On the limnology of Lake Tanganyika

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On the limnology of Lake Tanganyika

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Cover photos of R/V Tanganyika Explorer by V. T. Langenberg. Front: Light play through future door opening of wet laboratory including Greek chalk drawings of building scheme. Back: Trawling gear at the stern.

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Chapter 1

General Introduction

Research for the Management of the Fisheries on Lake Tanganyika (LTR)

The large lakes of the East African Rift Valley are amongst the oldest on earth. Lake Tanganyika is the largest and oldest of the Rift Valley lakes of East Africa and the second largest and deepest freshwater body in the world (Horne and Goldman, 1994). Lake Tanganyika is shared by four nations, i.e. Burundi, Tanzania, Democratic Republic of Congo and Zambia. It is an ancient lake with a history of geographical isolation of some 20 million years. Flora and fauna therefore have unique characteristics not found elsewhere (Coulter, 1991).

The lake is situated in a region characterised by low latitude, high temperatures and favourable light conditions year round and from ancient times, the lake's fish productivity has been a major source for the nutritional, economic and social wellbeing for the indigenous human populations

This unique ecosystem with its characteristic fluctuations in fish catches and continuous changes in species composition of the catch, defies standard fisheries planning, management and development practice (Hanek et al., 1997). Development programmes and studies undertaken under the Food and Agriculture Organization of the United Nations (FAO) auspices in the 1960s and 1970s in each of the four countries had concluded that simultaneous lake-wide research was needed to understand the observed phenomena, and more specifically how the lake demonstrates that high fish yields are not incompatible with apparently high water transparency, low nutrient concentrations, low algal biomass and other favoured water quality characteristics commonly found in oligotrophic waters.

To this end, the four riparian countries requested FAO's Committee for Inland Fisheries of Africa (CIFA) in 1977 to create a Subcommittee for the Development and Management of the Fisheries of Lake Tanganyika. This body was specifically requested to formulate and subsequently find funding for a regional fisheries research project on the lake. The Finnish International Development Agency (FINNIDA) eventually honoured the request for support of the four countries, and a FAO-executed regional research project of 5 years duration entitled "Research for the Management of the Fisheries on Lake Tanganyika" (henceforth named LTR) became operational in 1992 (Hanek et al., 1997). Financing of the Arab Gulf Programme for United Nations Development Organizations (AGFUND) could also be mobilised for part of the equipment component of the project.

It was felt that for the management of the fish stocks in the whole of Lake Tanganyika, a proper understanding of the hydrological, limnological and ecological mechanisms present in the lake is essential; such mechanisms were supposed to ultimately set the upper level for fish production. Earlier research on other African lakes had namely indicated the importance of these mechanisms in determining the chemical and biological characteristics of the upper productive waters (see Hecky and Bugenyi, 1992).

At the commencement of LTR, such information for Lake Tanganyika was scarce and could be readily characterised by its short-term observations and poor regional coverage (see Coulter, 1991). Consequently, at that time, scientific speculations were not adequate to give sufficient insight into the Lake Tanganyika's ecosystem functioning and productivity. Therefore, LTR's principal objective was to gather and synthesise data on the main hydrological, limnological and ecological variables, considered crucial to the further understanding of the mechanisms securing the biological basis for fish production in Lake Tanganyika (Hanek et al., 1997).

Consequent the considerable monitoring information gathered in the course of LTR-project new insights were obtained. However it became clear that in-depth analyses of the data banks were needed to scrutinise existing theories as well as to formulate new ones. Seen the considerable effort needed to fully analyse LTR's data banks, it was endorsed to also develop LTR's data through analyses carried out in different theses (e.g., Mannini, 1998). My studies specifically addressed the limnological dynamics and cycles in Lake Tanganyika using mostly data collected during the LTR-project.

Aim of thesis and background research questions

This study describes and analyses the intra- and interannual variations of the physical, chemical and biological properties of Lake Tanganyika in order to acquire a better understanding of the relations between constituents that are chemically and biologically active in the productive water layers of Lake Tanganyika.

More specifically, based on the knowledge available, five sets of research questions were formulated:

1 What are the spatial and temporal distributions of naturally occurring constituents that are physically, chemically and biologically active in the upper water layers of Lake Tanganyika?

