un certain type d'assemblage pendant des périodes très longues (Melack 1979). Hambright et Zohary (2000) ont démontré que la fréquence et la durée des perturbations physiques, alliées à la compétition interspécifique étaient les principaux facteurs qui contrôlaient le degré de diversité du phytoplancton lacustre. Théoriquement, les stratégies *r* (des "*pionniers*" selon Reynolds 1997) auraient moins de chances de se développer dans des milieux tropicaux très stables. Ainsi, même si d'autres facteurs (comme par exemple l'âge géologique du lac) ont une influence indéniable sur la diversité du phytoplancton lacustre, il n'est pas rare de constater que les lacs tropicaux ont une diversité inférieure à celle des lacs tempérés. Ceci est une des conclusions des travaux de Lewis (1978, 1990, 1996) aux lacs Lanao (Philippines) et Valencia (Venezuela).

Pourtant, si l'on analyse plus en profondeur la stratification des colonnes d'eau en zone tropicale et tempérée, la conclusion est que, *a priori*, les premiers sont beaucoup plus sensibles aux perturbations externes, notamment météorologiques et climatiques. Puisque les différences de densité sont de plus en plus importantes avec l'augmentation de la température (Fig. 1). En milieu tropical, des gradients peuvent se former plus vite et approcher plus la surface. De la même façon, une petite chute de la température (pendant la nuit, par exemple) génère une instabilité dans la colonne d'eau. Ainsi, le phénomène de stratification journalière (ou *atelmixis*, selon Barbosa & Padisák 2002) est très fréquent en milieu tropical. Souvent le résultat est une double stratification: une saisonnière ou pérenne (dans les lacs méromictiques) et une journalière, pendant les heures de fort ensoleillement et en absence de vent ou de pluie importants.

Melack (1979) a montré qu'il n'existe pas de gradient de latitude en ce qui concerne la périodicité des variations de production primaire au cours de l'année (même si les causes de ces variations sont différentes d'une région à l'autre). Par contre, les lacs tropicaux repris dans cette étude se sont montrés plus productifs que les lacs tempérés, si l'on intègre le cycle annuel complet. La même tendance a été vérifiée en termes de biomasse par Lewis (1990). La périodicité des successions algales dans les lacs tropicaux peut être divisée en trois grands types: (1) saisonnière, liée à l'augmentation des débits des rivières, aux fortes pluies ou à l'intensité du vent qui influencent le mélange vertical; (2) journalière, quand la variation au cours d'une

journée dépasse les variations saisonnières, ce qui veut dire que les variations sont d'amplitude très faible; ou plus rarement, (3) abruptes, quand une population très stable (pendant au moins 10 générations, soit ~30 à 100 jours) est brusquement remplacée par une autre qui restera aussi pendant une longue période. Un exemple qui illustre bien cette dernière situation (relativement rare), est le lac Nakuru (Kenya), où des assemblages dominés par *Arthrospira* ont été observés pendant trois ans de suite, puis remplacés par d'autres assemblages, pour revenir deux ans plus tard (Melack 1979).

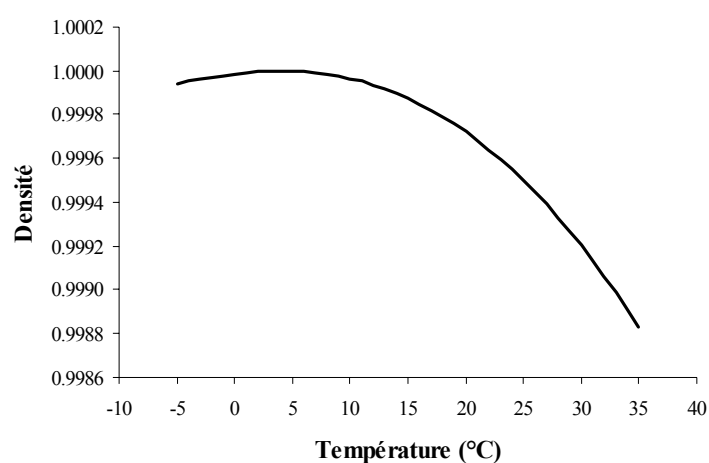


Figure 1: Variation de la densité en fonction de la température dans l'eau pure. A des températures élevées (comme dans les lacs tropicaux), les gradients de densité se forment plus facilement que dans les eaux plus froides.

La variabilité interannuelle semble aussi plus importante dans les régions tropicales. Malheureusement les études pluriannuelles sont extrêmement rares dans ces régions, mais les travaux de Lewis (1978, 1990, 1996) aux lacs Lanao (Philippines) et Valencia (Venezuela), de Richerson *et al.* (1986) au lac Titicaca (Pérou et Bolivie) et de Talling (1986) dans les grands lacs africains ont tous démontré que l'amplitude des variations interannuelles pouvait être plus importante que celle des variations saisonnières.

Autre que la latitude, l'altitude peut aussi être un facteur déterminant pour la distribution géographique des espèces phytoplanctoniques. Dans une étude phytogéographique dans la région Indo-Malayenne, Vyverman (1996) a mis en évidence un gradient de composition phytoplanctonique en fonction de l'altitude. Les masses d'eau de basse altitude sont riches en espèces

cosmopolites et pantropicales, mais entre 1700 et 2500 m d'altitude les taxons tropicaux sont progressivement remplacés par des espèces typiques de zones tempérées.

Toute la région des grands lacs en Afrique de l'est est surélevée par rapport au niveau de la mer, mais vu que les lacs situés le plus haut se trouvent plus proches de l'équateur (à l'exception du lac Albert), les différences de température dans les couches superficielles sont relativement faibles (Tab. I). Toutefois, leur composition et biomasse phytoplanctoniques sont distinctes (voir chapitre IV); Hecky & Kling (1987) ont rassemblé des données de phytoplancton de cinq lacs de l'Afrique de l'est (Albert, Edouard, Kivu, Tanganyika et Malawi) et définit quelques grandes lignes au sujet de leur écologie. Le cycle annuel est marqué par un mélange plus accentué durant la saison sèche dans tous les lacs, augmentant la disponibilité en nutriments mais réduisant l'accès à la lumière. Dans l'ensemble, la biomasse est plus élevée pendant cette saison même si le régime hydrodynamique très complexe (*upwelling*, vagues internes, *tilting*, etc.) dans certains lacs peut provoquer des épisodes de développement plus tardif.

Tableau I: Quelques généralités sur les grands lacs de l'Afrique de l'est (Zm = zone de mélange). Adapté à partir de Hecky & Kling (1987).

Lac	Latitude ; Longitude	Température dans la Zm (°C)	Altitude (m)
Albert	1°45' N ; 30°23' E	27.4 – 29.0	616
Edouard	0°30' S ; 29°45' E	24.7 – 27.2	912
Victoria	1°40' S ; 33°10' E	23.8 – 25.8	1135
Kivu	2°12' S ; 29°16' E	23.0 – 24.5	1460
Tanganyika	6°00' S ; 29°30' E	24.0 – 27.0	773
Malawi	12°30' S ; 34°30' E	22.1 – 22.3	474

Selon Hecky & Kling (1987) les lacs Albert, Tanganyika, et Malawi ont des biomasses plus faibles (au tour de 100 mg.m⁻³ en poids frais) que les lacs Kivu (1100 mg.m⁻³ en poids frais) et Edouard (>2000 mg.m⁻³ en poids frais). Dans cette étude, les cyanobactéries filamenteuses et coccoïdes étaient dominantes aux lacs Kivu et Edouard, respectivement. Durant les périodes de mélange profond aux lacs Albert, Malawi et Tanganyika, les diatomées dominantes appartenaient aux genres *Stephanodiscus* et *Nitzschia*. Curieusement, les espèces du genre *Aulacoseira* étaient absentes du lac Albert, probablement à cause des faibles concentrations en silice. Par contre, aux lacs Tanganyika et Malawi, *Aulacoseira* spp. étaient présentes durant des périodes d'*upwelling*.

A fin de compléter cette analyse, il faut citer le travail de Talling (1987) au lac Victoria: à l'époque, les diatomées des genres *Surirella*, *Cymatopleura* et *Nitzschia* dominaient pendant la saison sèche, alors que les cyanobactéries (comme *Anabaena*) étaient plus présentes en saison des pluies. Les algues vertes, par contre, étaient bien représentées toute l'année par un bon nombre d'espèces. Toutefois cette analyse ne semble plus être d'actualité. L'introduction de la perche du Nil et la croissante pression anthropogène sur les rives du lac Victoria ont transformé l'écosystème, avec des conséquences incontestables sur la composition et biomasse phytoplanctoniques (Kling *et al.* 2001, Hecky 1993). Les cyanobactéries (surtout *Anabaena* et *Cylindrospermopsis*) persistent durant toute l'année, avec des biomasses considérablement supérieures à celles observées par Talling dans les années 80.

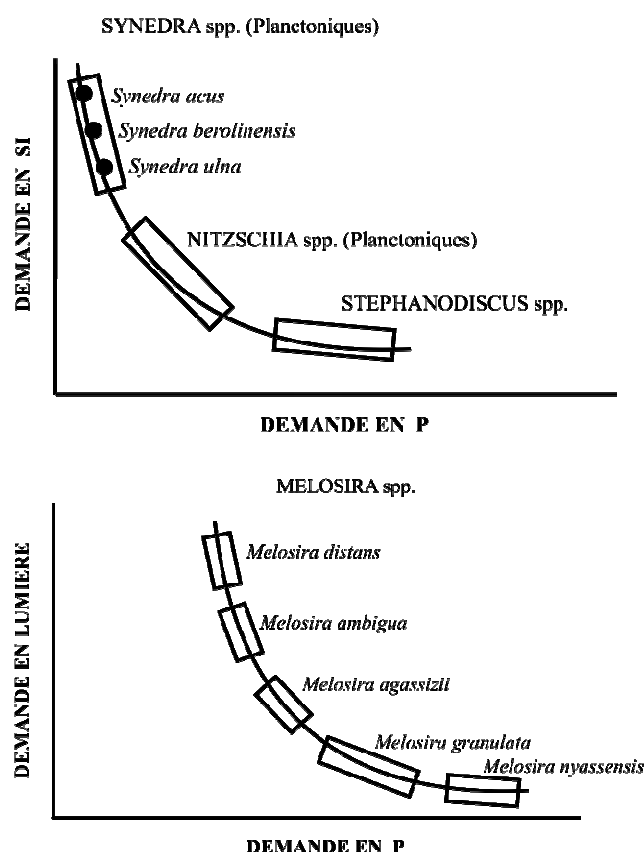


Figure 2: Relation hypothétique de la croissance des diatomées d'Afrique en fonction de la disponibilité de phosphore et silice et lumière (traduit de Kilham *et al.* 1986). "Melosira" correspond à "Aulacoseira" dans le texte.

Kilham *et al.* (1986) ont étudié la relation entre les diatomées africaines et les ratios Si:P. Les formes pennées plus longues (comme *Fragilaria*, ex-*Synedra*), plus exigeantes en silice, sont favorisées dans les lacs où le ratio Si:P est élevé, contrastant avec les diatomées centriques (comme *Stephanodiscus*) qui, moins exigeantes en Si, se développent dans les eaux à faible Si:P (Fig. 2). Les espèces du genre *Aulacoseira* seraient plutôt distribuées selon un gradient de lumière:P; *A. distans* et *A. ambigua* sont favorisées en conditions de forte lumière et faible concentration en phosphore, au contraire de *A. nyassensis* qui peut supporter des régimes de faible lumière mais nécessite beaucoup de phosphore; *A. agassizii* et *A. granulata* se positionnent dans une situation intermédiaire (Fig. 2). De plus, la taille des pores associés à chaque espèce seraient liés au régime lumineux: *A. distans* et *A. ambigua* possèdent de très petits pores et demandent beaucoup de lumière; *A. nyassensis* possédant des pores plus larges, peut croître dans des conditions de lumière moins favorables.

La limnologie tropicale présente ainsi des paradigmes parfois contradictoires à ceux de la limnologie dite "*classique*" (de zone tempérée). En 1898, Huitfeld-Kaas a établi une des premières lois de la limnologie: *les lacs peu profonds sont plus productifs que les lacs profonds*. Cette loi a été vérifiée à plusieurs reprises en zone tempérée dans des études à grande échelle comme celle réalisée par Fee (1979). Kilham & Kilham (1991) ont justement prouvé que les lacs tropicaux violent cette première loi de la limnologie, puisque la production primaire dans plusieurs lacs Africains s'était avérée équivalente aussi bien dans des lacs grands et profonds que dans les petits et pas très profonds. Dans le Chapitre VI dédié au picoplancton dans les régions tropicales, un autre paradigme de ce type est mis en cause par des résultats récents.

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Chapitre III

La diversité du phytoplancton pélagique du lac Kivu

... Ses eaux claires et transparentes sont un véritable désert...

"Exploration du Parc National Albert"
H. Damas
1935-1936

*Species diversity of pelagic algae of Lake Kivu
(Eastern Africa)*

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Chapitre IV

L'écologie du phytoplancton du lac Kivu

The great amount of nutrients trapped within the oxygen-free deep water of Kivu was strikingly demonstrated some years ago by a Belgian experiment for the commercial production of methane by pumping bottom water to the surface. This stimulated an abundant growth of phytoplankton and attracted a great many fish (pers. Comm. from A. Carpart). There is no doubt that the productivity of the deep and permanently stratified tropical lakes could be very greatly increased if means could be found for circulating a large amount of the lower water.

"The Inland Waters of Tropical Africa"
L. C. Beadle
1974

Phytoplankton ecology of Lake Kivu (Eastern Africa)

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Abstract

This paper reports a three year (2002-2004) survey on limnology and phytoplankton of Lake Kivu, a meromictic lake of the East African Rift, with peculiar geophysical and geochemical features. The phytoplankton survey combined HPLC analysis of marker pigments, flow cytometry, and epifluorescence and electron microscopy. Availability of similar data from a parallel study on Lake Tanganyika allowed a detailed comparison of phytoplankton composition and ecology in these two lakes. Lake Kivu combines a relatively shallow euphotic layer, usually smaller than its mixed layer, with relatively low nutrient content of the mixolimnion, and with unstable thermal stratification of the surface waters. With an annual average chlorophyll *a* in the mixed layer of 2.2 mg m^{-3} and low nutrient levels in the euphotic zone, the lake is clearly oligotrophic. As in other large African Rift lakes, seasonal variations of algal biomass and composition occurred, with substantial inter-annual variations, mainly related to variability of wind pattern and water column stability. Contrary to earlier reports which described Lake Kivu phytoplankton as dominated by cyanobacteria and green algae, we found that diatoms were the dominant group in the lake, particularly during the dry season episodes of deep mixing. During the rainy season, the stratified water column, with high light and lower nutrient availability, favoured dominance of filamentous, diazotrophic cyanobacteria and of picocyanobacteria, which represented a substantial fraction of autotrophic biomass. Different phytoplankton functional groups were identified in Lake Kivu, which place it in an intermediate position between the oligotrophic lakes Tanganyika and Malawi and the more eutrophic Lake Victoria. However, the dominant diatoms of Lake Kivu (*Urosolenia* sp. and the needle-like *Nitzschia bacata* Hust. and *Fragilaria danica* Lange-Bert.) are known from oligotrophic, P-deficient African lakes, and do not seem to be adequately included in the current functional classifications of freshwater phytoplankton.

Introduction

Lake Kivu, located between Rwanda and the Kivu Province (Democratic Republic of Congo), is the smallest of the East African Great Lakes. It is a deep (max. 489 m), meromictic lake, with an oxic mixolimnion up to 70 m, and a deep monimolimnion rich in dissolved gases, particularly methane (Tietze *et al.*, 1980; Schmid *et al.*, 2005). Lake Kivu has unique limnological characteristics, with temperature and salinity increasing in the deep water layers, due to the input of geothermal sources at the bottom of the lake (Degens *et al.*, 1973; Spigel and Coulter, 1996). As a consequence of high altitude (1463 m), the surface waters are slightly cooler than in other East African Great Lakes (24.9°C vs. 26.8°C in Lake Tanganyika). At present, the fish community of Lake Kivu comprises not more than 28 species, probably as a result of intense volcanic and tectonic activity in this region during the late Pleistocene and Holocene (Haberyan and Hecky, 1987).

By contrast with the knowledge of zooplankton (Kaningini *et al.*, 2003, Isumbisho *et al.*, *submitted*) and fish biology (de Jongh *et al.*, 1983; Spliethoff, 1983; Marshall, 1991; Snoeks *et al.*, 1997; Isumbisho *et al.*, 2004) that was promoted by the development of fisheries, the overall ecology of Lake Kivu is far from well known. In particular, data on phytoplankton, primary production and nutrients are scarce, and long-term surveys were never conducted. Hecky and Kling (1987) reported phytoplankton fresh weight biomass from 550 up to 2100 mg m⁻³ from March 1972 surface samples. Cyanobacteria and Chlorophytes accounted 70 to 90% of total biomass. The northern part of the lake was rich in peridinians, and diatoms were abundant only in an isolated bay (Kabuno bay). Therefore, the planktonic assemblage of Lake Kivu at that time appeared to be similar to that of the other East African Great Lakes, i.e. dominated by Chlorophytes and cyanobacteria, with diatoms at lower abundances (Hecky and Kling, 1987). Different diatom taxa were reported from the north and the south of the lake, and related to differences in Si:P dissolved ratio (Kilham *et al.*, 1986). In particular, needle-like *Fragilaria* and *Nitzschia*, favoured by high Si:P, dominated in the largest northern basin and in Kabuno Bay, while *Stephanodiscus* sp. was found in the southern Bukavu Bay, where dissolved Si:P was much lower. Another trait of Lake Kivu was its higher algal biomass than in the larger lakes Malawi and Tanganyika (Hecky and Kling, 1987), and a slightly higher primary production: 1.44 g C m⁻² d⁻¹ reported by Beadle (1981), which is actually an estimate based on the few measurements available at the time (Degens *et al.*, 1973; Jannasch, 1975). Based on palaeolimnological studies, Haberyan and Hecky (1987) have reconstructed the past ecology of Lake Kivu and have shown considerable changes in diatom assemblages from the sediment record, related to the volcanic activity in this region for the past few thousand years.

In this paper, we present limnology and phytoplankton data from a three-year survey (2002-2004) of Lake Kivu. Phytoplankton biomass and composition were assessed using HPLC analysis of marker pigments, processed with CHEMTAX. As a parallel study was carried out in Lake Tanganyika using the same techniques and sampling schedule (Descy *et al.*, 2005), we draw a comparison of the present phytoplankton ecology of these two Rift lakes. We conclude with a discussion on the phytoplankton assemblages of other large lakes from this region, in particular Lake Victoria and Lake Malawi.

Method

Sampling sites

Samples were collected in the 0-100 m water column, at 10 m intervals, with a 6-L Van Dorn bottle at Ishungu, in the southern basin of Lake Kivu (02°33.94'S, 28°97.65'E), twice a month from February 2002 to February 2005. In addition, four cruises took place: two during the rainy season (RS, 27 - 31 January 2003 and 23 February - 6 March 2004) and two in the dry season (DS, 26 August - 2 September 2003 and 9 - 12 September 2004). Cruises sampling points (Fig. 1) were distributed in the different basins: northern basin (01°68.08'S, 29°15.69'E), Eastern basin (01°96.17'S, 29°12.26'E) and Western basin (02°22.79'S, 28°97.35'E) as well as the two main bays, Kabuno Bay (02°61.62'S, 28°08.22'E) and Bukavu Bay (02°46.63'S, 28°85.71'E). The sampling protocol and equipment were identical to those used at the Ishungu (southern basin) station. Meteorological data were collected only for 2003 and 2004, by a Davis Weather Wizard III station (Davis Inotek Instruments, Baltimore, USA).

Limnological profiles

Limnological profiles using CTDs (Hydrolab DS4a, Loveland, USA), transparency measurements (Secchi disk depth) and nutrient analysis (using standard spectrophotometric techniques, [A.P.H.A., 1992], or Macherey-Nägel [Düren, Germany] analytical kits) were carried out during regular sampling at the Ishungu site and at all sites during the cruises. Detection limits for nutrients were: SRP (soluble reactive phosphorus): 0.16 µM; NH₄⁺: 0.29 µM; NO₃⁻: 1.43 µM; NO₂⁻: 0.14 µM. Euphotic depth (Z_{eu}, depth at which light is 1 % of subsurface light) was derived from estimates of the vertical light attenuation coefficient from Secchi depth, using a coefficient ($k = 1.34 / \text{Secchi disk depth}$) obtained by calibration with measurement of PAR downward attenuation with LICOR quantum sensors at each sampling site (n = 16). Average light in the mixed layer (expressed in µE m⁻² s⁻¹) was calculated according to Riley (1957):

$$I_{Z_m} = I_0 (1 - e^{(-Z_m \cdot K_e)}) / Z_m \cdot K_e$$

Where Z_m is the depth of the mixed layer, K_e the coefficient of light extinction, and I₀ the mean incident light.

Depth of the mixed layer (Z_m) was estimated from the depth of the top of the thermocline, as shown by the temperature and oxygen vertical profiles obtained with the CTDs. Thermal resistance to mixing (amount of work required to completely mix a water column with different temperatures) was calculated for the 0-100 m layer according to Birge (1910 and 1916):

$$\text{Work (ergs)} = (AC^2/12) \cdot (\rho_2 - \rho_1)$$

Where A is the area of the water column surface (1 cm^2 in this case), C is the height of water column (cm), ρ_2 is water density at the bottom of the water column, and ρ_1 the water density at the top of the water column (both in g cm^{-3}).

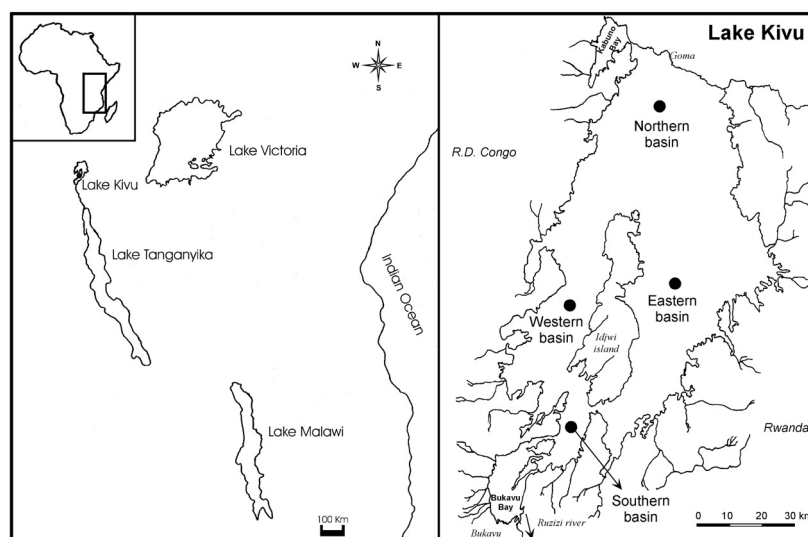


Figure 1: Geographic situation of Lake Kivu. Black dots are the sampling sites (see text for GPS coordinates).

Pigment analysis

In addition to water column samples every 10 m, occasional additional sampling was done at 5 m, in order to get a more detailed vertical distribution of the algae. Samples for pigment analysis followed a procedure described in Descy *et al.* (2000): 3 L were filtered on Whatman GF/F (Maidstone, U.K.) or Macherey-Nägel (Düren, Germany) GF/5 filters, of $0.7 \mu\text{m}$ pore size. Pigment extraction was carried out in 10 mL 90 % HPLC grade acetone. After two 15 min sonications separated by an overnight period at 4°C in the dark, extracts were stored in 2 mL amber vials in a freezer (at -25°C) for several months (under the regular sampling scheme) or for a 2-3 weeks at most (for the cruise samples). Transport to Belgium was carried out on ice in cooler boxes. HPLC analysis was carried out using the Wright *et al.* (1991) gradient elution method, with a Waters system comprising a PDA detector and a fluorescence detector. Calibration was made using commercial external standards (DHI, Denmark). Carotenoids not present in the standard were quantified against fucoxanthin, using as relative response the ratio of the specific absorbance coefficients at 440 nm (Jeffrey *et al.*, 1997) in methanol. Pigment concentrations were processed with the CHEMTAX software (CSIRO Marine Laboratories, Hobart,

Australia; Mackey *et al.*, 1996) using input ratio matrices adapted for freshwater phytoplankton (Descy *et al.*, 2000). Lake Kivu data processing followed a procedure similar to that of Descy *et al.* (2005), allowing estimating chlorophyll *a* (Chl *a*) biomass of Chlorophytes, Chrysophytes, diatoms, Cryptophytes, dinoflagellates and cyanobacteria, taking into account variations of pigment ratios with season and depth.

Picophytoplankton counts (flow cytometry)

Samples for flow cytometry counts were taken during cruises. Four milliliters of water were collected and fixed immediately with cold 10% glutaraldehyde (final concentration 1%), left in the dark for 10 min at room temperature and stored at -20°C. We used a FacsCalibur (Becton Dickinson, USA) flow cytometer equipped with a 15 mW Argon-ion laser (488 nm emission). At least 30000 events were acquired for each subsample (usually 90000 events). Fluorescent beads (1 µm, Fluoresbrite carboxylate microspheres, Polysciences Inc., Warrington, PA) were added at a known density as an internal standard. The bead standard concentration was determined by epifluorescence microscopy. We identified four different populations of picoautotrophic organisms: three picocyanobacteria (one *Synechococcus*-like that alone accounted for more than 70% of the events, and two undetermined picocyanobacteria, probably 2 and 4-celled *Synechococcus* colonies) and one picoeukaryote. These four groups of algae were easily identified in plots of SSC (side scatter) vs. FL3 (red fluorescence), and FL2 (orange fluorescence) vs. FL3 (red fluorescence). Data acquisition and analysis were performed with the program Paint-A-Gate (Becton Dickinson, USA). The flow cytometry results for the *Synechococcus*-like population were confirmed by epifluorescence microscopy counts performed in some of the 0-20 m samples (correlation between the results from the two methods was highly significant: $r = 0.99$, $P < 0.05$, $n = 20$, with a 1.01 slope).

Results

Regional climate and water column structure

Seasons, with their large variation in wind speed and precipitation, are the major factor responsible for variability in the water column structure of east African Great Lakes (Beadle, 1981). As in all Eastern Africa, the Lake Kivu region is characterized by a windy main dry season (long DS, from June to September) and a calmer rainy season (RS, October-May). In the Kivu region, however, there is a short DS around January when the winds can be stronger than in typical RS conditions. During DS, the daily range of air temperature increases, minimum temperatures occur (at night), but the mean air temperature is higher. The rest of the year (RS) temperatures are more stable, around 19°C, thanks to the high air humidity. Another feature of DS in relation to the hydrodynamic regime of Lake Kivu is the south-eastern dominant wind that reaches maximum velocity around July every year (Fig. 2).

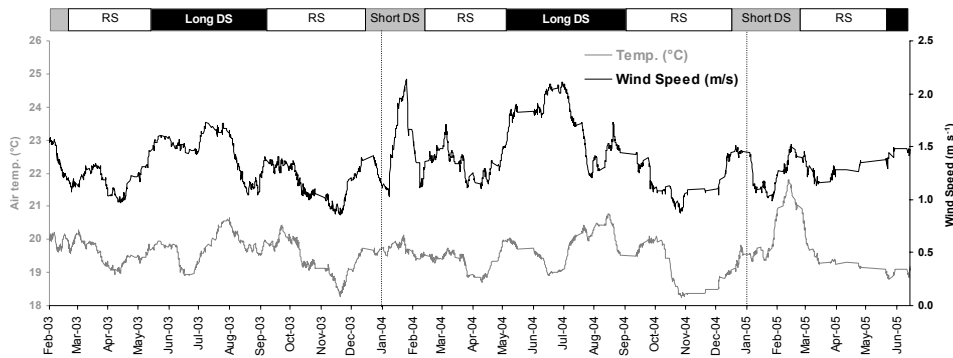


Figure 2: Wind speed and air temperature in the southern end of Lake Kivu (Bukavu, D. R. Congo) and season delimitation in 2003 and 2004.

During the study period, Lake Kivu mean surface water temperature was 24.9°C, while the mean annual air temperature was 19.6°C. Although the highest air temperatures were registered during DS, epilimnion temperature declined throughout this period, mainly due to evaporation and night cooling, attenuating the temperature density gradient, so that deeper vertical mixing occurs. However, the depth of the mixed layer is limited to 60-70 m (depth of the chemocline), which presents a steep salinity gradient (Fig. 3). Conductivity in the oxic layer oscillates between 950 and 1300 $\mu\text{S cm}^{-1}$, but it doubles at 100 – 120 m depth, below the chemocline. The pH is also a good indicator of this chemical gradient, showing an extreme contrast from around pH 9.1 in the oxic layer, but dropping to pH 6.5 at 100 m.

Along with weakening of the temperature-density gradient in the mixolimnion, the dominant south-eastern winds, more intense during DS, contribute to thickening of the mixed layer. The configuration of Lake Kivu, with a restricted littoral zone and several high mountains surrounding the lake basin, makes the eastern and northern basins more exposed to the DS winds. As a result, seasonal changes in the mixed layer were more diverse in these two basins. At the Ishungu site in the southern basin, the mixed layer depth during RS is usually around 25 m, while in DS it can reach 60 m (Fig. 3).

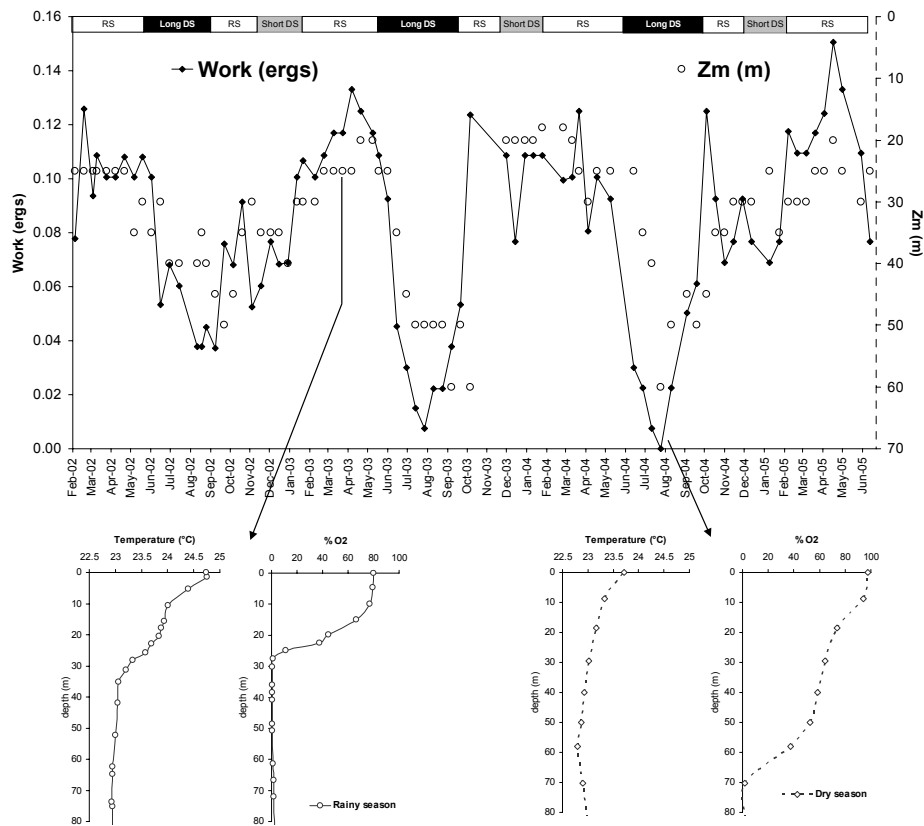


Figure 3: Mixed layer depth, Z_m (open circles) and thermal resistance to mixing (line) variation along seasons in Lake Kivu in the southern basin during the 2002 – 2004 period. Arrows indicate examples of rainy season (RS) and dry season (DS) temperature and oxygen profiles.

Bukavu Bay is not meromictic (Tietze *et al.*, 1980). It has a maximum depth of 100 m and complete mixing could be observed during the DS. On the other hand, Kabuno Bay has a permanent chemocline at 12 m, whatever the

wind strength (data not shown). This bay is actually isolated from the rest of the lake; the only connection is a 150 m wide, 16 m deep, channel (Damas, 1937).

By comparison, the vertical mixing regime off Kigoma (northern basin of Lake Tanganyika) is more variable due to internal waves and to the particular hydrodynamic complexity of this lake, although the depth of the mixed layer varies in a similar range to that of Lake Kivu: 25 m in RS, down to 80 m in DS (Descy *et al.*, 2005).

Nutrient and light conditions

Lake Kivu is less transparent than Lake Tanganyika (fig. 4): mean Z_{eu} at Ishungu in the southern basin was 18 m, while in Lake Tanganyika off Kigoma it was 39 m during the same period. The transparency tended to increase during DS in Lake Kivu. As a consequence of different degrees of light penetration the $Z_m:Z_{eu}$ ratio was usually higher in Lake Kivu (range at Ishungu: 0.9-3.8; mean 1.9) than in Lake Tanganyika (range: 0.42-1.88; mean 1.0). The DS mixing pattern is not similar in the two lakes and the maximum $Z_m:Z_{eu}$ ratio occurs later in Lake Kivu (southern basin) than off Kigoma (Lake Tanganyika) (Fig 4). Consequently, the average light in the mixed layer was about half in Lake Kivu compared with Lake Tanganyika (Fig. 5), and its temporal variation was different.

Nutrient concentrations in the euphotic zone of Lake Kivu were often below detection limits, but during DS, soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) mean concentrations reached detectable levels. Figure 6 shows DS vertical profiles of nutrient concentration in Lake Kivu compared to those in Lake Tanganyika. SRP in the euphotic zone of Lake Kivu was on average 0.44 μM in RS and 0.75 μM in DS; mean SRP in the euphotic layer of Lake Tanganyika was 0.19 (RS) – 0.43 (DS) μM in 2002 off Kigoma, with a DS maximum of 1.22 μM . Average DIN in Lake Kivu was 2.42 μM and 3.29 μM in RS and DS, respectively. This contrasts with lower DIN in Lake Tanganyika off Kigoma (mean RS DIN 0.48, mean DS DIN 0.69 μM). The difference stems from higher concentration of ammonium in the euphotic layer of Lake Kivu, while this nitrogen form was most often below detection level in Lake Tanganyika.

Dissolved reactive silica (DRSi) in the euphotic layer was a major difference between these two lakes: in Lake Kivu mean DRSi concentration was 100.1 μM vs. 25.5 μM in Lake Tanganyika. Naturally, this affects the dissolved Si:P ratios in the euphotic layer, which was 154 Lake Kivu Si:P vs. 103 in Lake Tanganyika.

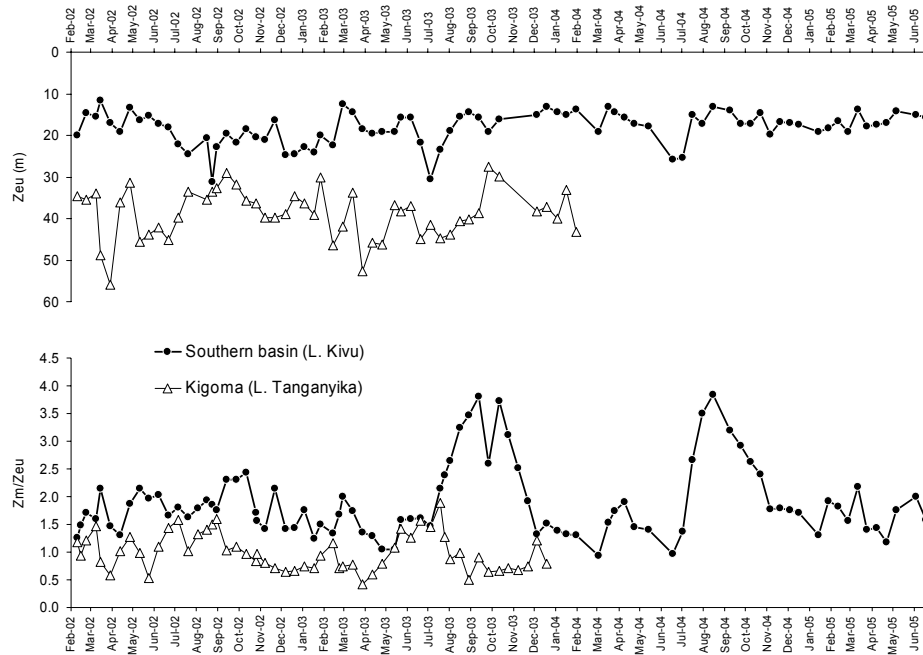


Figure 4: a) Euphotic depth (Z_{eu}) evolution in Lake Kivu in the southern basin (dots) and Lake Tanganyika off Kigoma (open triangles) during 2002 and 2003. b) Mixed layer depth (Z_m) : Euphotic depth (Z_{eu}) ratio at the same sites during the 2002-2004 period.

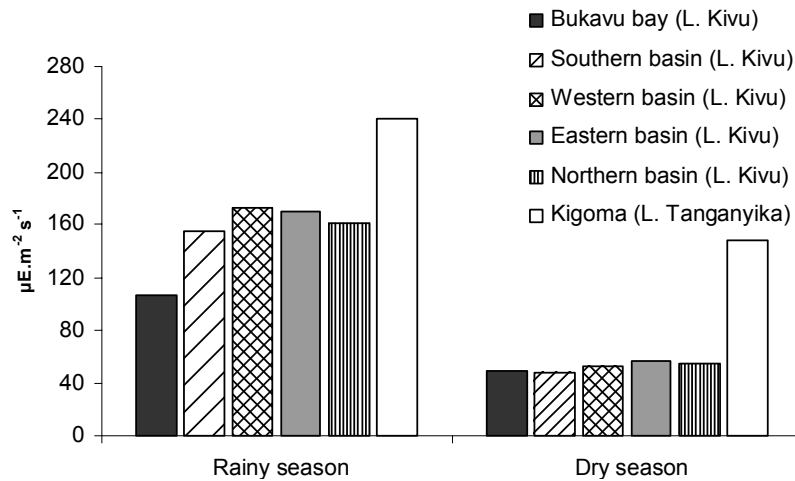


Figure 5: Average light in the mixed layer in lakes Kivu and Tanganyika off Kigoma for dry and rainy seasons.

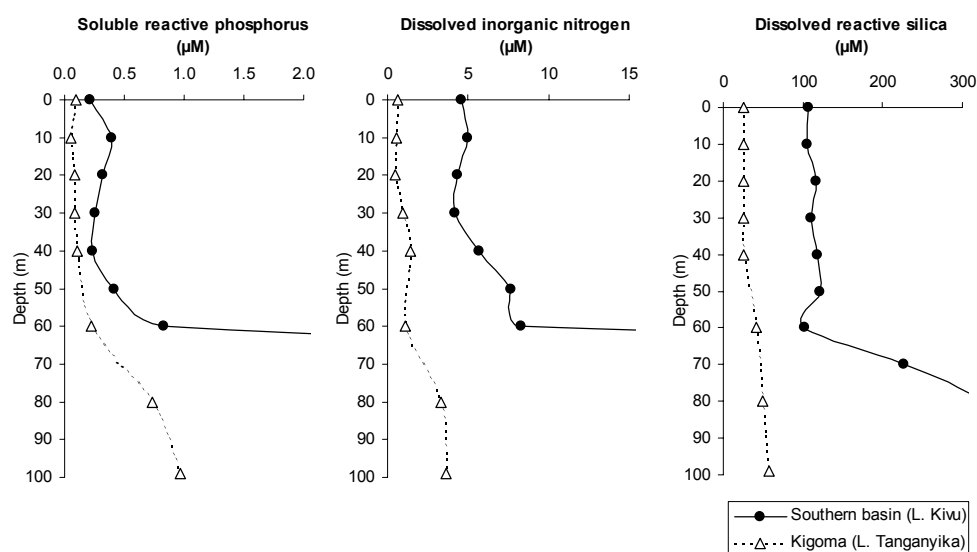


Figure 6: Main macronutrient profiles in Lake Kivu in the southern basin (dots) and Lake Tanganyika off Kigoma (open triangles). Measurements for depths below 60 m in L. Kivu are not depicted, because values are much higher than the detailed scale permits ($>10 \mu\text{M P-PO}_4$ for SRP at 70 m, $>130 \mu\text{M N}$ for DIN at 70 m, $>320 \mu\text{M Si}$ for DRSi at 80 m).

Phytoplankton biomass and composition

Phytoplankton biomass (Chl *a*) and composition were determined by HPLC pigment analysis followed by CHEMTAX processing of marker pigment concentrations. The results expressed in $\text{mg Chl } a \text{ m}^{-2}$ were determined by multiplying the average Chl *a* concentration (mg m^{-3}) within the 0-60 m layer by 60 m in order to obtain integrated values of the whole water column in a highly variable productive layer. During the 2002-2004 period (Fig. 7), Chl *a* average concentration was 76.9 mg m^{-2} in Lake Kivu at the southern basin vs. 37.4 mg m^{-2} in the 0-100 m layer off Kigoma (Lake Tanganyika) for the 2002 - 2003 period. Large temporal variations occurred in Lake Kivu: a large difference was observed in 2003 and 2004 between seasons, but not in 2002. There was a clear annual biomass maximum during DS, reaching $180 \text{ mg Chl } a \text{ m}^{-2}$ the 20th August 2003 and the 20th July 2004. In Kigoma (Lake Tanganyika), the DS peak occurred at the very end of DS in 2002 ($82 \text{ mg Chl } a \text{ m}^{-2}$) and was lower than the 2003 DS maximum ($94 \text{ mg Chl } a \text{ m}^{-2}$ on 2nd September).

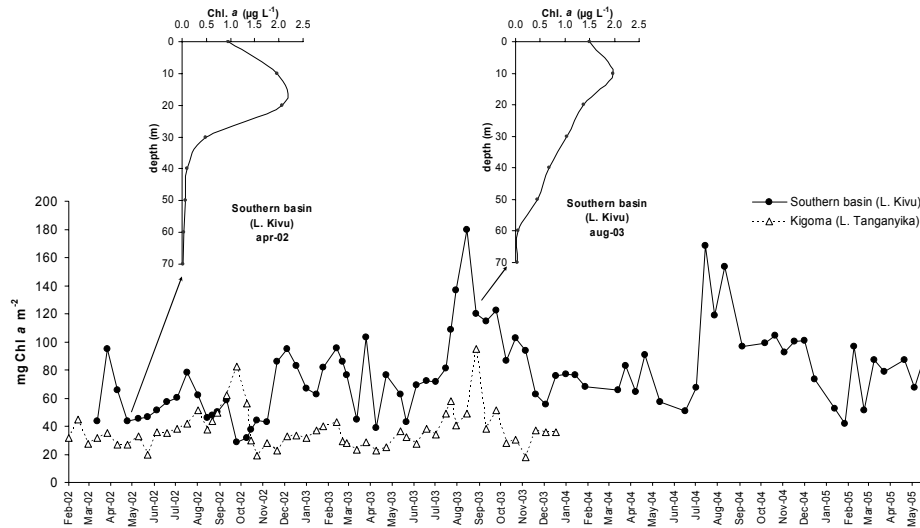


Figure 7: Chlorophyll *a* evolution in Lake Kivu southern basin (dots) and Lake Tanganyika off Kigoma (open triangles) during the 2002-2004 period. Arrows indicate examples of rainy season (RS) and dry season (DS) profiles in Lake Kivu (southern basin).