The vertical distribution of naturally occurring, chemically and biologically active, constituents in the upper water layers of Lake Tanganyika have been studied and described by several scientists since the early work of Beauchamp in 1939. In general, most scientists agree on the existence of strong vertical gradients of nutrient concentrations like nitrogen, oxygen, silicate and phosphate that result from the lake's meromictic condition (Beauchamp, 1940; Kufferrath, 1952; Degens et al., 1971; Ferro and Coulter, 1974; Ferro, 1975; Well and Chapman, 1976; Coulter, 1991; Hecky and Bugenyi, 1992; Crul, 1993; Edmond et al., 1993 and Plisnier et al., 1996).

Most scientific interpretations on the vertical distribution of important constituents and related mechanisms involved are based on short term measurements and many of them do not explain that the upper water layers are occasionally characterised by the occurrence of nutrient concentrations that are atypical to the oligotrophic and meromictic nature of the lake. The spatial and temporal distribution of epilimnetic constituents is still poorly defined, and even a complete annual cycle has not been observed previously on the lake.

2 What is the impact of the external influxes of constituents through terrestrial run-off, river inflow and atmospheric deposition on the chemical and biological characteristics of the upper waters of Lake Tanganyika? Is there a seasonal pattern?

In order to solve this question, we try to elaborate on the relative importance of respectively the external influxes of constituents through terrestrial run-off, river inflow and atmospheric deposition to the overall nutrient budget of Lake Tanganyika. In general, loading of plant nutrients (in particular phosphorus and nitrogen) determines the standing crop and primary productivity of phytoplankton (Moss, 1969; Melack et al., 1982; Carpenter and Kitchell, 1984; Patterson and Kachinjika, 1993; Järvinen et al., 1996). Because of Lake Tanganyika's long residence time and the existence of enormous potential of reduced constituents resident within the anoxic hypolimnion (Coulter, 1991), one might postulate that, concerning the lake's primary production, internal nutrient loading might be of greater importance than loading from external sources (run-off, rainfall, riverine inputs). However, the relative importance of loading through external sources to the nutrient balance of the lake in both long and short term has not been specifically studied. With the data collected an actual nutrient budget for both the epilimnion and the whole can be constructed, elaborating on the importance of external influx of nutrient to Lake Tanganyika's epilimnetic productivity.

3 What is the impact of the watercolumn stability on underwater PAR distribution, plant nutrients, and phytoplankton and zooplankton dynamics? How does it vary seasonally? Does it vary between different regions within the lake?

In the past, scientists have estimated the primary production in Lake Tanganyika from 0.1 to 3.1 $gCm^{-2}d^{-1}$ (Burgis, 1986; Hecky et al., 1978; Hecky et al., 1981; Hecky and Fee, 1981; Hecky and Kling, 1981; Melack, 1981) and suggested that this production was insufficient to maintain the annual fish yield of 125 kg ha^{-1} postulated by Coulter (1981). Hecky et al. (1978) suggested that the primary production of Lake Tanganyika in 1975 was insufficient to meet the respiratory demand of the plankton community let alone sustain populations at higher trophic levels. This discrepancy in productivity can be partly explained by the fact that algal and zooplankton dynamics, including the main factors affecting them, both short and long term, have not been specifically studied in Lake Tanganyika. Although some data on the relation between watercolumn stability (in terms of nutrient loading), underwater PAR distribution, chlorophyll concentrations and primary production are known, it still remains unknown how these factors relate and vary in time and space.

4 Do spatial and temporal distribution patterns of constituents (in particular plant nutrients, chlorophyll a concentrations and rates of primary production) vary seasonally and interannually as a result of changes in climatic conditions?

In Lake Tanganyika and other large tropical lakes, such as Lake Victoria (Talling, 1966) and Lake Malawi (Bootsma, 1993; Patterson and Kachinjika, 1993 en 1995), primary productivity seems determined to a large extent by the strength of the stratification and the upward flux of nutrients which primarily determines nutrient availability to phytoplankton permitting growth (Hecky and Fee, 1981). These influxes of nutrients and related mixing events are most likely to occur during the period of low air temperatures and Southerly trade winds (June - September) when general weakening of the thermocline occurs (Coulter, 1963 and 1991). LTR research carried out on Lake Tanganyika has indicated the importance of the influence that the annual distribution of temperature and winds has on the existing seasonal hydrodynamic pattern affecting many physical aspects of the lake (Kotilainen, 1995; Verburg et al., 1997).