The Chl *a* data collected during the cruises in Lake Kivu showed some season-related spatial variation (Fig. 8): the RS Chl *a* varied little in the four main basins (near 55 mg Chl *a* m⁻²), while more contrast among basins appeared in DS, with 160 mg Chl *a* m⁻² in the northern basin. The species composition and variation patterns were generally similar in open lake waters. The results from the survey in the southern basin can then be considered as representative of the whole lake situation. The isolated bays of Bukavu and Kabuno were two exceptional cases because of their very different limnology compared with the rest of the lake: the first showed higher biomass than the rest of the lake, particularly during DS when complete mixing occurred; in Kabuno Bay, the shallow epilimnion harbours low Chl *a* per m² (22.9 in RS and 33.7 in DS cruises), with less seasonal difference than in the open lake.

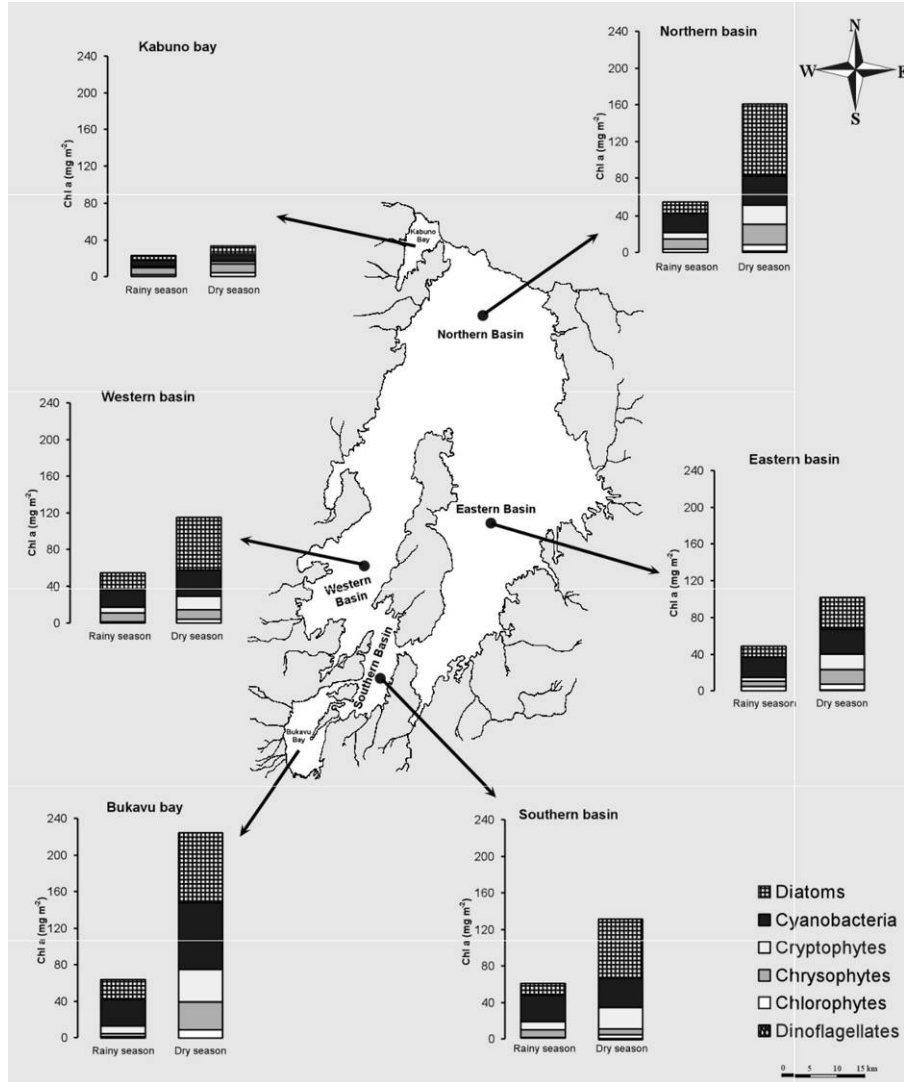


Figure 8: Spatial variability of phytoplankton biomass and composition from pigment analysis in the four major basins and two isolated bays (Kabuno and Bukavu) of Lake Kivu. The results correspond to epilimnion average observed during different seasonal cruises.

According to HPLC analysis, the phytoplankton in Lake Kivu was dominated by a diatom-cyanobacteria assemblage (Fig. 9a). The most common species in pelagic Lake Kivu were pennate diatoms (*Nitzschia bacata* Hust. and *Fragilaria danica* Lange-Bert.) and the cyanobacteria *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg and *Synechococcus* sp. Centric diatom *Urosolenia* sp. and various *Microcystis* species can also be very abundant. They form mostly distinct near surface populations under daily stratification conditions. Cryptophytes and chrysophytes presented a similar pattern, without noticeable seasonal variations; cryptophytes tended to occur in greater abundance in the deep epilimnion, close to the thermocline (data not shown). They are motile and have been shown to migrate in the water column. Chrysophytes occurred regularly, with one single identified species, *Paraphysomonas vestita* Stokes. During DS diatom dominance was even more abundant at all the sampling stations (Fig 8): this was as conspicuous in the temporal survey at the southern basin as in the cruise samples. Chlorophytes were barely represented. This contrasts sharply with the phytoplankton of Lake Tanganyika off Kigoma in 2002-2003 (Fig. 9b), which was characterised by a chlorophyte-cyanobacteria (including picocyanobacteria) assemblage, with a larger contribution of diatoms in DS (Descy *et al.*, 2005).

Finally, the $Z_m:Z_{eu}$ ratio was significantly correlated (Pearson correlation = 0.76, $P < 0.05$, $n=118$) with Chl *a* integrated over the 0-60 m layer for Lake Kivu and 0-100 m layer for Lake Tanganyika (Fig. 10a). In the three year pigment data series from the southern basin, diatom and cyanobacteria contributions to total Chl *a* were inversely correlated (Pearson correlation = 0.73, $P < 0.05$, $n= 70$), which suggests a prevalence of some well adapted species of cyanobacteria during stratified RS conditions (Fig. 10b), while diatoms dominated during the dry season.

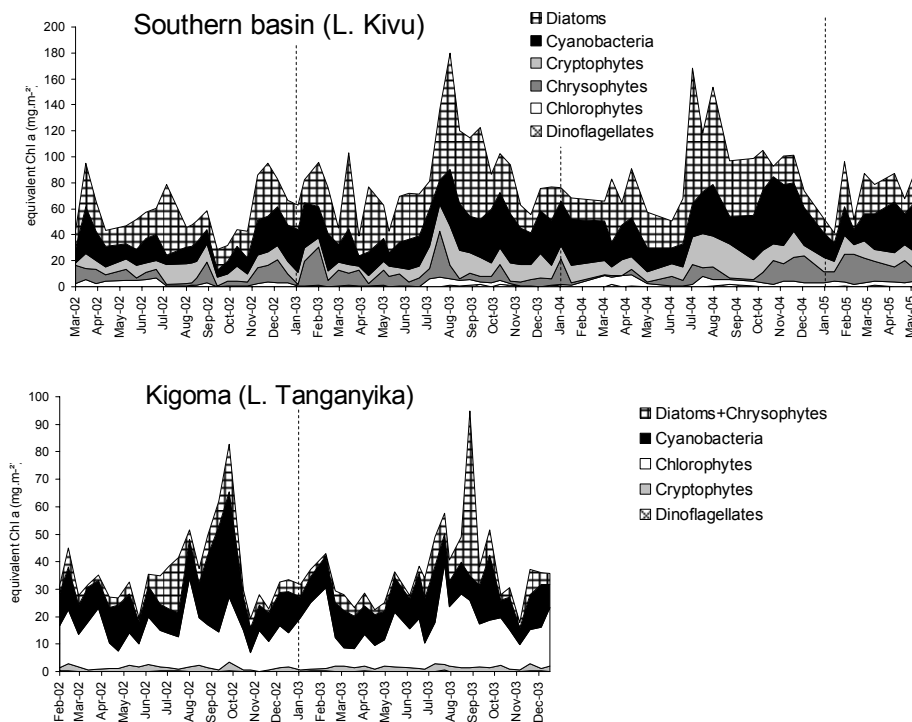


Figure 9: a) Phytoplankton biomass and composition from pigment analysis in Lake Kivu (southern basin) in the 2002-2004 period. b) Phytoplankton biomass and composition from pigment analysis in Lake Tanganyika off Kigoma in 2002 and 2003 (redrawn from Descy *et al.*, 2005).

Picophytoplankton counts (flow cytometry)

As expected, contrary to temperate lakes where picophytoplankton has a marked seasonal distribution cycle (Belykh and Sorokovikova, 2003; Callieri and Stockner, 2002), the autotrophic picoplankton (APP) was abundant at all seasons in Lakes Tanganyika and Kivu (and probably in other East African oligotrophic lakes). The spatial and temporal variations in those two lakes will be discussed in another paper. The flow cytometry counts during cruises showed *Synechococcus*-like densities in the range $1 \times 10^5 - 6 \times 10^5$ cells mL^{-1} (Fig. 11). Lake Tanganyika showed higher cell densities but the average cell biovolume was smaller: $0.37 \mu\text{m}^3$ vs. $0.43 \mu\text{m}^3$ in Lake Kivu. Therefore, in terms of biomass, the differences were attenuated: using a conversion factor of $0.47 \text{ pg C per } \mu\text{m}^3$ (Verity *et al.*, 1992) mean APP biomass was 1.1 g C m^{-2} for Lake Kivu in the southern basin and 1.8 g C m^{-2} in Lake Tanganyika off Kigoma. The $<2 \mu\text{m}$ fraction at the different cruise sampling points corresponded, in average ($n=15$), to 21% of the total Chl *a* within a 10-35% range. In Lake Tanganyika, this fraction was usually higher; Descy *et al.* (2005) reported a mean APP biomass of 50% in the southern basin.

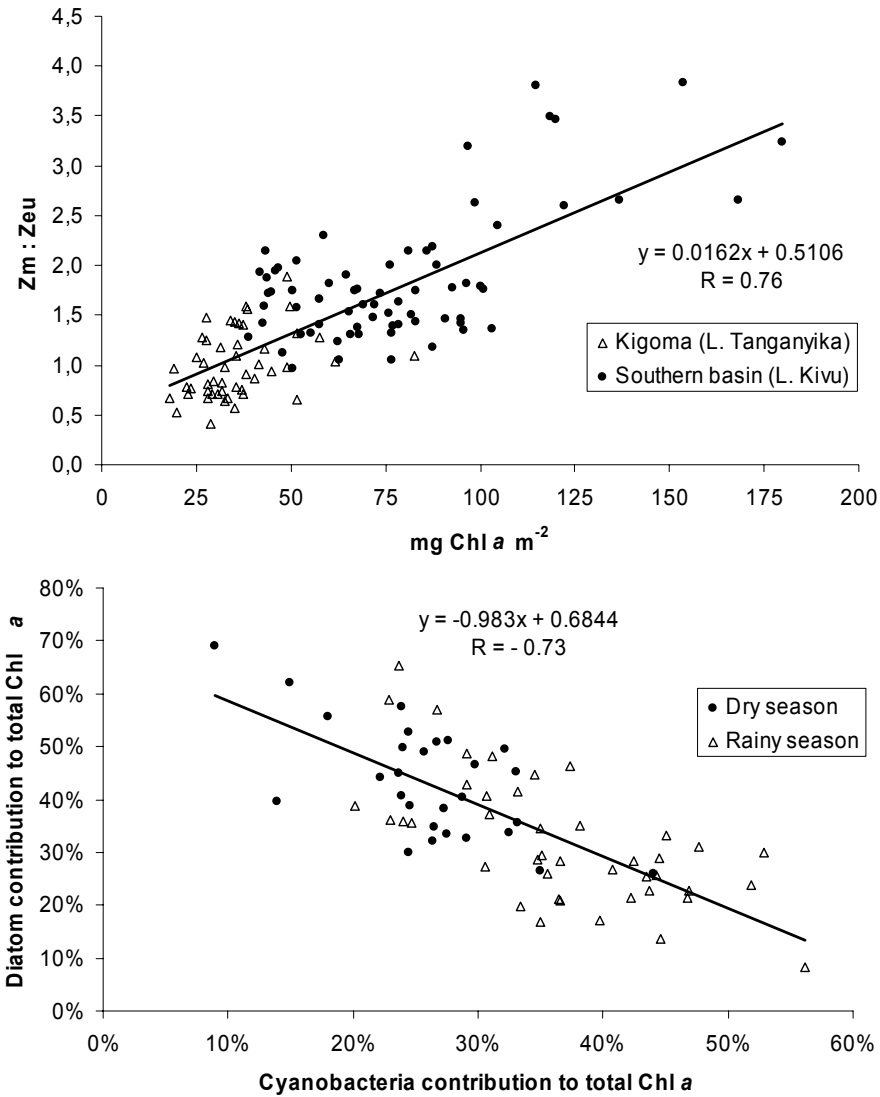


Figure 10: a) Relationship between phytoplankton biomass and the $Z_m : Z_{eu}$ ratio in lakes Kivu and Tanganyika (Kigoma). b) Relationship between diatoms and cyanobacteria contribution to total chlorophyll *a* in Lake Kivu.

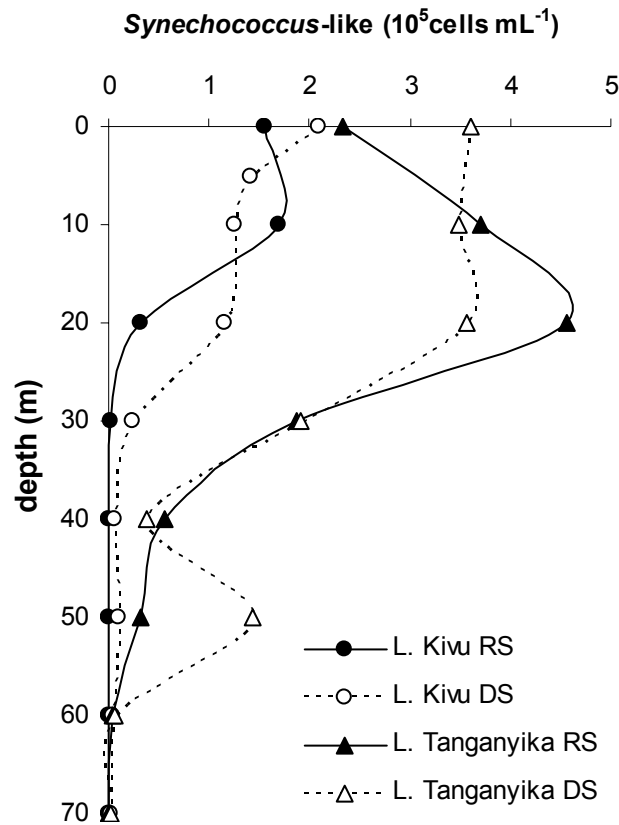


Figure 11: *Synechococcus*-like abundance profiles (from flow cytometry counts) in Lake Kivu at the southern basin (circles) and Lake Tanganyika off Kigoma (triangles) in the 2004s rainy season (RS - full lines) and dry season (DS - dashed lines).

Discussion

A biweekly limnological and HPLC-pigment survey of Lake Kivu in 2002 - 2004 showed an important interannual variability, rarely evaluated before in the East African Great Lakes. As expected from differences in wind stress and mixing conditions, Chl *a* was lower under stratified conditions (RS) and rose in DS, but this increase in phytoplankton biomass was much more important in 2003 and 2004 than 2002. The extent of the mixed layer and the duration of the deep mixing conditions, were the main factors driving this interannual variability in algal biomass. Although the meteorological data were not available for 2002, we can hypothesize that 2003 and 2004 DS winds were stronger and that the windy season lasted longer than in 2002. This can be derived from the observed vertical profiles of temperature: the thermal density gradient was weaker during the dry season in 2003-2004 than in 2002. This again demonstrates the sensitivity of tropical lakes to climate variability, as emphasized by several authors (e.g., Johnson and Odada, 1996) which implies that a survey of several years, with sufficient sampling periodicity, is necessary to assess productivity of tropical lakes. With mean annual Chl *a* concentration of 1.3 mg m^{-3} (average in the 0 to 60 m layer), Lake Kivu is clearly in the oligotrophic range.

As previous accounts of the phytoplankton of Lake Kivu were based on limited sampling over shorter periods of time than our three-year monitoring, comparison with other biomass estimates is limited. However, the picture of a more productive Lake Kivu, with phytoplankton biomass ten times higher than Lake Tanganyika reported by Hecky and Kling (1987) is certainly to be corrected. Indeed, Chl *a* per unit volume in Lake Kivu was only two to three times higher than in the pelagic zone of Lake Tanganyika off Kigoma, and the difference in algal biomass is even lower when expressed per unit area, owing to the greater extent of the mixed layer in Lake Tanganyika. Moreover, Hecky and Kling (1987), on the basis of microscope examinations of their few samples, described the phytoplankton assemblage of Lake Kivu as dominated by a cyanobacteria-chlorophyte assemblage. This is a major difference with our study, where, thanks to the combination of optical and electron microscopy (Sarmiento *et al.*, *submitted*) and of HPLC analysis of phytoplankton pigments, we found diatoms and cyanobacteria as the dominant groups on average over the three years, green algae being a minor component of the algal assemblage.

A review of the most characteristic taxa of the algal assemblages of the large lakes of Eastern Africa is synthesized in Table I. Considering only the dominant algal classes, phytoplankton of Lake Kivu seems more related to the shallower Lake Victoria (before anthropogenic eutrophication) than to the great, deep, oligotrophic lakes Malawi and Tanganyika. To some extent, this is not unexpected, as the two largest lakes are located farther from the

equator. However, a key common feature between Lake Victoria and Lake Kivu is the $Z_m:Z_{eu}$ ratio, usually greater than one which favours algae with high accessory pigment providing improved light harvesting capabilities. Also, despite the great depth of Lake Kivu, it never mixes vertically below 60-70 m, where the permanent chemocline is situated. Lake Victoria is shallower and vertical mixing involves contact with the sediment, which correlates with the greater nutrient availability and higher productivity of this large lake, even before its anthropogenic eutrophication. A key feature of Lake Kivu, pointed out by Spigel and Coulter (1996), is the weak thermal gradient in the mixolimnion, due to its location at high altitude, where air temperature is lower than in the regions of the other lakes. In addition, clear seasonal differences in dominant wind regime and mixing events driven by short but intense winds are likely to occur frequently, and alternate with episodes of stratification. To summarize, Lake Kivu combines a relatively shallow euphotic layer, usually smaller than its mixed layer, with relatively low nutrient content of the mixolimnion, and with unstable thermally stratified surface waters. In order to be successful in such an environment, phytoplankton units must be well adapted to low light regimes and resistant to nutrient stress. An additional advantage to survival would be the ability to achieve vertical migration in the stratified but unstable water column, in order to optimise nutrient uptake and light harvesting for photosynthesis. These conditions contrast with those of Lakes Tanganyika and Malawi, which combine stronger seasonality with complex hydrodynamics, creating sharp contrast between DS (deep mixing, increase of nutrients, reduction of light) and RS (shallow thermocline, low nutrients, high light): hence, the chlorophyte-cyanobacteria dominated assemblage reported for these large lakes, with diatoms developing during deep mixing events.

The taxonomic composition of the diatom assemblages of East African great lakes deserves more scrutiny and reveals important differences among lakes. In most of these lakes, needle-like or colonial *Nitzschia* appear first and are often followed by centrics like *Stephanodiscus* and *Aulacoseira*, when Si inputs decrease at advanced stages of the DS (Hecky and Kling, 1987). In Lake Kivu, long pennate diatoms, known to be good competitors at high Si:P ratio (i.e., at very low P availability), are always dominant and centrics, which develop at lower Si:P, are very rare. This is a specific trait of Lake Kivu as DRSi is relatively high in all seasons: we never measured $DRSi < 70 \mu M$ in the euphotic zone, and the three year average was $100 \mu M$, whereas average DRSi concentrations in the other lakes are much lower (Table II). With such a large amount of DRSi and low P in the euphotic zone, the diatom assemblage of Lake Kivu never shifts to centric *Stephanodiscus* or *Aulacoseira*-like during the DS, contrarily to the rest of the cited lakes. Moreover, the surface waters of Lake Kivu support a population of *Urosolenia* sp., a genus which is well-known for its oligotrophic affinities (see below) and tolerance to high light.