For Lake Tanganyika we lack almost completely any long term data sets of even the most basic chemical and physical measurements, and our knowledge of such variables as productivity or the dynamics of a particular constituent is inadequate to conclude or forecast on the overall effect that climate related parameters have on the lake's phytoplankton productivity.

5 How does the phytoplankton and zooplankton production relate to fish production? What ecosystem structures and functioning maintain the pelagic fisheries in Lake Tanganyika? How are they affected by climatic changes?

Lake Tanganyika is known for its productive pelagic fisheries, which is reported to yield higher catches per unit area than in most great lakes of the world (Coulter, 1981, 1991; Hecky et al., 1981; Lindqvist and Mikkola, 1989; Roest, 1992). Ultimately, the fish yield is a function of primary production, which in turn depends on solar radiation and external nutrient inputs. The fisheries yield in lakes usually ranges between 0.02 and 0.2 % of primary production (e.g. Morgan et al., 1980), while marine coastal seas often show values an order of magnitude higher (Nixon, 1988). For Lake Tanganyika, a preliminary estimate of 0.45 %, resembling those in the marine systems, has been given (Hecky et al., 1981; Hecky, 1984).

Several hypotheses have been presented to explain the high productivity of the pelagic fishery in Tanganyika (Hecky et al., 1981). Hecky (1991), noted that the food web of Tanganyika has a marine character. As in many productive marine systems, the primary grazer is a diaptomid copepod, and the dominant primary planktivores as well as the piscivores belong to predominantly marine fish families. The phytoplankton and bacterial biomasses are low but the growth rates are high. Organic carbon is not accumulated in the plankton but is channelled into fish biomass and harvested as fish yield. The long geological history of the lake, combined with the special ecological conditions of a deep, continuously warm tropical lake, may have resulted in the evolution of a trophic structure consisting of highly efficient species (Hecky, 1984).

However these assessments of ecosystem structure and fish production efficiency were based on fairly limited data and more comprehensive Knowledge of the trophic structure of the lake and the transfer efficiencies in the food chain is needed for reassessing the trophic structure and foodweb functioning of Lake Tanganyika.

Outline of thesis

The 5 sets of research questions are dealt with in Chapters 2-9 (Table 1.).

Table 1. Overview of the chapters of the thesis that relate to the 5 sets of research questions (keywords are given).

Research Questions	Chapters							
	2	3	4	5	6	7	8	9
Distribution spatio-temporal	x	x	x	x				
External influx				x		x		
Stratification, PAR, plankton		x		x	x			
Climatic influence	x	x	x	x				
Ecosystem structure				x	x		x	x

Chapter 2 reports on the yearly vertical distribution patterns of ten limnological variables (temperature, conductivity, pH, ortho-phosphate, nitrite, nitrate, ammonium, transparency, turbidity, dissolved oygen) at three locations throughout the lake. Relations between these patterns and the lake's hydronamical cycles are discussed as well as the importance of climatic conditions that act upon the lake. Chapter 3 addresses the vertical dynamics of thermal stratification, underwater PAR distribution and chlorophyll a. Mechanisms on how hydrodynamic aspects may control biological productivity are suggested. Chapter 4 reports on the spatial en temporal distribution of *in vivo* fluorescence as measure for photosynthetic pigments in Lake Tanganyika algae. The formation of algal blooms in relation to hydrodynamical events is discussed. Chapter 5 describes how in Lake Tanganyika Wedderburn numbers can be constructed to elaborate on changes in thermal properties, mixing and upwelling. Chapter 6 is based on field data collected during a lake-wide cruise. The spatial and temporal heterogeneity in nutrients, chlorophyll a and major zooplankton species in relation with wind-driven phenomena is addressed. In Chapter 7 a nutrient budget for Lake Tanganyika is constructed based on one year of field data on riverine input and atmospheric deposition. Their importance to biological productivity throughout the seasons is discussed. Chapter 8 holds extensive descriptions of the performance of most important constituents that make up Tanganyika's trophic structure. Field and laboratory data to quantify carbon flows through Tanganyika's foodweb are used to gain insight in the mechanisms that relate primary production to fish yields in Lake Tanganyika. Chapter 9 addresses the development in Tanganyika fish catches over the last 45 years in particular in relation to climate change, lake productivity and fisheries intensification. It was stressed that for future research it is of importance to distinguish these two factors because all four riparian countries that crucially depend on its fishery resources are placing hope in rational fisheries and catchment management.

Compared to chapter 2-9, chapter 10 does not present a scientific synopsis based on limnological field and laboratory measurements. Chapter 10 concerns the survival of the great lacustrine biodiversity found in ancient lakes. Are these unique faunas to survive, then they have to be managed along with vital resource uses. Currently, the acceleration of exploitation and catchment development poses urgent problems to the remarkable and unique faunas that have evolved in these lakes. The chapter elaborates on common approaches to conservation and development of ancient lake's resources. Major difficulties or deficiencies in recent management practices for Lake Tanganyika as well as two other comparable lakes Malawi and Baikal are described and discussed.

This item is included in this thesis because we wish to bring to the attention that independent scientists have to play an important role in the fate of ancient Lake biodiversity. Encouraging sustained international scientific, political and popular interest in the remarkably diverse faunas of Lake Tanganyika should lead to a more generalised public awareness of the threats to biodiversity and is a requirement for ensuring their survival. In chapter 10 we are concerned less with describing changes and threats in these ancient lakes, than with proposing certain concepts that are at present important when considering the sustainable conservation and development of ancient lakes.

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Chapter 2

Limnological annual cycle inferred from physico-chemical fluctuations at three stations of Lake Tanganyika

Plisnier. P.D., Chitamwebwa, D., Mwape, L. M. †, Tshibangu, K. †, Langenberg, V.T. and Coenen, E.

Hydrobiologia 407: 45–58, (1999)

Abstract

Ten variables were measured at least twice per month at three locations of Lake Tanganyika (East Africa) over one year (1993–94). Upwelling was observed in the south of the lake during the dry, windy season from May to September. Stratification was variable in strength but always present in the north. The lake showed a marked tilting of the epilimnion during the dry season (0-20 m in the South, 60–70 m in the North). This period was followed by oscillations of water masses towards an equilibrium when the strong winds from the south east ceased. Conductivity and pH fluctuations indicated dampened oscillations, particularly at the ends of the lake. Movements of the epilimnion toward an equilibrium position generated and/or re-enforced internal waves. These waves were inferred from fluctuations of chemical and physical characteristics of the lake. The concentrations of inorganic P and N commonly fluctuated by a factor of 3 or more in the epilimnion. The period of long-period internal waves was estimated to be ca. 28–33 days. Turbidity changes suggested pulse production caused by internal waves linked to non-random patchiness in nutrients and organisms. Turbulence resulting from highly dynamic physical events also induces random-patchiness in water composition. The lake water generally showed oligotrophic characteristics near the surface but had high concentrations of nutrients in deep water. The results showed that the trophic state of Lake Tanganyika, like that of the oceans, seems to depend largely on regeneration processes. The annual Limnological cycle in Lake Tanganyika appears closely linked to the climatic conditions.

Keywords: Lake Tanganyika, limnology, upwelling, internal waves, patchiness

Résumé

Au lac Tanganyika, durant une année (1993-1994) dix paramètres limnologiques furent mesurés à trois stations au moins deux fois par mois. Au sud, une remontée des eaux profondes fut observée lors de la saison sèche et venteuse. Une stratification verticale permanente, variable en intensité, fut observée au nord du lac. L'épilimnion accusait une inclinaison nette durant la saison sèche (20m au sud, 60-70m au nord). La cessation du vent du sud provoque une oscillation vers l'équilibre des masses d'eau. Les fluctuations de la conductivité et du pH traduisent une diminution de ces oscillations, surtout aux deux extrémités du lac. Des ondes internes furent générées et/ou renforcées par des mouvements de l'épilimnion. L'existence de telles ondes fut déduite des fluctuations des caractéristiques chimiques et physiques du lac. Au sein de l'épilimnion, les concentrations de P et N inorganiques variaient normalement d'un facteur de 3 ou plus. La période des ondes internes de longue durée fut estimée à 28-33 jours. La variabilité de la turbidité suggère des pics abrupts en production causés par les ondes internes reflétant une distribution non aléatoire de nutriments et d'organismes. Des processus physiques très dynamiques provoquent une turbulence causant des inégalités très localisées dans la composition de l'eau. Les eaux superficielles furent généralement oligotrophes, tandis que celles de profondeur contenaient des concentrations élevées de sels nutritifs. Les résultats indiquent que l'état trophique du lac Tanganyika, comme celui des océans, dépendrait principalement de processus régénérateurs. Le cycle limnologique annuel du lac paraît être intimement lié aux conditions climatiques.