Table I: Annual succession of the functional groups¹ (according to Reynolds *et al.*, 2002) and some of the dominant phytoplankton species in the East African Great Lakes. A short dry season takes place in the January to May period in lakes Victoria and Kivu. From May to September is the dry season in all East Africa. The rest of the year it is rainy season. (*) Adequate assemblage not found in the functional classification¹ of Reynolds *et al.* (2002).
¹ – See Appendix I for more details on the functional groups

Lake (pelagic)	Functional Group ¹	Some of the main species	References
Malawi	Jan.-May	<i>Synechococcus</i> (?), <i>Planktolingbya</i> , <i>Lobocystis</i> , <i>Coenococcus</i>	Patterson and Kachinjika, 1995
	May-Sept.	<i>Nitzschia</i> , <i>Aulacoseira</i> ... then <i>Stephanodiscus</i> / <i>Cyclotstephanos</i> , <i>Mougeotia</i>	Hecky and Kling, 1987
	Sept.-Dec.	As in Jan-May but <i>Anabaena</i> and <i>Gymnodinium</i> can bloom	
Tanganyika	Jan.-May	<i>Synechococcus</i> , <i>Chroococcus</i> , <i>Lobocystis</i> / <i>Dictyosphaerium</i> , <i>Oocystis</i>	Descy <i>et al.</i> , 2005
	May-Sept.	<i>Nitzschia</i> ... then <i>Stephanodiscus</i>	Hecky and Kling, 1987
	Sept.-Dec.	As in Jan-May but more Chrysophyceae, <i>Strombidium</i> ; <i>Anabaena</i> can bloom	
Victoria (50's)	Jan.-May	<i>Synechococcus</i> (?), <i>Planktolingbya</i> (if mixing occurs: <i>Nitzschia</i> , <i>Aulacoseira</i> , <i>Stephanodiscus</i>)	Talling, 1957
	May-Sept.	<i>Nitzschia</i> ... then <i>Aulacoseira</i> , <i>Stephanodiscus</i>	Talling, 1987
	Sept.-Dec.	As in Jan-May <i>Anabaena</i> and <i>Anabaenopsis</i> can bloom	
Victoria (90's)	Jan.-May	As in the 50's, but cyanobacteria persist; when mixing occurs, only <i>Nitzschia</i>	Hecky, 1993
	May-Sept.	? Persistence of N ₂ -fixing cyanobacteria (<i>Anabaena</i> , <i>Cylindrospermopsis</i>)?	Lehman and Branstrator, 1993
	Sept.-Dec.	Persistence of N ₂ -fixing cyanobacteria (<i>Anabaena</i> , <i>Cylindrospermopsis</i> , ...)	
Kivu	Jan.-May	<i>Synechococcus</i> , <i>Planktolingbya</i> , <i>Nitzschia</i>	This study
	May-Sept.	<i>Nitzschia</i> , <i>Fragilaria</i> (<i>Synedra</i>); <i>Urosolenia</i> can bloom	
	Sept.-Dec.	As in Jan-May but <i>Microcystis</i> can bloom	

Table II: Overview of silica concentrations in the epilimnion of some East African Great Lakes.

Lake	epilimnion Si μM	References
Malawi	20	Haberyan and Hecky, 1987
	14.2	Patterson and Kachinjika, 1995
	16	Branchu, 2001
Tanganyika	1.2	Degens <i>et al.</i> , 1973
	15	Branchu, 2001
	25.5	Descy <i>et al.</i> , 2005
Victoria	> 45	Talling and Talling, 1965
	2.3	Lehman and Branstrator, 1993
Kivu	231	Degens, 1973
	100	This study

A very convenient and commonly used approach to synthesize the ecology of lacustrine phytoplankton is the functional classification of algal assemblages proposed by Reynolds *et al.* (2002). In Lake Kivu, in stratified conditions (RS), the low nutrient and higher available light favours specialised cyanobacteria: a coexistence of assemblages Z (*Synechococcus*) and M (*Microcystis*) is often observed. However, we couldn't find an adequate functional group for the DS assemblages. From our results and from other studies in the East African Lakes (Table I), the assemblages found during the DS (usually needle-like or centric diatoms) seem to be a very particular feature from this region, not found in other tropical lakes. Moreover, the dominant taxa are often specific to tropical regions or even strictly African (as *Nitzschia bacata* Hust. in Lake Kivu or *Nitzschia asterionelloides* O. Müll. in lakes Tanganyika and Malawi). For this reason, the DS assemblages are not quoted in the Table I.

Daily stratification in tropical lakes is very common and well known since Worthington (1930). A secondary thermocline can form in the surface water during the day, and is broken down when the sun sets. In Lake Kivu this phenomenon was frequently observed and could be part of the reason for the recurrent high surface biomass observed recurrently (up to 8 mg Chl *a* m^{-3}), accompanied by a high abundance of the centric diatom *Urosolenia* (A assemblage), tolerant to nutrient depletion and high light intensity. The real abundance of *Urosolenia* could be overlooked when using optical microscopy. Not only the valves are very thin and delicate, which renders observation more difficult, but fixation with formaldehyde seems to destroy

them further (E. Rott, personal comm.). Otherwise, it could be that these organisms simply do not settle, and are consequently absent from microscopic counts at the inverted microscope. In our study, HPLC pigment analysis coupled with scanning electronic microscopy allowed detection of these diatoms. Although this genus is frequently listed in taxonomical works in tropical freshwaters, very little is known about their abundance and ecology. Instead of proliferation in a specific layer, other possible explanation for these surface accumulations of *Urosolenia* cells would be the migration upward the water column as described in several works for marine *Rhizosolenia* species (Villareal and Lipschultz, 1995; Villareal *et al.*, 1996, 1999; Heather and Villareal, 2005). As *Urosolenia* plastids occupy a small proportion of the entire valve, the large cells surrounded by a thin silica wall could have a similar function as colony mucilage in *Microcystis aeruginosa* (Walsby and Reynolds, 1980), i.e. reducing their sinking rate, by reducing the overall cell density. Moreover, the same authors stated that *Urosolenia* long spines contributed to form resistance to sedimentation.

Another group of organisms that was completely missed in classical microscopic counts is autotrophic picoplankton, which represents around one fourth of total Chl *a* in Lake Kivu. Flow cytometry and epifluorescence have confirmed that *Synechococcus* biomass in both lakes Tanganyika and Kivu was in the same order of magnitude, even if it corresponds to higher relative abundance in Lake Tanganyika. This means that the Chl *a* differences between this two lakes fits exclusively for the >2µm fraction, which could be a result of different grazing pressure related to two different trophic structure. In Lake Kivu, the planktivorous sardine *Limnothrissa miodon* Boulenger, introduced from Lake Tanganyika 45 years ago, has no natural predators. Zooplankton, dominated by copepods, has lower biomass than other East African Great Lakes (Isumbisho *et al.*, *in press*). A reduction of the grazing control of edible phytoplankton may have resulted from grazer control after the sardine introduction, which could explain why phytoplankton biomass is comparatively high in Lake Kivu.

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Appendix I: Functional groups of phytoplankton
(extracted from Reynolds *et al.* 2002)

Code	Habitat	Typical representatives	Tolerances	Sensitivities
A	Clear, often well-mixed, base poor, lakes	<i>Urosolenia</i> , <i>Cyclotella comensis</i>	Nutrient deficiency	pH rise
B	Vertically mixed, mesotrophic small-medium lakes	<i>Aulacoseira subarctica</i> <i>Aulacoseira islandica</i>	Light deficiency	pH rise, Si depletion, stratification
C	Mixed, eutrophic small- medium lakes	<i>Asterionella formosa</i> <i>Aulacoseira ambigua</i> <i>Stephanodiscus rotula</i>	Light, C deficiencies	Si exhaustion, stratification
D	Shallow, enriched turbid waters, including rivers	<i>Synedra acus</i> <i>Nitzschia spp</i> <i>Stephanodiscus hantzschii</i>	Flushing	nutrient depletion
N	mesotrophic epilimnia	<i>Tabellaria</i> <i>Cosmarium</i> <i>Staurodesmus</i>	Nutrient deficiency	stratification pH rise
P	eutrophic epilimnia	<i>Fragilaria crotonensis</i> <i>Aulacoseira granulata</i> <i>Closterium aciculare</i> <i>Staurastrum pingue</i>	Mild light and C deficiency	stratification Si depletion
T	deep, well-mixed epilimnia	<i>Geminella</i> <i>Mougeotia</i> <i>Tribonema</i>	Light deficiency	Nutrient deficiency
S1	turbid mixed layers	<i>Planktothrix agardhii</i> <i>Limnithrix redekei</i> <i>Pseudanabaena</i>	highly light deficient	flushing conditions
S2	shallow, turbid mixed layers	<i>Spirulina</i> <i>Arthrospira</i> <i>Raphidopsis</i>	light deficient conditions	flushing
S _N	warm mixed layers	<i>Cylindrospermopsis</i> <i>Anabaena minutissima</i>	light-, N- deficient conditions	flushing
Z	clear, mixed layers	<i>Synechococcus</i> prokaryote picoplankton	low nutrient grazing	light deficiency
X3	shallow, clear, mixed layers	<i>Koliella</i> , <i>Chrysococcus</i> <i>Pseudopedinella</i> eukaryote picoplankton	low base status	mixing, grazing
X2	shallow, clear mixed layers in meso-eutrophic lakes	<i>Plagioselmis</i> <i>Chrysochromulina</i>	stratification	mixing, filter feeding
X1	shallow mixed layers in enriched conditions	<i>Chlorella</i> , <i>Ankyra</i> <i>Monoraphidium</i>	stratification	nutrient deficiency filter feeding

Code	Habitat	Typical representatives	Tolerances	Sensitivities
Y	usually, small, enriched lakes	<i>Cryptomonas</i>	low light	phagotrophs
E	usually small, oligotrophic, base poor lakes or heterotrophic ponds	<i>Dinobryon</i> <i>Mallomonas</i> (<i>Synura</i>)	low nutrients (resort to mixotrophy)	CO ₂ deficiency
F	Clear epilimnia	colonial Chlorophytes e.g. <i>Botryococcus</i> <i>Pseudosphaerocystis</i> <i>Coenochloris</i> <i>Oocystis lacustris</i>	low nutrients	?CO ₂ deficiency high turbidity
G	Short, nutrient-rich water columns	<i>Eudorina</i> <i>Volvox</i>	high light	nutrient deficiency
J	shallow, enriched lakes	<i>Pediastrum</i> , <i>Coelastrum</i> <i>Scenedesmus</i> <i>Golenkinia</i>	high light,	settling into low light ponds and rivers nutrient poverty
K	short, nutrient-rich columns	<i>Aphanothece</i> <i>Aphanocapsa</i>	deep mixing	
H1	dinitrogen-fixing Nostocaleans	<i>Anabaena flos-aquae</i> <i>Aphanizomenon</i>	low nitrogen low carbon,	mixing, poor light, low phosphorus
H2	dinitrogen-fixing Nostocaleans of larger mesotrophic lakes	<i>Anabaena lemmermanni</i> <i>Gloeotrichia echinulata</i>	low nitrogen	mixing, poor light,
U	summer epilimnia	<i>Uroglena</i>	low nutrients	CO ₂ deficiency
L_O	summer epilimnia in	<i>Peridinium</i> <i>Woronichinia</i> <i>Merismopedia</i>	segregated nutrients	prolonged or deep mesotrophic lakes mixing
L_M	summer epilimnia in eutrophic lakes	<i>Ceratium</i> <i>Microcystis</i>	very low C, stratification	mixing, poor light
M	dielly mixed layers of small eutrophic, low latitude	<i>Microcystis</i> <i>Sphaerocavum</i>	high insolation	flushing, low total light
R	metalimnia of mesotrophic	<i>P. rubescens</i> <i>P. mougeotii</i>	low light, instability strong segregation	stratified lakes
V	metalimnia of eutrophic stratified lakes	<i>Chromatium</i> , <i>Chlorobium</i>	very low light, strong segregation	instability
W1	small organic ponds	Euglenoids, <i>Synura</i> <i>Gonium</i>	high BOD	grazing
W2	shallow mesotrophic lakes	bottom-dwelling <i>Trachelomonas</i>	?	?
Q	small humic lakes	<i>Gonyostomum</i>	high colour	?

Chapitre V

Le rôle de la production primaire et du phytoplancton dans l'augmentation de la concentration en méthane dans le lac Kivu

Samedi 16 juin 1894 – Nous sommes dans un site idéalement beau, tout proche du rivage nord du lac Kivu. Nos tentes ne sont qu'à quelques mètres du bord, et quand nous écartons nos portes de toile, dans l'air lourd et chaud où nous sommes enfermés passe le souffle frais de la brise venant du lac. (...) Pendant l'absence de Prittwitz, je m'étais occupé à acquérir des notions précises sur le lac que nous avions découvert. A la fraîcheur du soir, nous mîmes à l'eau notre petit canot pliant, pour faire quelques sondages, mais déjà assez près du rivage notre sonde, longue de 53 mètres, n'atteignait pas le fond.

"A travers l'Afrique de l'est à l'ouest"
M. le Comte de Götzen
1897

*Role of primary production and phytoplankton dynamics in
the increasing methane concentrations in the deep waters of
Lake Kivu (Eastern Africa)*

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Abstract

With a volcanic origin, Lake Kivu is deep and meromictic, and shows a very particular limnology. Recent investigations on its chemistry revealed an increasing methane production in its deep waters during the past 30 years, leading to an accumulation of gas and the subsequent lowering of the energy required to trigger a devastating release of gasses. An important fraction of this methane is produced by the anoxic degradation of settling material from the 'biozone'. There are two different hypotheses that could explain the increasing gas: anthropogenic eutrophication or biological changes in the trophic chain. The biological history of Lake Kivu is marked by the introduction of the planktivorous sardine from Lake Tanganyika *Limnothrissa miodon* in the late 50s that was responsible for major changes in the zooplankton community. The role of primary producers and the probable changes on the export ratio of the organic matter into deep waters after this introduction is discussed in this paper. A several year data set on primary production is presented, which is quite rare for a tropical lake. The two principal algal groups (cyanobacteria and diatoms) were studied in detail in their vertical and temporal distribution with marker pigments analysis, sestonic elemental ratios and pigment-degradation products. The actual primary production on Lake Kivu doesn't seem substantially different from some punctual measurements made in the past, which discards the eutrophication hypothesis. We believe that the export ratio of organic matter into the deep waters was largely affected by biological changes, namely in zooplankton and in phytoplankton, that could explain part of the methane increase in the past 30 years in Lake Kivu.

Introduction

Lake Kivu is notorious for its peculiar geochemical and limnological features. Its deep-waters are anoxic and harbour one of the largest quantities of dissolved methane known on Earth (Tietze *et al.*, 1980). The origin of such an amount of gas is not yet clearly defined. Schoell *et al.* (1988) suggested two possible sources of carbon for the two principal forms of gas: magmatic for the carbon dioxide and bacterial (by methanogenesis) for the methane. In the same study, theoretical models validated by culture experiments with an *inoculum* from the sediments of Lake Kivu, showed that methane was generated by two biological processes: the reduction of the magmatic carbon dioxide and the decomposition of organic sediment material by methanogenic bacteria.

Recent investigations on Lake Kivu chemistry (Schmid *et al.*, 2005) have revealed that methane production has increased during the past 30 years, leading to an accumulation of gas in the deep waters and the subsequent lowering of the energy input required to trigger a devastating release of gasses. The latest estimates indicate that the gas concentrations could reach saturation during this century. The most significant variations observed have been the increasing concentrations of methane (by 15-20% during the past 30 years), silica (by 30-35%), calcium (by 25–30%) and phosphate (more than 300%) in the deep waters, and a decrease of these elements in the surface layers. The origin of these huge and rapid modifications in the biogeochemical cycles of elements in Lake Kivu is still poorly understood.

The most plausible hypothesis is a rapid increase of sedimentation flux. In this paper we discuss two hypotheses for this increasing flux of organic matter. The first is a hypothetical increase of the primary production following eutrophication of surface waters caused by the increasing lakeside human population. Since some decades, land use along the banks of Lake Kivu is turned over to deforestation and agriculture. We may thus reasonably hypothesize an important increase of external nutrient loading to surface waters of Lake Kivu. However, the most important agglomeration is situated in the south end of the lake, at the city of Bukavu, where a relatively isolated bay harbours the only outlet, the Ruzizi river, that flows out in the surroundings of the city (Fig. 1). The impact of this city in the open lake, 20 km away towards the north, is then not very probable.

Another hypothesis, raised up by Schmid *et al.* (2005) but still unexplored, is an increased export of organic matter and nutrients to the deep waters, resulting from changes in the trophic chain after the introduction of the sardine *Limnothrissa miodon* Boulenger to Lake Kivu in the late 1950s. At present, Lake Kivu is the sole natural lake in which *Limnothrissa miodon*, an endemic sardine originally from Lake Tanganyika, has been introduced

(Collart, 1954), initially to fill an empty niche (Simberloff, 1995). Indeed, prior to the introduction, no planktivorous fish was present in the pelagic waters of Lake Kivu. Following this introduction, the sardine has gained substantial economic and nutritional importance for the lakeside human population (Spliethoff *et al.*, 1983; de Iongh *et al.*, 1983; Marshall, 1991b, 1995; Roest, 1999). But from an ecosystem standpoint, the introduction of planktivorous fishes may result in important modifications of plankton community structure (e.g., Carpenter & Kitchell, 1993). Dumont (1986) already envisioned such a modification of Lake Kivu zooplankton community structure following the introduction of *Limnothrissa*. Recent observations showed the disappearance during the last decades of a large grazer, *Daphnia curvirostris* Eylmann, and the dominance of mesozooplankton community by three species of cyclopoid copepod: *Thermocyclops consimilis* Kiefer, *Mesocyclops aequatorialis* Kiefer and *Tropocyclops confinis* Kiefer (Isumbisho *et al.*, *in press*).

In this paper, we present the results from a survey in Lake Kivu spanning several years, and covering the vertical and temporal variations of phytoplankton. A large number of plankton primary production measurements were carried out to encompass seasonal variations, and phytoplankton nutritional status was approached by seston C:N:P ratios. Finally, we discuss the role played by primary production and grazing in the enrichment of deep waters by settling of organic matter derived from the euphotic layer, in relation with the increase of methane in Lake Kivu reported by Schmid *et al.* (2005).

Methods

Study site and sampling

Lake Kivu, located between Rwanda and the Kivu Province (Democratic Republic of Congo), is the smallest of the East African Great Lakes. It is a deep (max. 489 m), meromictic lake, with an oxic mixolimnion of ca. 70 m, and a deep monimolimnion rich in dissolved gases. Lake Kivu is a volcanic lake and presents some particular limnological features, such as stepwise increases of temperature and salinity in the deep-water layers (Degens *et al.*, 1973; Spiegel and Coulter, 1996). As a consequence of high altitude (1463 m), the surface waters are slightly cooler than in other East African Great Lakes (24.9°C vs. 26.8°C in Lake Tanganyika). Recent studies have confirmed the oligotrophic status of Lake Kivu, and details about nutrient concentrations, general features and phytoplankton biomass and community composition can be found in Sarmiento *et al.* (*in press*, 2006). The present study presents data collected at Ishungu in the southern basin of Lake Kivu (02°33.94'S, 28°97.65'E, Fig. 1). A previous study with sampling points distributed in the various basins indicated no significant differences between the different basins in either phytoplankton biomass or primary production (Sarmiento *et al.*, 2006), so that Ishungu was considered representative of the entire lake.

Water samples were collected twice a month from February 2002 to February 2005 at 10-m intervals in the 0-100 m water column using a 6-L Van Dorn bottle. Occasional additional samplings were done at 5 m-depth, in order to get a more detailed vertical distribution of the algae. For each sampling depth, 3 L of water were filtered on Whatman GF/F (Maidstone, U.K.) or Macherey-Nägel (Düren, Germany) GF/5 filters (both have a similar 0.7-µm pore size), and the filters were then immediately frozen for later HPLC pigment analysis. 3 L of water were also filtered on pre-ignited Whatman GF/F filters (1.2-µm pore size) for elemental (C, N and P) analysis. Supplementary water samples were collected and immediately preserved with Lugol solution and glutaraldehyde at 1 to 2 % final concentration for observation in light microscopy, epifluorescence microscopy and scanning electronic microscopy (see Sarmiento *et al.*, *in press*).

Limnological profiles were obtained using multiparametric sonde (Hydrolab DS4a, Loveland, USA); the downward attenuation coefficient (k) was determined from transparency measurements (Secchi disk depth) and photosynthetic active radiation (PAR) measured with Li-Cor quantum sensors. The depth of the mixed layer (Z_m) was estimated by locating the top of the thermocline, as shown by the temperature and oxygen vertical profiles obtained with the multiparametric sonde.

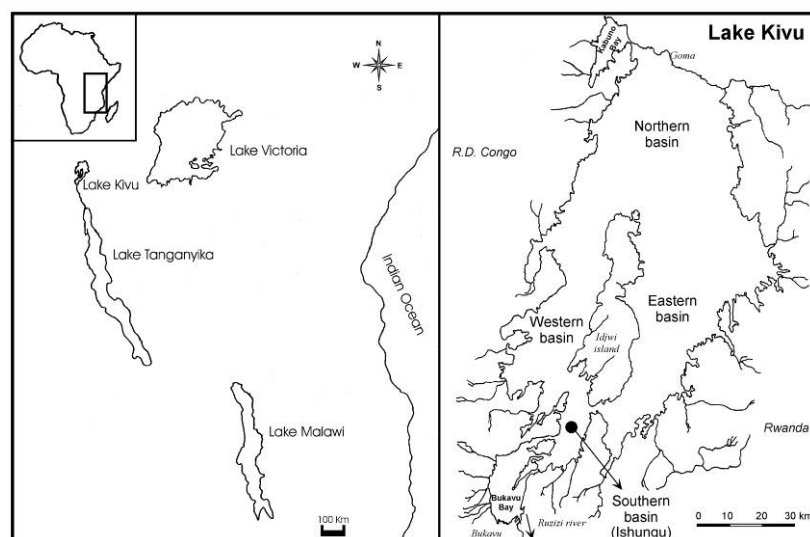


Fig. 1: Geographic situation of Lake Kivu. Black dot indicates the sampling site (see text for GPS coordinates).

Pigment analysis

Samples for pigment analysis followed a procedure described in Descy *et al.* (2000). Pigment extraction was carried out in 10 ml 90 % HPLC-grade acetone. After two 15-min sonications separated by an overnight period at 4°C in the dark, extracts were stored in 2-mL amber vials in a freezer (at -25°C) for several months. Transport to Belgium was carried out on ice in cooler boxes. HPLC analysis was carried out using the gradient elution method of Wright *et al.* (1991), with a Waters system comprising a PDA detector and a fluorescence detector. Calibration was made using commercial external standards (DHI, Denmark). Carotenoids not present in the standard were quantified against fucoxanthin, using as relative response the ratio of the specific absorbance coefficients at 440 nm in methanol (Jeffrey *et al.*, 1997a). Pigment concentrations were processed with the CHEMTAX software (CSIRO Marine Laboratories, Hobart, Australia; Mackey *et al.*, 1996) using input ratio matrices adapted for freshwater phytoplankton (Descy *et al.*, 2000). Data processing followed a procedure similar to that of Descy *et al.* (2005) and Sarmiento *et al.* (2006), allowing estimates of chlorophyll *a* (Chl *a*), biomass of Chlorophytes, Chrysophytes, diatoms T1 and T2, Cryptophytes, dinoflagellates and cyanobacteria T1 and T2, taking into account variations of pigment ratios with season and depth. The distinction between cyanobacteria “type 1” (T1) and “type 2” (T2) was based on different zeaxanthin:Chl *a* ratios and on the presence of echinenone

in cyanobacteria T2. Type 1 diatoms (diatoms T1, containing the usual diatom pigments) were essentially composed of pennate diatoms (*Nitzschia bacata* Hust. and *Fragilaria danica* Lange-Bert.). The presence of a particular carotene, similar to $\beta\Psi$ -carotene described in Jeffrey *et al.* (1997b), enabled us to distinguish “diatoms type 2” (or T2), corresponding to the centric diatom *Urosolenia* sp. identified by electron microscopy and occurring frequently in the surface samples.

Estimating primary production

Primary production rate was determined in 27 field incubations (^{14}C incorporation at different seasons following Steeman-Nielsen, 1952) and completed with calculations (using mean P^B_{max} and I_k derived from the 27 incubations, and fortnightly field measurements of Chl *a*, *k* and solar irradiance). Eighteen 120-mL glass bottles filled with water from a pooled mixolimnion sample were incubated *in situ* just below the surface with $\text{NaH}^{14}\text{CO}_3$. Duplicate sets of bottles were placed at mid-day for 1.5 h into a nine-case incubator providing a range from 0–60% of natural light energy. Radioactivity was measured using a Beckman scintillation counter (LS 6000 SC) with Filter-Count (Packard) as scintillation cocktail and the external standard method for quench correction. Photosynthesis parameters were determined following Vollenweider’s (1974) equation. Solar irradiance was measured throughout the study period using a Davis Weather Wizard III station light sensor (Davis Inotek Instruments, Baltimore, USA) located in the city of Bukavu. Those data were converted to PAR using a correction factor determined by comparison with several Li-Cor sensor irradiance measurements. Daily depth-integrated primary production ($\text{g C m}^{-2} \text{d}^{-1}$) was calculated using photosynthesis parameters, continuous surface irradiance data, and vertical light attenuation (Kirk, 1983). Calculations of daily production over the years used fortnightly measurements of Chl *a*, *k*, and mean P^B_{max} ($4.08 \mu\text{g C } \mu\text{g Chl}^{-1} \text{h}^{-1}$) and I_k ($310 \mu\text{E m}^{-2} \text{s}^{-1}$), obtained from 27 incubations distributed along the study period. Annual primary production ($\text{g C m}^{-2} \text{y}^{-1}$) was estimated by multiplying the mean daily primary production by 365.

Seston elemental ratios (C:N:P)

Particulate C and N were analyzed using a Carlo-Erba NA1500 elemental analyzer. Particulate P was analyzed by spectrophotometric determination of phosphate after digestion with potassium persulphate and boric acid (Valderrama, 1981). The elemental ratios were expressed as the ratio of the means in molar units.

Results

Phytoplankton distribution in the water column and primary production

Chlorophyll *a* concentration in the 0-60-m layer at Ishungu ranged from 0.76 to 4.55 mg m⁻³ (1.3 mg m⁻³ global average), and vertical and temporal variations followed a seasonal pattern, reflected by the extent and duration of the dry season mixing. During the dry season, Chl *a* increased in the top 20 m, and became detectable in deeper waters as well, following the deepening of the mixed layer (Fig. 2). The euphotic depth varied between 11.7 and 31.2 m (average 18.1 m).

Particulate primary production varied between 0.37 and 1.50 g C m⁻² d⁻¹ (Table I), and exhibited a seasonal pattern with peaks during the dry season, although high productions occurred also during the rainy seasons (Fig. 2). Seasonal averages were significantly different (t-student test, $P > 0.05$), with higher values in the dry season (0.80 ± 0.32 g C m⁻² d⁻¹) than the remainder of the year (rainy season, 0.67 ± 0.21 g C m⁻² d⁻¹). The average daily primary production in the southern basin of Lake Kivu was 0.71 ± 0.25 g C m⁻² d⁻¹. The calculated annual primary production, in g C m⁻² y⁻¹, was 223 in 2002, 286 in 2003 and 275 in 2004.

The vertical and temporal distribution of the two dominant algal groups (diatoms and cyanobacteria) is illustrated in Figs. 3 and 4. In the top 30 m (approximately the average euphotic depth), diatoms and cyanobacteria contributed equally (32% each) to total Chl *a*. The vertical and temporal distribution of these two diatom pigment types was very distinct. Diatoms T1 were well represented all year round, increased significantly under conditions of deep mixing (dry season), and were distributed from the surface to 60 m depth. In contrast, diatoms T2 were present sporadically in high concentrations, and mainly in the 0-10m surface layer (Fig. 3).

The highest concentration of pheophytin (Chl *a* degradation product) was found between 20 and 50 m, and tended to decrease below, but significant concentrations were measured at the bottom of the mixolimnion during the dry season (Fig. 6). A significant correlation was found between diatoms T1 and pheophytin concentration in the water column (Pearson correlation = 0.53, $p < 0.01$, $n = 66$).

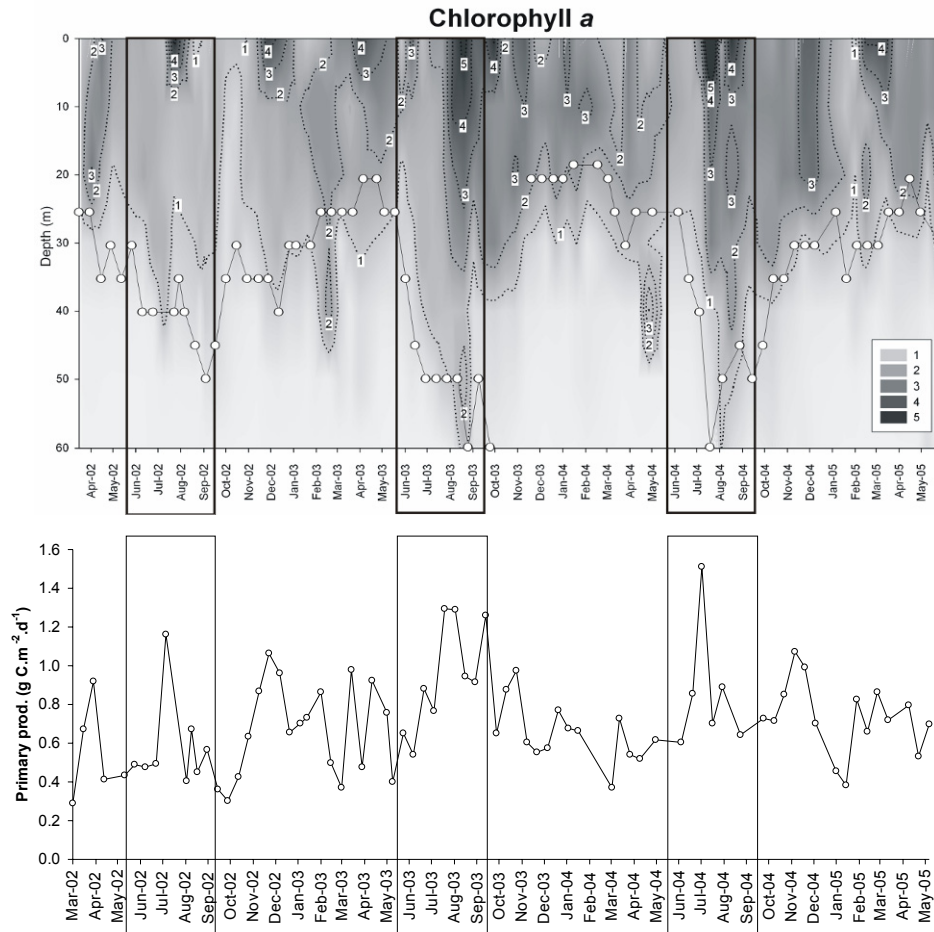


Fig. 2: Chlorophyll *a* (vertical distribution within the top 60 m, in mg m^{-3}) and primary production (integrated in the mixed layer) in the southern basin of Lake Kivu during the 2002-2005 period. Rectangles highlight the annual dry season (June to October).

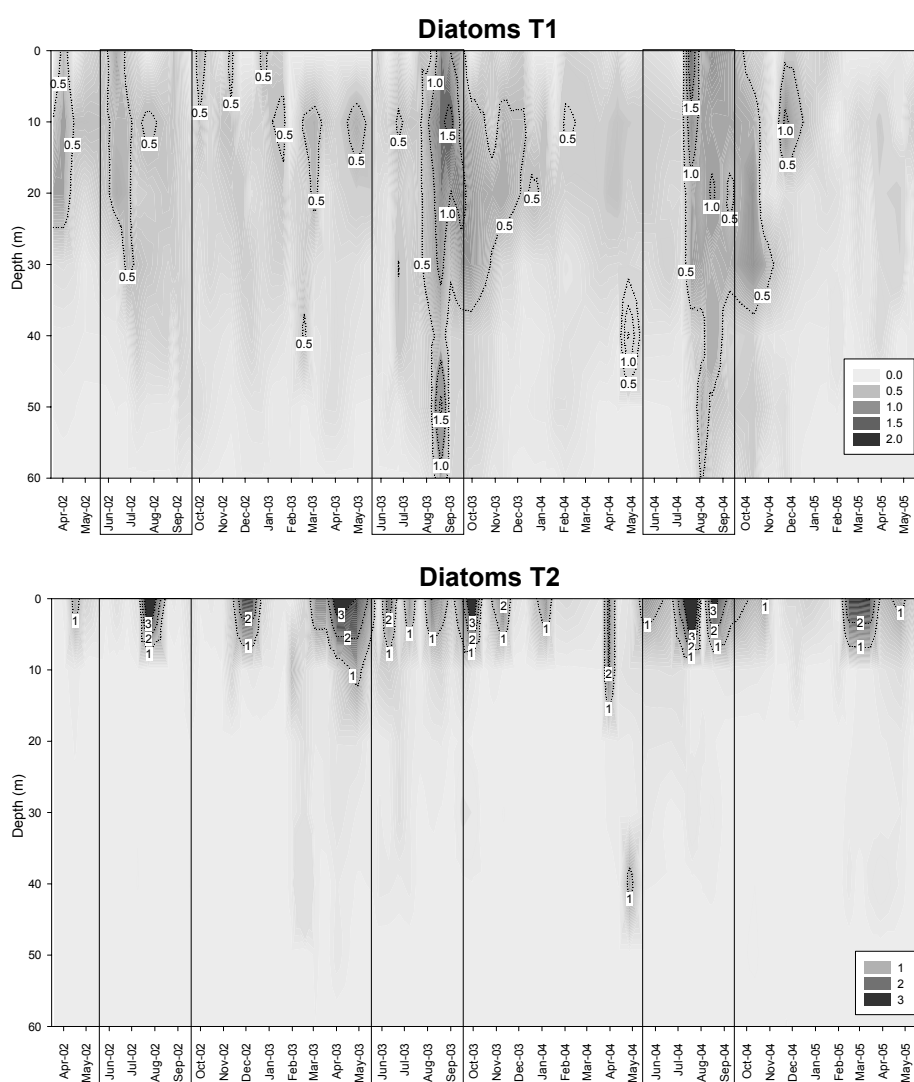


Fig. 3: Diatoms T1 and T2 (vertical distribution within the top 60 m, in mg m^{-3}) in the southern basin of Lake Kivu during the 2002-2005 period. Rectangles highlight the annual dry season (June to October).

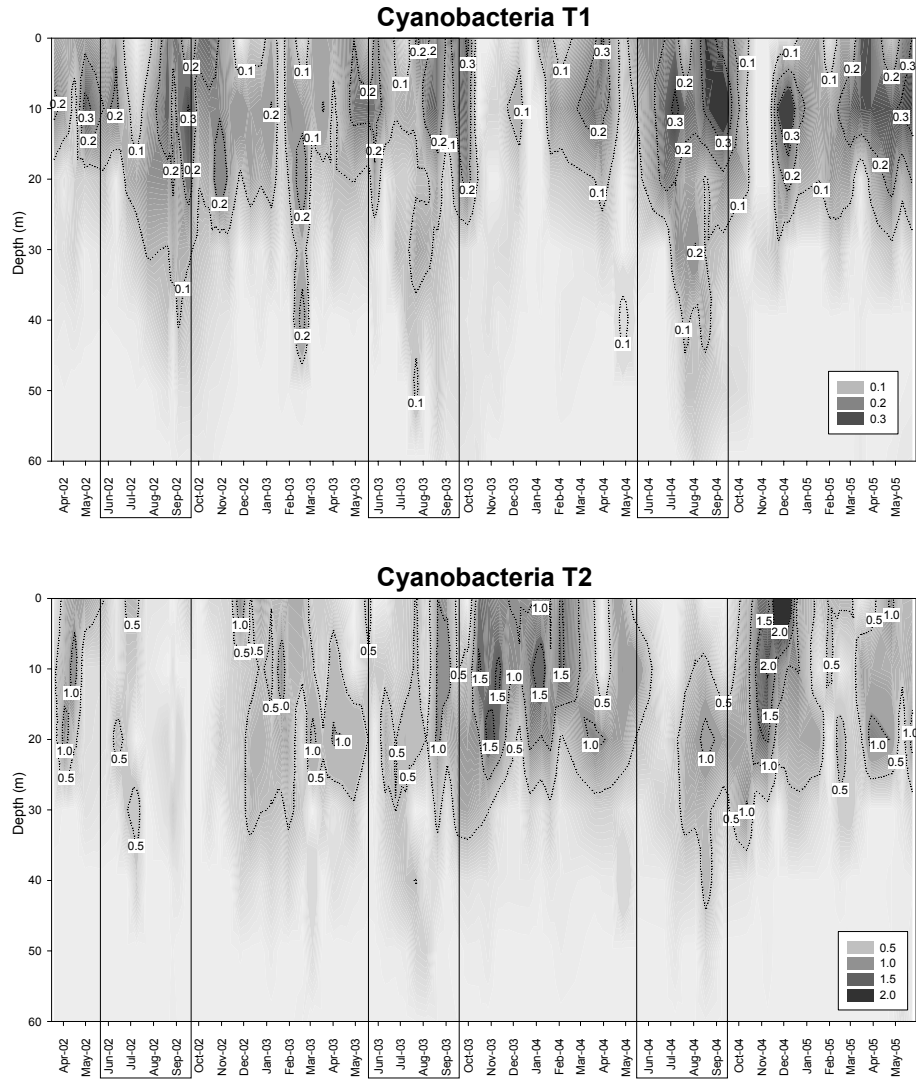


Fig. 4: Cyanobacteria T1 and T2 (vertical distribution within the top 60 m, in mg m^{-3}) in the southern basin of Lake Kivu during the 2002-2005 period. Rectangles highlight the annual dry season (June to October).

The major cyanobacteria T2 species were filamentous forms, such as *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg and *Cylindrospermopsis* cf. *curvispora* Wat., while *Synechococcus* sp. and various *Microcystis* species were the most represented species in the T1 group. Cyanobacteria T1 were present all year round in relatively small amounts, while cyanobacteria T2 were much more abundant, particularly during the rainy seasons (well stratified waters, low nutrients, but high light conditions) and usually in the top 20 to 30 m (Fig. 4).

Sestonic C:N:P ratios

The elemental ratios of the seston always remained well above the Redfield ratio and followed a clear seasonal pattern (Fig. 5). From generally high values during the rainy season, both the C:N and C:P ratios tended to decrease during the dry season. Following elemental thresholds defined by Healey and Hendzel (1980) and Guilford & Hecky (2000) to estimate nutrient deficiency of phytoplankton in lakes, the C:P ratios of seston in Lake Kivu indicated a moderate P-deficiency during the dry seasons and a severe P limitation during part of the rainy seasons. The C:N ratios indicated however a moderate N limitation throughout the whole study period, except in some dates during the dry seasons where no N-limitation occurred. The average ratios for the study period was 9.6 for C:N and 256.3 for C:P (Table I). The average N:P ratio was 26.8, clearly indicating P limitation.

Table I: Review on the primary production, Chlorophyll *a*, and sestonic C (carbon), N (nitrogen) and P (phosphorous), as well as the stoichiometry ratios (C:N, C:P and N:P) in Lake Kivu.

Primary prod. (g C m ⁻² d ⁻¹)	Chl <i>a</i> (µg l ⁻¹)	C (µg l ⁻¹)	N (µg l ⁻¹)	P (µg l ⁻¹)	C:N	C:P	N:P	n	Reference
1.03 – 1.44	-	-	-	-	-	-	-	<14*	Degens <i>et al.</i> , 1973
0.66 – 1.03* (Mars 1972-73)	-	-	-	-	-	-	-	8	Jannasch, 1975
0.33 (October 1990)	0.29 – 0.85	404.3	43.6	2.34	10.9	458.6	42.1	3 (pelagic)	Descy, 1990
0.37 – 1.50 (Mars 2002 – May 2005)	0.76 – 4.55	433.1	54.1	4.8	9.6	256.3	26.8	75 (27**)	This study

* The exact number of incubations was not stated in this reference;

** The average was calculated over 75 modelised values, but only 27 incubations were made.

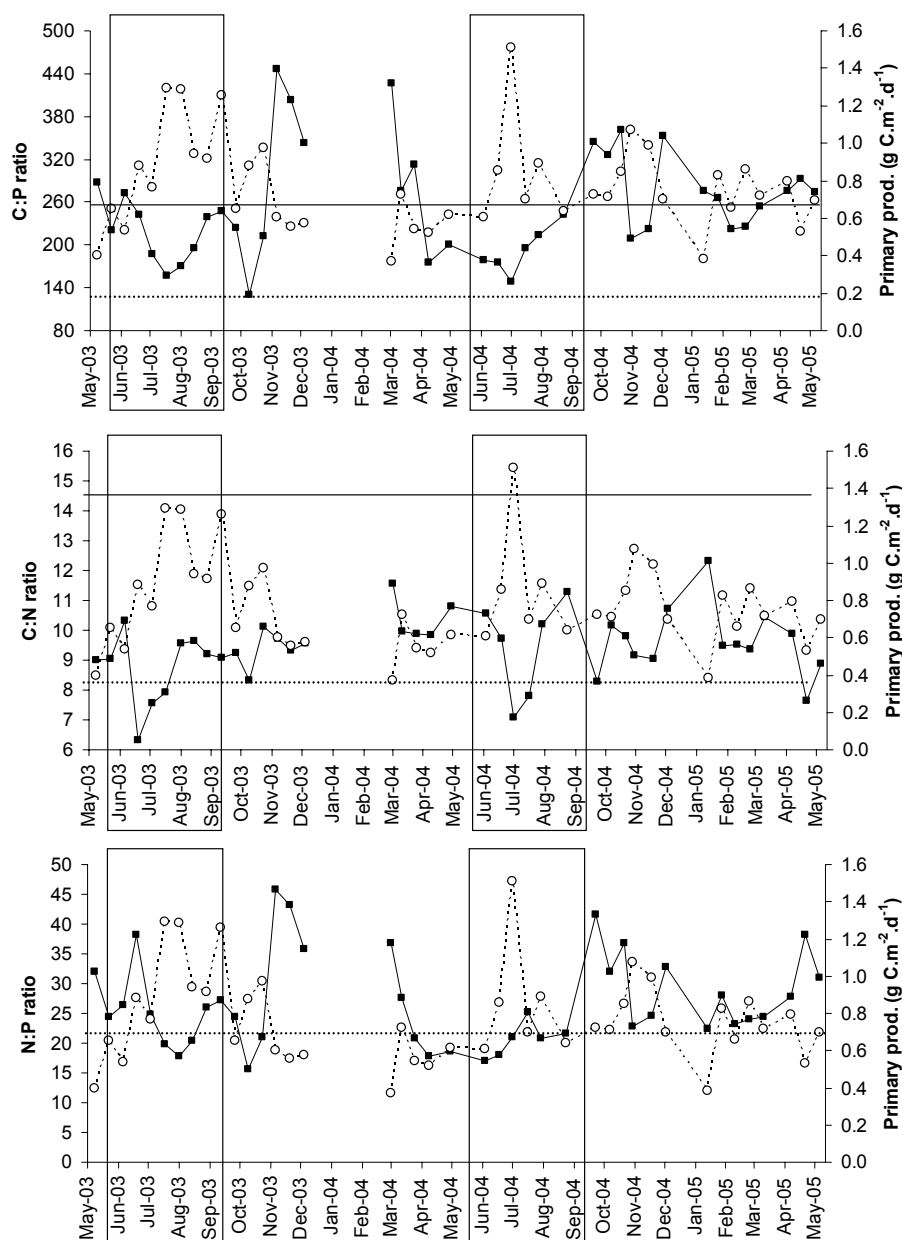


Fig. 5: Sestonic elemental ratios (C:P and C:N; bold squares) and primary production (open circles) in the southern basin of Lake Kivu during the 2003-2005 period. Rectangles highlight the annual dry season (June to October). Dotted horizontal line indicates the lower value of a moderated deficiency; bold horizontal line indicates the lower value of an extreme deficiency (from Healy and Henzel, 1980).