Mots clés: Lac Tanganyika; Limnologie; Remontée des eaux; Ondes internes; Répartition spatiale inégale.

Introduction

Lake Tanganyika is situated between 3°30' and 8°50' S and 29°05' and 31°15' E. It occupies a deep and narrow trough of the western branch of the Rift Valley of East Africa (Coulter, 1994). The lake is ca. 650 km long and 50 km in average wide. There are three distinct basins: the Kigoma basin in the north (max depth: 1310 m), the Kungwe basin in the centre (max depth: 885 m) and the Kipili basin in the south (max depth: 1410 m). Lake Tanganyika is meromictic with anoxic monimolimnion. It has the second largest volume of anoxic water in the world after the Black Sea. The generally high Secchi disk transparency, low nutrient concentrations in the epilimnion and low phytoplankton densities led early investigators to conclude that the pelagic environment was oligotrophic (Beauchamp, 1939). Van Meel (1987) noted from observations of dense phytoplankton blooms and diurnal vertical movements of zooplankton and fish, that certain areas of the lake were productive. This led him to classify the lake as pseudo-eutrophic, i.e. possessing both oligotrophic and eutrophic characteristics. A quantitative estimated overall annual rate of primary production (0.8 g Cm^{-2} d^{-1}) was compared with that of other tropical lakes and it was concluded that the rate of primary production in Lake Tanganyika is not high (Hecky and Fee, 1981). However, Hecky and Kling (1981) noted that the carbon transfer efficiency derived from the percentage proportion of clupeid production to primary production was extremely high (0.45%). The most intensively exploited areas yield higher catches per unit than any other great lake, with a carbon transfer efficiency from primary production to fish production as high as the most efficient marine fisheries. They suggested that the high efficiency of the trophic structure in Lake Tanganyika could be due to (a) a relatively short food chain leading to harvestable fish and (b) the great age of the lake which has allowed for the selection of trophically efficient populations. To improve understanding of the basis of the biological production, a regional research project was proposed: ‘Research for the Management of the fisheries on Lake Tanganyika’ (LTR). This project is financed since 1992 by the Finnish International Development Agency FINNIDA and implemented by the Food and Agriculture Organisation of the United Nations (FAO). LTR started investigations in 1993 and the first known simultaneous limnological annual sampling and measuring at different locations on the lake (Bujumbura/Uvira, Kigoma and Mpulungu) was completed in July 1994 (Plisnier et al., 1996). The objectives of the LTR limnological component were to obtain information on changes in time and space of some of the main physical and chemical parameters of the lake. The regular LTR monitoring provided observations on some of the main hydrodynamic events during an annual cycle as summarized here. Previously, hydrodynamic events known or suggested for the lake have been synthesised by Coulter (1991). The hydrodynamic of Lake Tanganyika and its modelisation is actually studied in the frame of LTR (Huttula and Podsetchine, 1994).

Material and methods

In 1993–94, LTR mainly investigated the pelagic zone. Three different types of sampling were established:

1. Regular sampling (2–4 times per month),
2. Intensive sampling (24 h cycle, every 6 weeks) and
3. Seasonal sampling (every 3 months).

Results of regular sampling and partial results of intensive sampling are reported here. The position of each sampling site (Figure 1) was recorded with a GPS (global positioning system), Raystar 390 of Raytheon, with an estimated accuracy of 15–100 m. Sampling started in August 1993 for all the variables studied except dissolved oxygen measurements (November 1993 at Bujumbura, April 1994 at Kigoma and Mpulungu). Regular sampling was normally performed every Tuesday morning at 0900 h (GMT + 2 h), except during the intensive sampling period. Regular sampling site of each station was located >4 km from the shore where the depth of the lake was > 120 m. Temperature, pH, conductivity and turbidity were measured every 10 m and the other variables every 20 m, from the surface to 100 m. Transparency, water temperature, dissolved oxygen, pH and conductivity, were measured directly from the boat. For the determination of NH_4-N, NO_2-N, NO_3-N, total-P, PO_4-P and turbidity, water samples were kept in a cooler box and taken to the laboratory for immediate determination. If measurements could not be completed the first day, NO_2-N and/or NO_3-N were kept for less than 24 h below 4 °C.