Primary production and the seston elemental ratios varied inversely: the increase in primary production during the dry season corresponded to a decrease of the elemental ratios. A significant negative correlation was observed between primary production and both C:N (Pearson correlation = -0.53, $p < 0.05$, $n = 40$) and C:P (Pearson correlation = -0.57, $p < 0.05$, $n = 40$) ratios. No relation was found between primary production and N:P ratio.

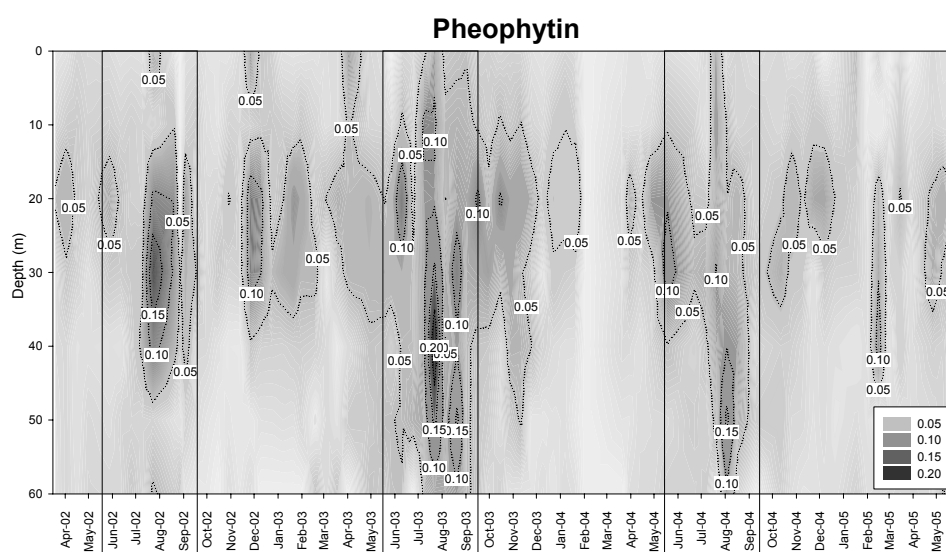


Fig. 6: Pheophytin vertical distribution within the top 60 m (in mg m^{-3}), in the southern basin of Lake Kivu during the 2002-2005 period. Rectangles highlight the annual dry season (June to October). Rectangles highlight the annual dry season (June to October).

Discussion

Fortnightly HPLC-pigment surveys on Lake Kivu in the 2002–2005 period showed a relatively constant pattern with some variations of Chl *a* in a relatively short range. The seasonal signal reported for the large East African lakes was also seen in Lake Kivu, with maxima of phytoplankton biomass and production during the well-mixed dry season, although increases of algal biomass also occurred at times during the rainy season. Actually, in this region of East Africa, the annual rainy season is often interrupted by a short dry season and, given the weak temperature-density gradient in the mixolimnion of Lake Kivu, deep vertical mixing may occur locally at different times of the year. The inter-annual variability of the dry season peak was also noteworthy, specially comparing the low productive 2002 dry season with the rest of the study period. The same remark had been made in other tropical lakes by Talling (1986) and Richerson *et al.* (1986).

Regarding primary production, past estimates made in Lake Kivu were based on few measurements (see Tab. I) and no paper explicitly studied seasonal variations of primary production in Lake Kivu. Yet, it is generally accepted that large East African Lakes may present a marked seasonality between dry and wet seasons depending on variations in wind velocity and air temperature (Tilzer, 1990; Talling, 1987; Sarmiento *et al.*, 2006). Deep mixing in tropical lakes generally stimulates primary production by internal loading of limiting nutrients from deep waters, but in some cases vertical mixing below the euphotic zone may sufficiently alter light conditions in the water column to limit phytoplankton growth (Lewis, 1974). For example, in the East African Great Lakes (Victoria, Malawi, Kivu and Tanganyika), phytoplankton biomass typically increases during the dry season, when surface nutrients are replenished by deep mixing (Talling, 1986; Hecky and Kling, 1987; Patterson and Kachinjika, 1995; Descy *et al.*, 2005; Sarmiento *et al.*, 2006).

Primary production in the large East African Great lakes is highly dependent on nutrients transported from the deep to the surface waters. Nutrient enrichment experiments in lakes Malawi, Victoria (Guildford *et al.*, 2003; Lehman and Branstrator, 1993, 1994) and Tanganyika (Jarvinen *et al.*, 1999; de Wever *et al.*, *submitted*) have systematically shown positive responses of phytoplankton to N, P and Fe enrichment, generally, with a lowering of the seston elemental ratios (C:N and C:P). These authors concluded that P, N (and in some cases Fe) were common limiting factors for algal growth. In Lake Kivu, the phytoplankton seemed to be subjected to a moderate to severe P-limitation. A moderate N-limitation may also intervene when the mixolimnion is well stratified (Fig. 5). As expected, cyanobacteria were more successful during those periods, especially filamentous forms (cyanobacteria “T2”) such as *Planktolyngbya limnetica*. This species is

particularly well adapted to tropical conditions and can grow under extremely low light intensities (less than $1 \mu\text{E m}^{-2} \text{s}^{-1}$ PAR, Reynolds *et al.*, 1983). During the dry season, deep nutrient-rich waters partially mix with the epilimnetic waters, and pennate diatoms (T1) became dominant. In these conditions, nutrient limitation can be reduced and sestonic C:P and C:N ratios decreased. A possible explanation for these sub-surface accumulations of *Urosolenia* cells (diatoms T2) could be the upward migration in the water column as described in several studies on marine *Rhizosolenia* species (Villareal and Lipschultz, 1995; Villareal *et al.*, 1996, 1999; Heather and Villareal, 2005), or simply a local development under daily stratification conditions, very common in this region (Worthington, 1930). The ecology of this particular taxon is discussed in Sarmiento *et al.* (2006).

Our study is the first long-term phytoplankton monitoring in Lake Kivu, and a substantial number of primary production measurements allowed a reliable assessment of average daily and annual phytoplankton production (average for the whole study period: $261 \text{ g C m}^{-2} \text{y}^{-1}$). Unfortunately, addressing changes in phytoplankton production and biomass over decades is not straightforward. The earliest estimate made for Lake Kivu, $375 \text{ g C m}^{-2} \text{y}^{-1}$, dated from the beginning of the 70s (Degens *et al.*, 1973) and was based on comparatively few measurements (Table 1). The range of daily rates measured in the 1970s was $0.66 - 1.44 \text{ g C m}^{-2} \text{d}^{-1}$, which is close to the range reported in the present study ($0.37 - 1.50 \text{ g C m}^{-2} \text{d}^{-1}$). Then, there is no indication of a significant change in primary production over the last three decades in the pelagic zone of Lake Kivu. We can thus play down the hypothesis that chemical changes observed during these last 3 decades in the deep waters results from the eutrophication of surface waters (Schmid *et al.* 2005). If primary production has stayed constant during these last 3 decades, and if we assumed that the increasing gas concentrations in deep waters results from higher sedimentation of biogenic materials, it implies that the export ratios of matter (i.e., the share of what is produced that sediments) has been completely changed and increased. Then, a more likely hypothesis explaining methane increase is that a change of trophic structure resulting from the sardine introduction has increased the export ratios of biogenic matter.

Previous quantitative estimates of phytoplankton biomass and composition in Lake Kivu can be found in Hecky and Kling (1987), who studied some surface samples from March 1972. These authors described the planktonic assemblage of Lake Kivu as being similar to that of the other East African Great Lakes, i.e. dominated by Chlorophytes and cyanobacteria, with diatoms at lower abundances. No pennate diatoms (“needle-like” *Nitzschia* and *Fragilaria*) were observed in the open lake at that time. Nowadays, they can be found in significant numbers (on average about 30 % of the standing phytoplankton biomass), particularly during the dry season. Although no

significant changes in species diversity was pointed out by Sarmento *et al.* (*in press*), significant changes in their abundance may have taken place during the last 3 decades.

Diatoms are denser than other non-siliceous algae, and have higher specific sedimentation rates (Reynolds, 1984; Padisák *et al.*, 2003). During the dry season, when diatoms reach maximum development in the lake, the light gradient in the mixed layer is very steep, as vertical mixing extends down to 60 m while the euphotic zone is never deeper than 35 m (Sarmento *et al.*, 2006). Such conditions of deep mixing are known to favour diatoms (Reynolds, 1984), but they may also accelerate the senescence process in some algal cells. Dead or senescent algae sink faster than viable cells, by a factor of three to five (Smayda and Boleyn, 1965; Eppley *et al.*, 1967; Smayda, 1970, 1974; Reynolds, 1973; Titman and Kilham, 1976; Wiseman and Reynolds, 1981). Increased sedimentation of diatoms could also occur when the water column re-stratifies at the beginning of the rainy season, as a result of photoinhibition and higher specific sinking rates (Reynolds, 1984).

The significant positive correlation found between diatoms T1 and pheophytin suggests an export flux of particulate organic matter toward the deep anoxic water. The increased contribution of diatoms to phytoplankton, and their subsequent loss through sedimentation might have contributed to enhanced losses of silica, phosphorus and organic carbon from the surface waters of Lake Kivu. It has been noted an important decrease of surface dissolved reactive silica over the last three decades (Sarmento *et al.*, 2006).

A further hint at this scenario is that in the current phytoplankton assemblage of Lake Kivu, the diatom *Urosolenia* sp. forms distinct near-surface populations. Hecky and Kling (1987) did not observe this species in their 1972 samples. These diatoms are well known by their capacity to grow under extreme oligotrophic conditions (Reynolds *et al.*, 2002) and their significant development in Lake Kivu would be a sign that P-limitation may have become more stringent in the surface waters, possibly as a result of increased losses of P to the deeper waters. So, the modification of the phytoplankton composition supports the hypothesis that methane enrichment of the deep waters is induced by changes in the vertical particulate flux.

Another biological factor that may have contributed to increasing nutrient export from the surface waters of the lake is the significant change in zooplankton community brought about by the introduction of *Limnothrissa miodon* (Isumbisho *et al.*, *in press*). Marshall (1991a) reported a drastic reduction of zooplankton biomass and an increase in phytoplankton after the introduction of the same sardine in Lake Kariba. In Lake Kivu, the most obvious consequence has been the disappearance of the large grazer, *Daphnia curvirostris*, reported by Dumont (1986), and a diminution of the

average total zooplankton biomass (Isumbisho *et al.*, *in press*). The elimination of this large cladoceran likely resulted in a reduction of the grazing pressure on that fraction of the phytoplankton that is edible by filter-feeding zooplankton, mostly the nanoplankton size class. This single fact may explain why present-day Chl *a* concentration in Lake Kivu is higher than in Lake Tanganyika (Descy *et al.*, 2005; Sarmiento *et al.*, 2006), despite similar surface light, daylight duration and nutrient conditions (although P limitation seems more severe in Lake Kivu). It is worth noting that, despite a 2 or 3 fold difference in algal biomass, rates of phytoplankton production and average daily primary production lie in the same range in both Lake Kivu and Lake Tanganyika. So, the higher algal biomass in Lake Kivu is to be related to the fate of the algal biomass – particularly less grazing due to the disappearance of the sole large grazer, and possibly, to lower edibility of the phytoplankton – rather than to higher primary production. In other words, as primary production stayed constant and grazing rates decreased, more algae biomass was susceptible to sediment.

Furthermore, a zooplankton community comprising only copepods is susceptible of inducing larger particulate export than a cladoceran-dominated community. Copepods produce coherent faecal pellets that sink rapidly and favour particle export to the sediment (Deuser *et al.*, 1981; Martin *et al.*, 1987; Dunbar and Berger, 1981; Lampitt, 1985). Moreover, when considering the stoichiometric constraints that determine zooplankton homeostasis (Sterner and Elser, 2002), they may favour N retention in the surface layers and regulate excess P by increasing P egestion. For instance, Darchambeau *et al.* (2005) showed that a cladoceran-dominated community favoured P recycling in the epilimnion, whereas when copepods became dominant, more P was exported through sedimentation of faecal pellets. This would support the hypothesis that the introduction of the efficient planktivore *Limnothrissa miodon* triggered large-scale geochemical changes in Lake Kivu, resulting from the spectacular change in zooplankton structure. This would provide a tentative explanation to the observed depletion of Si and P in the surface waters of Lake Kivu, while deep waters are now conversely enriched in these elements (Schmid *et al.* 2005). So, modifications of grazing pressure, internal nutrient recycling (Elser and Urabe, 1999) and nutrient sedimentation (Sarnelle, 1999; Darchambeau *et al.*, 2005) due to perturbations of zooplankton community are very probable in Lake Kivu. We may fairly hypothesize that the shift from *Daphnia* to copepod dominance resulted to a lower internal nutrient recycling and a higher sedimentation flux of egested material (Sarnelle, 1999; Darchambeau *et al.*, 2005), although further research is needed.

In summary, our results support the hypothesis that increased methane production and deep water enrichment in Si and P in Lake Kivu are the consequence of increased particulate export, brought about by a major

change in the lake food web, rather than the result of increased primary production. Testing this hypothesis for increased C, Si and P exports in Lake Kivu will require quantifying the vertical fluxes of these elements, using sediment traps deployed at different depths, but particularly at the oxic anoxic interface. In parallel, a food web simulation model, incorporating nutrient recycling and stoichiometric constraints of the plankton compartments, should be developed in order to reconstruct the geochemical effects of the present trophic functioning of the ecosystem, i.e. with a copepod-dominated zooplankton, possibly submitted to top-down control by the planktivorous clupeid, without a top predator.

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Chapitre VI

Etude du picoplancton des lacs tropicaux par la cytométrie de flux: l'exemple du lac Kivu

L'étude des conditions écologiques d'un lac demande l'emploi de techniques spéciales (...). Il fallait donc emmener un véritable laboratoire. D'autre part, le programme de nos recherches supposait des déplacements nombreux, par camion, par baleinière ou par porteurs. Nos instruments devaient donc être à la fois effectifs, d'un maintien aisé et assez robustes pour supporter le traitement d'un "Safari".

"Exploration du Parc National Albert"

H. Damas

1935-1936

*Flow cytometric study of tropical lake picoplankton:
Lake Kivu (Eastern Africa)*

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*Abundance and distribution of picoplankton in tropical, oligotrophic Lake Kivu, eastern Africa
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Abstract

This work is one of the first applications of flow cytometry in the characterisation of freshwater photosynthetic picoplankton (PPP) and heterotrophic bacteria (HB) in a tropical region. Over three cruises organised at different seasons, covering the four major basins of the Great East African Lake Kivu, phycoerythrin-rich cells dominated the PPP. Spatial, seasonal and vertical variations on PPP and HB cell numbers were relatively subtle (constantly high), which represents an important difference to temperate lakes that show high fluctuations in cell abundances during a year cycle. As in the ocean, the prevalence of the microbial food web and the seasonality are intimately linked to the physics of the systems. In open lake waters, where allochthonous carbon inputs are most probably inconsequential, HNA HB subpopulation was significantly correlated with Chl *a*, while no significant correlation existed for LNA or total bacteria. Our results join the idea that HNA HB subpopulation corresponds to active bacteria, whose growth is highly dependent on dissolved primary production. Additionally, an overview on the PPP concentrations across aquatic systems is presented, which suggests that abundance of *Synechococcus*-like cyanobacteria is higher in large, oligotrophic, tropical lakes than in any other aquatic system.

Introduction

The importance of photosynthetic and heterotrophic picoplankton in aquatic food webs was largely covered in the last decades (e. g. Pomeroy, 1974; Azam *et al.*, 1983; Stockner & Antia, 1986; Weisse, 1993; Fogg, 1995; Bell & Kalff, 2001). Most of the records are from marine systems, but some freshwater data on picoplankton are now published, but the great majority concern exclusively temperate lakes. Records for tropical lakes are rare, even if high picoplankton abundance in those warm and oligotrophic waters would be expected (Agawin *et al.*, 2000). Lake Tanganyika is one of the rare tropical lakes where picoplankton has attracted the attention of some scientists by its astonishingly high abundances (Vuorio *et al.*, 2003; Pirlot *et al.*, 2005; Descy *et al.*, 2005; Unrein and Sarmento, 2005). Hecky *et al.* (1981) were the first to hypothesise a major role played by heterotrophic bacteria (HB) in the trophic chain of Lake Tanganyika, earlier than the landmark paper by Azam *et al.* (1983) that firstly described the microbial loop in the oceans.

Photosynthetic picoplankton (PPP) abundance seems particularly affected by water temperature and trophic state. Agawin *et al.* (2000), in a literature review, showed the increasing importance of picophytoplankton in warm and oligotrophic waters. The reduced contribution of picophytoplankton in warm productive waters is hypothesized here to be due to increased loss rates, whereas the dominance of picophytoplankton in warm, oligotrophic waters is attributable to the differential capacity to use nutrients as a function of differences in size and capacity of intrinsic growth between picophytoplankton and larger phytoplankton cells. Bell & Kalf (2001) reported a significant positive relationship between picoplankton abundance and total chlorophyll *a* (Chl *a*) in a large number of lakes and over a large biomass range. Actually, the relation between trophic state and the PPP abundance appears to be complex. However, one theory seems to make consensus: the PPP abundance and production increases with the increasing trophic state while their contribution to total phytoplankton biomass and production decreases both in marine and freshwater ecosystems (Stockner, 1988; Søndergaard, 1991; Stockner, 1991).

Transparency (light conditions on the water column) has also a major impact in the PPP communities, on selecting the dominant pigment-type. Vörös *et al.* (1998) showed that phycocyanin-rich cells are typical from low light regimes, while more transparent waters usually favour phycoerythrin-rich cells. These results match with laboratory experiments on *Synechococcus* marine strains (Glover *et al.*, 1986; Waterbury *et al.*, 1986) and freshwater strains (Wyman & Fay, 1987; Hauschild *et al.*, 1991; Callieri *et al.*, 1996), that showed that phycoerythrin rich cells grew better in green

light (generally more penetrating in clear water columns in opposition to red light, that penetrates farther in turbid environments).

The seasonal fluctuation pattern of PPP abundances is now well known for temperate lakes (Crosbie *et al.*, 2003; Weisse, 1993; Stockner *et al.*, 2000; Weisse, 1988; Weisse & Kenter, 1991; Gaedke & Weisse, 1998; Belykh & Sorokovikova, 2003). The annual maximal peak always takes place in spring or summer, contrasting with relatively low numbers in the rest of the year. At present, no reference can be found in the literature concerning seasonal patterns of PPP in tropical freshwaters.

Another vital compartment of the microbial food web is the HB. Coupling between bacterioplankton and phytoplankton is generally accepted (Cole *et al.*, 1988), but this relationship is not as simple as it seems: Coveney & Wetzel (1995) noticed that, in an oligotrophic temperate lake, HB biomass followed Chl *a*, except when the maximum Chl *a* occurred in the metalimnion, where temperature was probably reducing bacterial growth. Temperature was then pointed as a primary factor for HB growth. Biddanda *et al.* (2001) established a relation between trophic state and HB biomass in temperate lakes, where smaller organisms predominate in oligotrophic conditions. We could, then, expect a high HB biomass in tropical lakes (by the favourable temperature conditions) and especially in oligotrophic ones. Indeed, Pirlot *et al.* (2005) found that the HB carbon corresponded to approximately half of the phytoplankton carbon in Lake Tanganyika ($\sim 2 \text{ g C m}^{-2}$).

Although several marine studies have demonstrated the efficiency and sensitivity of flow cytometry (e. g. Li & Wood, 1988; Gasol & del Giorgio, 2000), the technique has rarely been applied by limnologists in field studies of picoplankton (but see Crosbie *et al.*, 2003), and even less in tropical regions. Moreover, freshwater PPP and HB are usually studied separately, but from a functional point of view it is likely that they occupy a similar position in the microbial trophic web, as protozooplankton (heterotrophic nanoflagellates, ciliates, rotifers and nauplii) take both as a major source of carbon (e. g. Simek *et al.*, 1996; Nagata *et al.*, 1996).

In this paper we present data from one of the first flow cytometry studies in a tropical deep lake (Lake Kivu, East Africa), from three cruises at different seasons in 2003 and 2004. Finally, an overview on the PPP concentrations across aquatic systems is presented, which suggests that abundance of *Synechococcus*-like cyanobacteria is higher in large, oligotrophic, tropical lakes than in any other aquatic system.

during the cruises. Depth of the mixed layer (Z_m) was estimated from the depth of the top of the thermocline, as shown by the temperature and oxygen vertical profiles obtained with the multiparameter sonde.

Samples for Chlorophyll *a* (Chl *a*) and secondary pigment analysis followed a procedure described in Descy *et al.* (2000): 3 L were filtered on Whatman GF/F (Maidstone, U.K.) or Macherey-Nägel (Düren, Germany) GF/5 filters, of 0.7 μm pore size. Pigment extraction was carried out in 10 ml 90 % HPLC grade acetone. After two 15 min sonications separated by an overnight period at 4°C in the dark, HPLC analysis was carried out using the Wright *et al.* (1991) gradient elution method, with a Waters system comprising a PDA detector and a fluorescence detector. Calibration was made using commercial external standards (DHI, Denmark).

Fractionated Chl *a* measurements were made from an average euphotic layer sample made by mixing equal volumes of lake water sampled from 0 to 20 m; 3 l were filtered on a Millipore membrane of 2 μm pore size ($> 2\mu\text{m}$ fraction), and the filtrate was filtered on a GF/5 filter ($< 2\mu\text{m}$ fraction). Both filters were extracted and analysed in HPLC by the procedure described above.

Picoplankton cell number was measured with a FacsCalibur flow cytometer, and some PPP samples were counted with an epifluorescence microscope for methods intercalibration. For the flow cytometry countings, 4 ml of lake water were collected at each depth and fixed immediately with cold Glutaraldehyde 10% (final concentration 1%), left in the dark for 10 min. at room temperature and then stored at -20°C. Two subsamples were taken for separate counts of heterotrophic and photosynthetic picoplankton. For heterotrophic bacteria, a 400 μl sample was added with a diluted SYTO-13 (Molecular Probes Inc., Eugene, OR, USA) stock (10:1) at 2.5 $\mu\text{mol l}^{-1}$ final concentration, left for about 10 min in the dark to complete the staining and run in flow cytometry. We use a FacsCalibur (Becton Dickinson) flow cytometer equipped with a 15 mW Argon-ion laser (488 nm emission). At least 30000 events have been acquired for each subsample (usually 90000 events). Fluorescent beads (1 μm , Fluoresbrite carboxylate microspheres, Polysciences Inc., Warrington, PA) were added at a known density as internal standard. The bead standard concentration was determined by epifluorescence microscopy. Bacteria were detected by their signature in a plot of 90° light scatter vs. green fluorescence. Bacteria were separated in two populations: HNA and LNA bacteria by the 90° light scatter vs. green fluorescence plot (Gasol *et al.*, 1999). In a red fluorescence - green fluorescence plot (Fig. 2), beads fall in a line, bacteria in another one, and noise in a third one (respectively with more red fluorescence than green fluorescence). Picocyanobacteria fall in between noise and bacteria. This

method is based on del Giorgio *et al.*, (1996) and discussed in Gasol & del Giorgio (2000). For photosynthetic picoplankton, we used the same procedure as for heterotrophic bacteria, but without addition of SYTO-13. Small algae were easily identified in plots of 90° light scatter vs. red fluorescence, and orange fluorescence vs red fluorescence. Data acquisition and analysis were performed with the Paint-A-Gate program (Becton Dickinson).

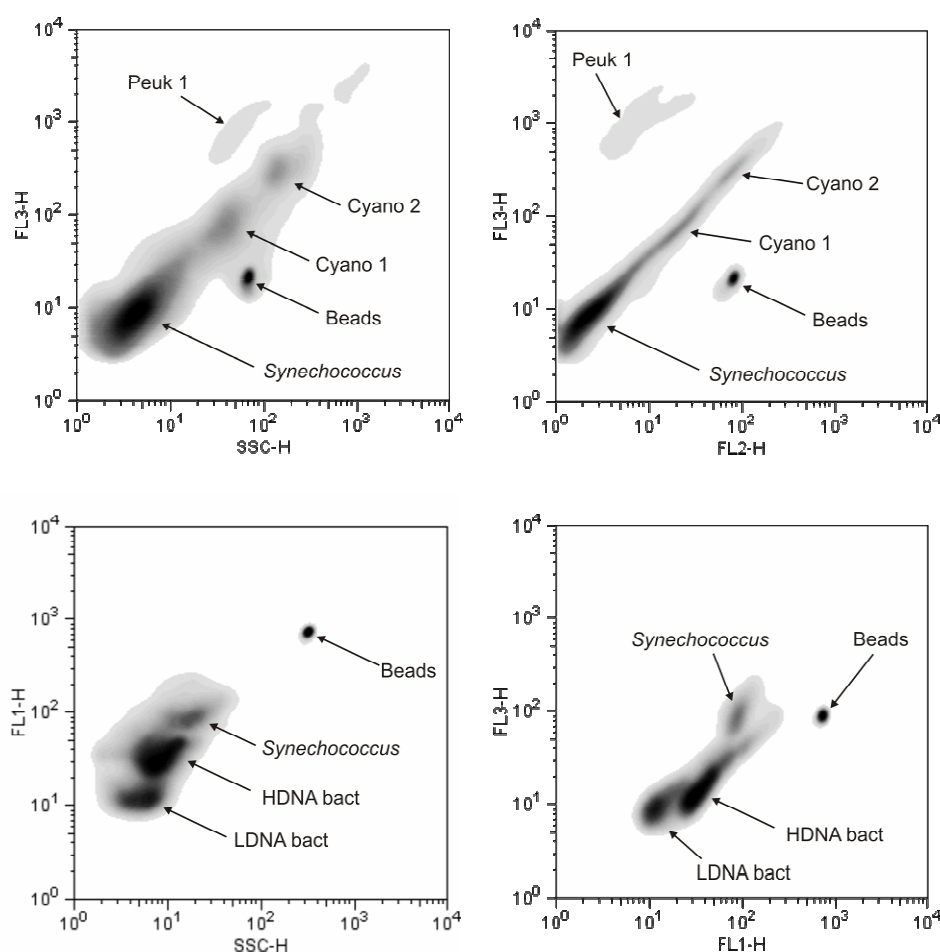


Fig. 2: Typical cytograms from a Lake Kivu sample showing the picoplankton populations (autotrophic in the top and heterotrophic in the bottom).

Samples for epifluorescence microscopy were preserved by adding filtered (0.22 μm Millex [Millipore, Billerica, MA, U.S.A.]) glutaraldehyde (1% final concentration) and stored at -20°C until analysis. For PPP enumeration in epifluorescence microscopy, 10 ml of water sample were filtered onto a 0.8 μm polycarbonate black filter (Nuclepore, Whatman International Ltd, Maidstone, U.K.) using a 5 μm backing filter. On average 1000 cells from 10 randomly chosen fields were enumerated using a Zeiss Axioplan microscope at a $1000\times$ magnification.

Results

The results are presented by geographic sectors that reflect the exposure to winds: the northern/eastern basins correspond to open lake conditions, more exposed to winds, and the southern/western basins, smaller and more protected by the surrounding mountains.

The environmental conditions during the three cruises were slightly different as a result of the dominant south-eastern dry season winds that induce deep mixing events. The mixed layer (Z_m) attained 60 m in the dry season cruise, while in the rainy season it was only 25 m. In the transition between seasons, the lake began to re-stratify, and the epilimnion was 50 meters deep, although its delimitation was not very clear. The light conditions were rather similar between basins and seasons: the depth of the euphotic zone (Z_{eu}) ranged between 15.3 and 18.2 m, and was slightly deeper in the rainy season (Tab. I).

Algal biomass (expressed in Chl *a*) in the Z_{eu} was higher in the dry season cruise, reaching 3.76 µg l⁻¹ in the northern/eastern basins and 2.70 µg l⁻¹ in the southern/western basins. The results for the rainy season and for the transition cruises corresponded to the mean values previously reported for Lake Kivu (in the 1.25 – 1.62 µg Chl *a* l⁻¹ range). Fractionated Chl *a* results show a relatively constant pattern: in average, the < 2µm fraction contributed 21.2% of total Chl *a* (Tab. I).

We identified 4 different populations of photosynthetic picoplankton in the flow cytometry countings (Fig. 2): three of phycoerythrin-rich picocyanobacteria (*Synechococcus*-like) and one constituted of picoeukaryotes (Peuk 1). These results were confirmed by epifluorescence microscopy. A summary of cell numbers, along with as the other variables are presented in Tab. I., We observed sporadically anoxygenic photosynthetic bacteria populations in the northern basin and in the isolated Kabuno bay, under the chemocline. These results were confirmed by HPLC detection of bacteriochlorophylls (data not shown).

Table I: Summary of some general features and picoplankton results in the two sectors of Lake Kivu at different seasons (Zm – depth of the mixed layer, Zeu – depth of the euphotic layer, HB – Heterotrophic bacteria, PPP – Photosynthetic picoplankton, Peuk – picoeukaryotes).

	<i>Temp.</i>	<i>Zm</i>	<i>Zeu</i>	<i>Mean</i> <i>Chl a</i>	<i>%</i> <i>Chl a</i>	<i>HB</i>	<i>PPP</i>	<i>HB : PPP</i>	<i>Peuk</i>
	(°C)	(m)	(m)	(µg l ⁻¹)	< 2µm	(10 ⁶ cell ml ⁻¹)	(10 ⁵ cell ml ⁻¹)	(cell ml ⁻¹ ratio)	(10 ³ cell ml ⁻¹)
Dry season									
Northern / Eastern basins	23.1	60	16.5	3.76	n.a.	1.53	1.15	12.4	2.4
Southern / Western basins	23.2	60	15.3	2.7	28.3	1.25	1.29	12.3	1.56
Transition									
Northern / Eastern basins	23.4	50	17.6	1.62	17.2	1.34	0.74	12.4	5.89
Southern / Western basins	23.2	50	17.4	1.52	17.5	1.73	1.42	9.24	8.47
Rainy season									
Northern / Eastern basins	24.1	25	17.6	1.49	23.8	1.78	1.37	12.4	n.a.
Southern / Western basins	24.2	25	18.2	1.25	19	1.77	1.39	11.4	n.a.

The PPP (*Synechococcus*-like coccoid cyanobacteria) abundances in the euphotic zone ranged between 0.5 and 2.0 10^5 cell ml^{-1} . As expected, the vertical profiles revealed higher abundances within the Zeu than at depth, with a sharp decrease around 30 m depth. In the northern/eastern basins, seasonal variation in PPP abundance was greater than in the southern/western basins (fig. 3). Average cell biovolume, determined by epifluorescence microscopy, was 0.43 μm^3 ; using a conversion factor of 0.47 pg C μm^{-3} (Verity *et al.*, 1992), mean PPP biomass in the euphotic zone was 1.1 g C m^{-2} .

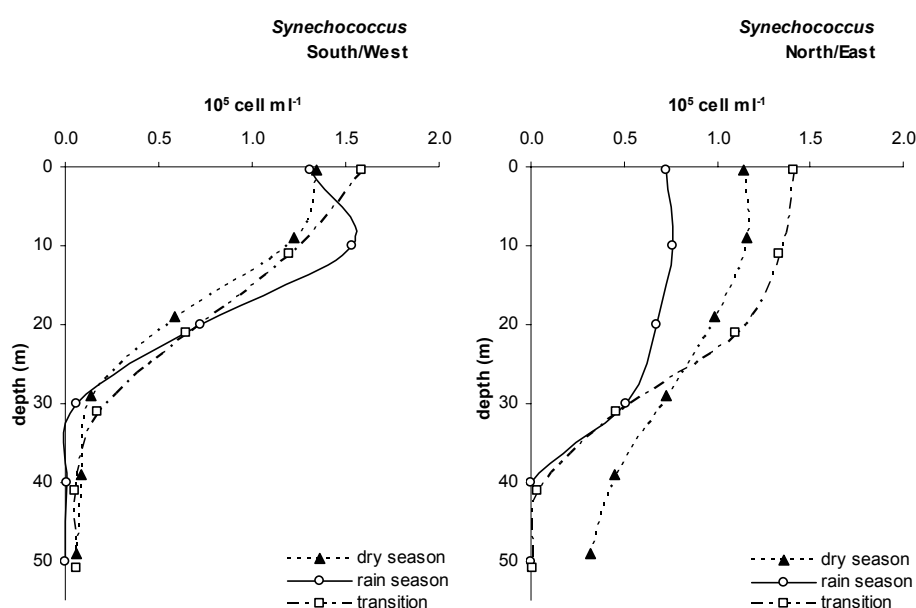


Fig. 3: Profiles of photosynthetic picoplankton (*Synechococcus*-like) in the two sectors (northern/eastern and southern/western basins) of Lake Kivu at different seasons (2003/2004).

Heterotrophic bacteria (HB) concentrations were relatively constant, in the 1 - 2 10^6 cell ml^{-1} range. HNA bacteria were dominant in the euphotic layer, contributing with 64%, on average, of the total number of heterotrophic bacterial. This proportion decreased with depth, reaching ~30% in the anoxic hypolimnion (60-70 m). The vertical distribution of HB did not show any clear seasonal pattern (fig. 4).

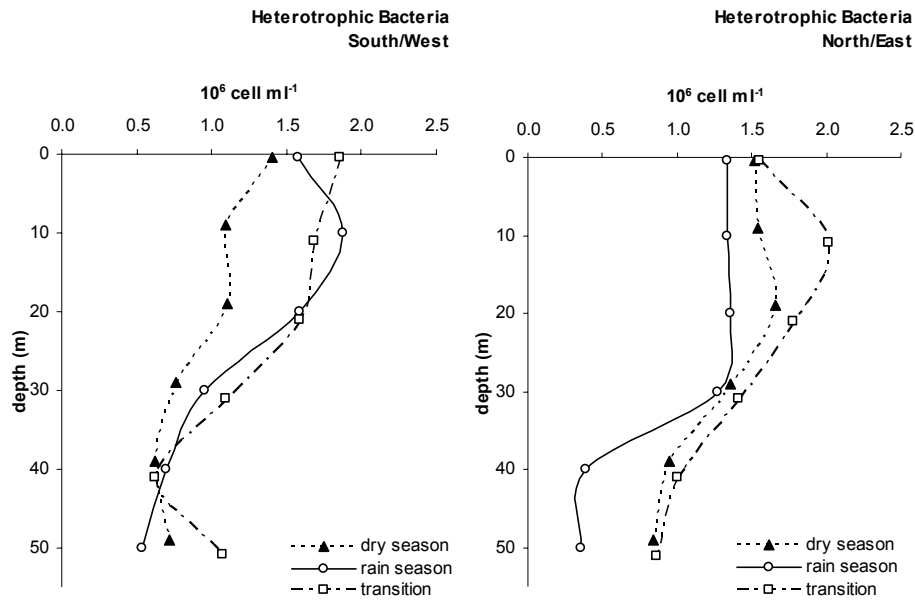


Fig. 4: Profiles of heterotrophic bacteria in the two sectors (northern/eastern and southern/western basins) of Lake Kivu at different seasons (2003/2004).

We tried to correlate phytoplankton biomass with LNA, HNA and total heterotrophic bacteria, but the only significant correlation was between Chl *a* and HNA (Pearson correlation coefficient = 0.90, $p < 0.01$). We also included some data from Lake Tanganyika (Fig. 5) redrawn from Stenuite *et al.* (submitted) in order to enlarge the data range, and we found the same correlation with a similar slope (Pearson correlation coefficient = 0.86, $p > 0.01$).

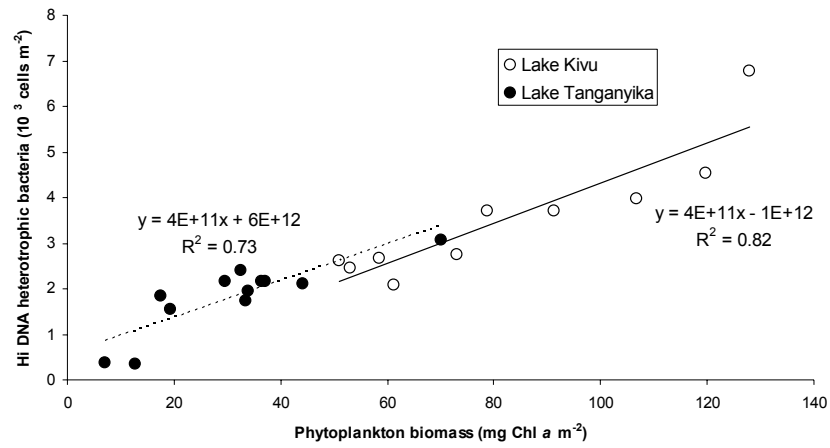


Fig. 5: Relation between phytoplankton biomass (Chl *a*) and HNA heterotrophic bacteria integrated over the euphotic layer of lakes Kivu and Tanganyika.

Discussion

This study reports one of the first applications of flow cytometry in the characterisation of freshwater photosynthetic picoplankton (PPP) and heterotrophic bacteria (HB) in a tropical region. As expected, in a lake with relatively high transparency, phycoerythrin-rich cells dominated the PPP (Vörös *et al.*, 1998). Spatial and seasonal variations were relatively subtle, and distribution in the water column was rather constant. Within the euphotic layer, PPP and HB abundances were, in each case, in the same order of magnitude in all the sampling stations, at all seasons. This is an important difference when compared with temperate lakes, which show large fluctuations in cell abundances during the annual cycle.

However, a slight seasonal pattern was observed in the northern and eastern regions of the lake. The shape of the vertical profiles was the main difference, suggesting that cell abundance followed the deeper vertical mixing. These results seem to confirm that these regions of the lake, being more exposed to the dry season winds, experience higher influence of the physical factors than the more protected southern and western regions. Besides this slightly contrasted vertical distribution of picoplankton, there were no significant differences among all lake regions in Chl *a* nor in Zeu. More investigations are necessary to understand why picoplankton responded to seasonal factors in the parts of the lake most exposed to wind, while total phytoplankton biomass remained similar.

Regarding transparency and Chl *a*, Lake Tanganyika is usually considered as more oligotrophic than Lake Kivu (Hecky & Kling, 1987; Sarmento *et al.*, 2006). This is verified by the larger proportion of picocyanobacteria in Lake Tanganyika: Descy *et al.* (2005) reported that more than 50% of total Chl *a* was in the $<2\ \mu\text{m}$ fraction, in the southern basin; this tendency is confirmed by Pirlot *et al.* (*submitted*), although the contribution of PPP to total phytoplankton biomass is lower in the northern part of Lake Tanganyika. In terms of PPP cell abundance, the figures are consistently higher in Lake Tanganyika ($3.4 \times 10^5\ \text{cells ml}^{-1}$ against $1.2 \times 10^5\ \text{cells ml}^{-1}$ in Lake Kivu; average in the euphotic zone). Then, Lake Kivu, which has higher Chl *a* and vertical light extinction than Lake Tanganyika, has a lower contribution of PPP ($< 2\ \mu\text{m}$ fraction) to total phytoplankton, but not a higher PPP cell number. This contrasts with the view that PPP abundance increases with the increasing trophic state while their contribution to total phytoplankton biomass decreases (Stockner, 1988; Søndergaard, 1991; Stockner, 1991; Stockner *et al.*, 2000). Does this deviation from the pattern observed in temperate regions imply that tropical lakes are different, as far as PPP is concerned? Whatever the answer might be, these apparent differences draw the attention on the risk of making generalisations in limnology. In the comparison we make here between the two large tropical lakes, factors such

as nutrient limitation (greater P limitation in Lake Kivu; see Sarmento *et al.*, *submitted*), variability of light climate, competition with other phytoplankton, and food web structure (more complex in Lake Tanganyika, possibly with more protozooplankton) may be of greater significance than trophic status in determining PPP abundance and contribution to autotrophs biomass in these two lakes.

The review presented in Tab. II shows that cell abundance per unit area of euphotic zone in the oligotrophic lakes Kivu and Tanganyika is comparable to those of eutrophic temperate lakes. This may be related to the higher mean primary production in large tropical lakes than in their temperate counterparts, that was already pointed out by Kilham & Kilham (1990, 1991), due to higher and rather constant irradiance (see also Talling, in Beadle, 1981), a deep euphotic zone and more efficient nutrient recycling in the water column, favoured by higher biological activity in the warm mixed layer. Interestingly, *Synechococcus*-like cell abundance is still much higher in those tropical lakes than in oceanic waters with an even greater euphotic zone and much lower Chl *a*. The reason for this apparent paradox might be, again, that there are other factors than light and nutrient availability which structure picoplankton communities in fresh and marine waters.

The abundance of heterotrophic bacteria (HB) didn't show any clear seasonal pattern, and varied between 1 and 2 10^6 cell ml⁻¹ in the euphotic zone. Again, similar observations of constancy of HB numbers compared to large seasonal changes in Chl *a* were reported by Pirlot *et al.* (*submitted*) for Lake Tanganyika, suggesting a balance between production and mortality losses of HB. Interestingly, we found that abundance of HNA bacteria was significantly correlated with Chl *a* in both lakes Tanganyika and Kivu, while no significant correlation existed for LNA or total bacteria. The interpretation of the meaning of these two bacterial subpopulations (HNA and LNA) is a controversial issue, but our results seem to confirm that the HNA population would correspond to active bacteria, as their numbers respond to phytoplankton biomass increase, and probably to organic carbon availability from algal excretion and mortality. Servais *et al.* (2003) showed that, in different aquatic ecosystems (marine, brackish and freshwater), HNA and LNA subpopulation cells were composed by the same dominant species and that an important heterogeneity of physiological states coexisted at the same time. Curiously, in one of the first papers published on this issue, Li *et al.* (1995) reported the same kind of correlation between the fluorescence intensity of HNA bacteria (at that time called type-II) and Chl *a*, while LNA (or type-I) fluorescence intensity was rather constant across the Chl *a* range.

Table II: Review on some general features and *Synechococcus*-like (maximum and mean) concentrations integrated in the euphotic layer (when available, otherwise, in the mixed layer), in different environments, latitudes and trophic state. (EM – Epifluorescence microscopy, FC – Flow cytometry; ****annual mean, ***spring/summer, **autumn/winter, *single sample/cruise). Note: *Prochlorococcus* was not taken into account for marine data.

Environment	Trophic state	Temp (°C)	Zeu (m)	Mean Chl <i>a</i> (µg l ⁻¹)	max <i>Synechococcus</i> -like (10 ¹⁰ cell m ⁻²)	mean <i>Synechococcus</i> -like (10 ¹⁰ cell m ⁻²)	Method	Reference
Marine								
South Atlantic - gyre*	ultra-oligotrophic	20	82	0.2	297	69	FC	Gasol <i>et al.</i> , unpublished
South Atlantic*	ultra-oligotrophic	25.6	95	0.2	221	64	FC	Gasol <i>et al.</i> , unpublished
Atlantic - Equatorial water*	ultra-oligotrophic	24.5	69	0.4	89	49	FC	Gasol <i>et al.</i> , unpublished
North Atlantic (near the African coast)*	oligotrophic (upwelling)	23.1	62	0.5	1044	134	FC	Gasol <i>et al.</i> , unpublished
Brackish water								
San Francisco bay (freshwater - seawater transect)***	eutrophic (variable)	17.7	-	9.7	52	9	EM	Ning <i>et al.</i> , 2000
Freshwater								
11 Antarctic lakes***	different trophic status	-9.9	-	1.9	0.3	0.1	FC	Andreoli <i>et al.</i> , 1992
4 boreal lakes in Finland****	different trophic status	~15	3.3	8.3	202	26	EM	Jasser & Arvola 2003
7 temperate lakes in Denmark	different trophic status	~15	1 – 15	7-200	495	<30	EM	Søndergaard 1991
48 lakes in North America*	Oligo- to mesotrophic	~22	3 – 15	8.7	140	~100	EM	Lavallee & Pick 2002

Environment	Trophic state	Temp (°C)	Zeus (m)	Mean Chl <i>a</i> (µg l ⁻¹)	max <i>Synechococcus</i> -like (10 ¹⁰ cell m ⁻²)	mean <i>Synechococcus</i> -like (10 ¹⁰ cell m ⁻²)	Method	Reference
Southern Lake Baikal*	oligotrophic	~12	~15	-	3000	~1500	EM	Nagata <i>et al.</i> , 1994
Lake Baikal****	oligotrophic	~6	~15	-	1485	150	EM	Belykh & Sorokovikova 2003
2 lakes in British Columbia***	oligotrophic	15.4	-	0.8	78	36	EM	Stockner & Shortreed 1985
Lake Maggiore (subalpine lake) in Italy****	oligotrophic	11.8	15	2.9	825	185	EM	Callieri & Piscia 2002
Lake Skrzynka (shallow lake) in Poland***	oligo-mesotrophic	~15	-	-	763	199	EM	Szelag-Wasielewska 1999
Lake Biwa in Japan****	mesotrophic	~15	15	6.5	2170	186	EM	Wakabayashi & Ichise 2004
Lake Constance (pre-alpine lake) in central Europe***	meso-eutrophic	~12	-	-	314	~100	EM	Weisse 1988
Furuike Pond (pond) in Japan****	hypereutrophic	~15	-	~100	152	45	EM	Hirose <i>et al.</i> , 2003
4 semi-tropical productive shallow lakes in Florida*	hypereutrophic	~25	0.8	111.4	677	341	EM	Carrick & Schelske 1997
Lake Apopka (semi-tropical shallow lake) in Florida****	hypereutrophic	25	0.8	105.1	2384	1088	EM	Carrick & Schelske 1997
Lake Tanganyika (large tropical lake)****	oligotrophic	26.8	44	-	2670	890	EM	Vuorio <i>et al.</i> , 2003
Lake Tanganyika (large tropical lake)****	oligotrophic	26.8	39	0.6	3190	1323	FC	Stenuite <i>et al.</i> , submitted
Lake Kivu (large tropical lake)****	oligotrophic	24.9	18	2.2	630	216	FC	This study

HB and PPP abundance has been shown to correlate with water temperature in lakes and oceans (e. g. Caron *et al.*, 1985; Murphy & Haugen, 1985; Jochem, 1988; Maeda *et al.*, 1992; Coveney & Wetzel, 1995). In tropical lakes, the warm waters all year round are favourable to high abundances of these micro-organisms, enhancing the role of the microbial food web. Most studies in tropical limnology conducted so far have neglected the microbial food web, following the models from temperate regions where picoplankton is abundant only sporadically in a specific period.

Finally, Schallenberg & Burns (2001) found that PPP in oligotrophic lakes is an early indicator of change in trophic status, but that they can respond in complex ways to nutrient enrichment. Several East African Great Lakes, in particular Lake Tanganyika, were already cited as affected by global warming, and changes in phytoplankton composition over the last decades have been reported (Verburg *et al.*, 2003; Cocquyt & Vyverman, 2005). In this context, this study represents a reference point for future investigations on the effects of climatic and other anthropogenic changes in a unique lacustrine environment.

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Chapitre VII

Discussion générale et perspectives

En quatre-vingt ans, depuis la date de sa découverte jusqu'à aujourd'hui, le Nyamulagira a laissé ses laves s'échapper une bonne dizaine de fois. Trois fois elles ont atteint les eaux du lac Kivu: pas le cratère Kateruzi en 1912, par le cratère Tshambene, en 1938, et en 1948 par le cratère Muhuboli (...).

Le Niragongo lui, dans cette brève époque historique que Götzen avait ouverte, n'a pas délivré une seule éruption de son cratère.

"Niragongo ou le volcan interdit"

H. Tazieff
1975

Le 17 Janvier 2002 le Niragnongo est entré en éruption et 10^6 m^3 de lave se sont déversés dans le lac, après avoir traversé la ville de Goma.

Discussion générale et perspectives

Pour la première fois, une étude approfondie et à long terme sur la limnologie et l'écologie de phytoplancton du lac Kivu a été menée. L'étude s'est structurée en deux approches complémentaires: un suivi régulier dans le bassin Sud (Ishungu), avec des campagnes d'échantillonnage toutes les deux semaines, de février 2002 à mai 2005, totalisant un peu plus de trois ans; et quatre croisières (deux en 2003 et deux en 2004) à des saisons différentes, permettant d'évaluer la variabilité spatiale dans l'entièreté du lac. Profitant du fait qu'une étude similaire a eu lieu au lac Tanganyika pendant la même période, et puisque le lac Tanganyika est l'un des lacs le plus connus dans la région, il est inévitable de faire des comparaisons, en se servant de l'exemple du lac Tanganyika comme une référence de lac tropical, oligotrophe et méromictique.

L'utilisation de plusieurs techniques complémentaires comme l'analyse en HPLC des pigments marqueurs, cytométrie de flux, microscopie optique, en épifluorescence et électronique de balayage, s'est avérée indispensable pour la compréhension du système dans sa globalité. Par exemple, l'abondance réelle de la diatomée *Urosolenia* sp., n'aurait pas pu être estimée sans la microscopie électronique à balayage, effectuée dans des échantillons fixés à la glutaraldéhyde, qui est une méthode beaucoup moins agressive que la fixation classique au formaldéhyde. Un autre exemple de cette complémentarité de techniques est fourni par les résultats de la cytométrie de flux concernant le picoplancton, compartiment largement négligé par le passé dans les études de microscopie inversée. Une des conclusions de cette étude, sur le point de vue méthodologique, est que dans ces grands lacs tropicaux, comme dans l'océan, le simple comptage en microscope inversé est largement insuffisant. La multiplication des prélèvements, en vue d'obtenir une résolution spatiale (dans la colonne d'eau et à des différents points du lac) et temporelle suffisantes, doit être favorisée. Pour accomplir une telle tâche, des techniques automatisées sont plus indiquées, et l'analyse des pigments marqueurs par HPLC a montré ses avantages à ce point de vue.

Dans un premier temps (chapitre III), nous avons prêté une attention particulière à la composition floristique du phytoplancton pélagique du lac Kivu. En zone pélagique, les quatre bassins présentent la même composition algale. Par contre, la structure physique de la colonne d'eau s'est avérée un important facteur de diversification, avec quelques espèces typiques du métalimnion ou du bas de l'épilimnion, comme *Cryptaulax* sp., *Cryptomonas* sp., cf. *Rhodomonas* sp. et *Merismopedia trolleri* Bach. Le gradient vertical de lumière et nutriments, dans des conditions relativement stables tout au long de l'année, est une des sources de variabilité les plus importantes dans ce lac. Les espèces les plus communes sont des diatomées

pennées *Nitzschia bacata* Hust. et *Fragilaria danica* (Kütz.) Lange-Bert., et des cyanobactéries *Planktolyngbya limnetica* (Lemm.) Komárková-Legnerová and Cronberg et *Synechococcus* sp.. La diatomée centrique *Urosolenia* sp. et la cyanobactérie *Microcystis* sp. sont fréquemment très abondantes, principalement au voisinage de la surface en conditions de stratification journalière.

De légères différences ont été observées relativement à la situation décrite dans les rares études trouvées dans la littérature. Ainsi, les données existantes ne sont pas concluantes quant à un possible impact de l'introduction de la sardine planctonivore *Limnothrissa miodon* Boulenger (endémique du lac Tanganyika) sur la diversité du phytoplancton pélagique du lac Kivu. On peut néanmoins noter que les diatomées pennées, aujourd'hui très bien représentées dans la zone pélagique, n'étaient citées comme abondantes que dans une baie isolée (Kabuno), dans les études précédentes. Si ces changements dans l'abondance de certains taxons pélagiques se confirment, notamment par l'étude de carottage dans les sédiments, ce serait un argument de plus à l'appui de l'hypothèse de modifications biogéochimiques consécutives à l'introduction de la sardine. Une des conséquences aurait pu être une augmentation du flux de sédimentation des matières organiques et des nutriments vers l'hypolimnion (cf. chapitre V).

Quant à l'écologie du phytoplancton du lac Kivu, on peut dire que les groupes d'algues dominantes correspondent aux prévisions théoriques pour ce type de lac: dominance de diatomées pendant les épisodes de mélange profond durant la saison sèche, et dominance de cyanobactéries pendant la saison des pluies, avec une colonne d'eau stratifiée et les conditions de lumière plus favorables, mais moins de nutriments. Par contre, si l'on compare le phytoplancton du lac Kivu à celui des autres lacs de la région, il est *a priori* surprenant de trouver plus de similitudes avec le lac Victoria (avant l'eutrophisation des deux dernières décennies) qu'avec les lacs Tanganyika ou Malawi. La zone euphotique au lac Kivu est relativement peu profonde, presque toujours moins épaisse que la zone de mélange, comme au lac Victoria. De plus, la stratification thermique des couches superficielles est assez instable. Des mélanges partiels peuvent se produire régulièrement, notamment pendant la petite saison sèche (janvier/février), de sorte que la zone de mélange peut atteindre le chimiocline (~70 m). Tous ces facteurs régulateurs sont aussi rencontrés au lac Victoria, qui se trouve à la même latitude et à une altitude comparable, et qui est soumis à des conditions météorologiques très semblables. La seule différence importante est que, en période de mélange, le lac Victoria se déstratifie complètement et que le mélange atteint les sédiments. En d'autres mots, au contraire du lac Kivu, le lac Victoria n'est pas méromictique, ce qui expliquerait les valeurs de

biomasse inférieures au lac Kivu (la moyenne annuelle de chlorophylle *a* dans la zone de mélange étant de 2.2 mg m^{-3}).

Un trait (très probablement) commun entre tous ces grands lacs tropicaux est l'abondance constamment élevée de picoplancton phototrophe (chapitre VI). Au lac Kivu, les variations spatiales, saisonnières et verticales ont été relativement légères au cours de nos trois croisières. Il est très probable que la température joue ici un rôle primordial, permettant à ces organismes à croissance rapide et ayant des besoins en nutriments relativement faibles, un succès incomparable, en termes de concentration cellulaire. Un ratio surface:volume élevé augmente considérablement la superficie de contact et l'absorption de nutriments, pour un besoin en carbone limité, vu les petites dimensions de ces organismes. De plus, avec des pigments photoprotecteurs (comme la zéaxanthine) qui leur permettent de tolérer des fortes intensités lumineuses notamment proches de la surface, et des pigments hautement efficaces pour la captation de la lumière (comme la phycoérythrine) dans les eaux relativement transparentes, où les longueurs d'onde correspondant aux lumières bleu et verte sont plus pénétrantes, les picocyanobactéries du type *Synechococcus* sont hautement compétitives.

En zone pélagique, les apports allochtones de carbone sont probablement négligeables et la croissance des bactéries hétérotrophes, particulièrement de la sous-population HNA (très probablement correspondant aux bactéries actives), dépend fortement de la production primaire dissoute (excrétion, mortalité, etc.). Dans le futur, certains aspects du réseau trophique microbien du lac Kivu mériteront d'être éclaircis. Des estimations préliminaires (résultats non publiés) semblent indiquer une abondance de nanoflagellés hétérotrophes proche de celle observée au lac Tanganyika. Par contre, il semble y avoir beaucoup moins de ciliés de grande taille au lac Kivu. D'un autre côté, les rotifères y sont bien représentés en zone pélagique: en particulier, une espèce de *Bdelloides* (pourtant connus comme étant essentiellement benthiques) est abondante par moment. Ces derniers pourraient jouer un rôle important dans le réseau trophique microbien, ce qui distinguerait substantiellement le lac Kivu des autres lacs environnants, où les rotifères sont absents.

Dans l'ensemble, le réseau trophique au lac Kivu semble peu efficient. Les relations phyto-zooplancton seront discutées plus en profondeur dans le travail de M. Isumbisho qui a été mené en parallèle. Quelques pistes de réflexion peuvent être émises: la production primaire aux lacs Kivu et Tanganyika est du même ordre de grandeur; en revanche, la biomasse algale est environ deux fois plus élevée au lac Kivu. La seule explication plausible est une exploitation inefficace des ressources algales par le zooplancton. Cette biomasse algale, souvent carencée en nutriments, en particulier en phosphore, ne pouvant pas se diviser éternellement, finit par sédimenter. Des

résultats préliminaires non publiés d'une trappe à sédiments placée à la limite supérieure de la zone anoxique ont montré la présence d'algues vivantes à cette profondeur, indiquant qu'une bonne partie de la biomasse algale, non exploitée, traverse le chimiocline et se perd dans les eaux profondes. Voici un autre aspect à éclaircir dans les recherches futures: les flux de carbone entre le mixolimnion et l'hypolimnion. En effet, des travaux récents sur la géochimie des eaux profondes dans ce lac ont indiqué une production croissante de méthane pendant les 30 dernières années, menant à une accumulation du gaz et à l'abaissement de l'énergie nécessaire pour déclencher un dégagement massif de gaz, qui serait dévastateur pour les populations environnantes.

La production primaire actuelle, de $0.71 \text{ g C m}^2 \text{ j}^{-1}$ ($\sim 260 \text{ g C m}^2 \text{ a}^{-1}$), ne semblant pas spécialement différente des quelques mesures ponctuelles faites dans le passé, l'hypothèse d'une eutrophication anthropogène semble peu probable. Par contre, des changements dans la composition phytoplanctonique, avec plus de diatomées dans la situation actuelle, pourraient expliquer en partie l'augmentation hypothétique du flux d'exportation de matière organique vers les eaux profondes. Un autre aspect très important qui pourrait avoir également un impact sur les flux d'exportation est le changement de la composition zooplanctonique suite à l'introduction de la sardine. Il a été prouvé dans plusieurs études que les cladocères favorisent le recyclage de nutriments en milieu lacustre, alors qu'une communauté dominée par des copépodes favorise plutôt l'exportation (en particulier de phosphore) par l'intermédiaire des pelotes fécales. Ainsi, on peut avancer que le flux d'exportation de matière organique vers les eaux profondes a très probablement été affecté par des changements biologiques, peut-être à plusieurs niveaux (changement dans les communautés phyto et zooplanctoniques) ce qui pourrait expliquer en partie l'augmentation de méthane pendant les 30 dernières années au lac Kivu. A ceci on pourrait ajouter une possible intervention humaine, soit par des apports directs dans le lac, soit par le réchauffement global (déjà signalé au lac Kivu), ou par l'érosion des zones côtières, ou encore par l'exploitation industrielle du gaz qui a démarré depuis quelques mois. Le cadre semble plutôt complexe. La modélisation intégrée de tous ces facteurs serait un outil nécessaire, si on vise une meilleure compréhension du phénomène, et si on envisage des prévisions valables.

On peut donc suggérer que de futurs travaux sur le lac Kivu soient suffisamment bien intégrées pour couvrir le fonctionnement biogéochimique du lac, avec pour objectifs de reconstruire le passé (conséquences de l'introduction de *Limnothrissa*), notamment via des études sur les sédiments et une approche par modélisation pour simuler les flux de matière, mais aussi de prévoir l'avenir. Ainsi, si le futur de la pêche basée sur le *sambaza* est déjà une préoccupation actuelle, l'évolution des concentrations en méthane

et dioxyde de carbone des eaux profondes est une problématique cruciale à plus long terme, à la fois dans le cadre de l'exploitation des ressources énergétiques et pour la menace qu'elle pourrait représenter pour les populations locales si la tendance à l'augmentation des concentrations en gaz se confirme.

Contributions des différents auteurs

Chapitre III: *Species diversity of pelagic algae of Lake Kivu (Eastern Africa)*

- H. Sarmento:** échantillonnage (partiellement), mesures sur le terrain (partiellement), analyses de nutriments (partiellement), identifications taxonomiques, dessins, photos en microscopie optique et électronique de balayage, traitement des résultats, rédaction;
- M. Leitao:** identifications taxonomiques, dessins, photos en microscopie optique, relecture;
- M. Stoyneva:** identifications taxonomiques, photos en microscopie, rédaction, relecture;
- P. Compère:** identifications taxonomiques, rédaction, relecture;
- A. Couté:** identifications taxonomiques, dessins, relecture;
- M. Isumbisho:** échantillonnage, mesures sur le terrain, analyses de nutriments, relecture;
- J.-P. Descy:** relecture, supervision.

Chapitre IV: *Phytoplankton ecology of Lake Kivu (Eastern Africa)*

- H. Sarmento:** échantillonnage (partiellement), mesures sur le terrain (partiellement), analyses de nutriments (partiellement), analyses de pigments, cytométrie de flux, traitement des résultats, rédaction;
- M. Isumbisho:** échantillonnage, mesures sur le terrain, analyses de nutriments, traitement des résultats, relecture;
- J.-P. Descy:** rédaction, relecture, supervision.

Chapitre V: *Role of primary production and phytoplankton dynamics in the increasing methane concentrations in the deep waters of Lake Kivu (Eastern Africa)*

- H. Sarmento:** échantillonnage (partiellement), mesures sur le terrain (partiellement), analyses de nutriments (partiellement), analyses de pigments, analyses de la composition élémentaire (C,N,P), traitement des résultats, rédaction;
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- L. Viroux:** rédaction, relecture;
- B. Leporcq:** assistance technique;
- J.-P. Descy:** rédaction, relecture, supervision.

Chapitre VI: *Flow cytometric study of tropical lake picoplankton: Lake Kivu (Eastern Africa)*

- H. Sarmento:** échantillonnage (partiellement), mesures sur le terrain (partiellement), analyses de nutriments (partiellement), analyses de pigments, analyses en cytométrie de flux, traitement des résultats, synthèse bibliographique, rédaction;
- F. Unrein:** analyses en cytométrie de flux, synthèse bibliographique, traitement des résultats, rédaction, relecture;
- M. Isumbisho:** échantillonnage, mesures sur le terrain, analyses de nutriments, traitement des résultats, relecture;
- S. Sténuite:** participation aux analyses en cytométrie de flux;
- J. M. Gasol:** synthèse bibliographique, rédaction, relecture, supervision;
- J.-P. Descy:** rédaction, relecture, supervision.

Liste des abréviations

BOD	Biological Oxygen Demand
C	Carbon
CH ₄	Methane
Chl <i>a</i>	Chlorophyll <i>a</i>
CO ₂	Carbon dioxide
CTD	Multiparametric probe
DIN	Dissolved Inorganic Nitrogen
DS	Dry season (in Eastern Africa)
EM	Epifluorescence Microscopy
FC	Flow Cytometry
FL2	Orange fluorescence (in flow cytometry)
FL3	Red fluorescence (in flow cytometry)
HB	Heterotrophic Bacteria
HNA	Heterotrophic bacteria subpopulation with High Nucleic Acid content
HPLC	High Performance Liquid Chromatography
K	Downwards attenuation coefficient
LM	Light Microscopy
LNA	Heterotrophic bacteria subpopulation with Low Nucleic Acid content
N	Nitrogen
P	Phosphorous
PAR	Photosynthetic Active Radiation
Peuk	Picoeukaryotes
POC	Particulate Organic Carbon
PPP	Phototrophic Picoplankton
RS	Rainy season (in Eastern Africa)
SEM	Scanning Electron Microscopy
Si	Silica
SRP	Soluble Reactive Phosphorus
SSC	Side scatter (in flow cytometry)
Temp.	Temperature
Zeü	Euphotic layer
Zm	Mixed layer

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