When necessary, samples were preserved with acidification for NH_4-N and NO_3-N or addition of mercuric chloride for PO_4-P and NO_2-N. Transparency measurements, taken at the start of the sampling period, were made with a 20 cm diameter Secchi disk. The mean value of measurements made by three observers was recorded. Water samples were collected using 7.4 and 2.0 l capacity Limnos samplers. Water temperature (accuracy ±0.1 °C) was first measured with a thermometer placed inside the water bottle. The thermometer was read as soon as the bottle reached the deck. This method was replaced in April with in situ measurements taken down to 80 m using a digital thermometer, coupled to an oxygen meter (made by Yellow Springs Instrument Co.), with the same accuracy as before. For deeper water, the probe was placed in the sampler and read when the bottle reached the surface.

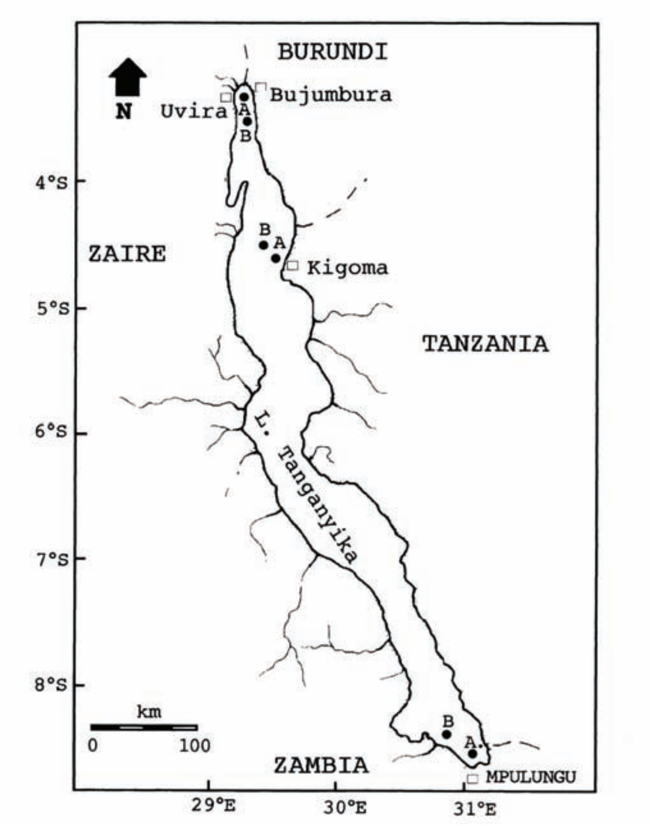

Figure 1. Location of sampling sites in Lake Tanganyika off Bujumbura/Uvira, Kigoma and Mpulungu (A = regular sampling, B = intensive sampling).

Other water temperature measurements were collected with a CTD-12 (accuracy ±0.01 °C) and with automatic Anderaa thermistor strings (with a similar precision but with an accuracy of ±0.1 °C). Dissolved oxygen (DO) was measured with a dissolved oxygen meter, model 50B of Yellow Springs Instrument Co., equipped with a YSI 5739 probe and a YSI 5795A submersible stirrer (precision ±0.01 mg l^{-1} DO). The cable allowed in situ measurements down to 80 m. For deeper water the probe was carefully introduced into a 7.4 l sampling bottle after each vertical haul. Calibrations were made in the air and corrected for altitude before each sampling period. pH readings were taken with a portable Hach pH meter, model 43800-00 (precision ±0.01). For conductivity (µS cm^{-1}), a Hach conductivity meter, model 44600, was used. The instrument automatically compensates for temperature deviation from 25 °C. Turbidity measurements (nephelometric turbid unit, NTU) were made with a Hach turbidity meter model 2100A (precision ±0.01 NTU). All the above instruments were regularly calibrated at each station. The chemical parameters were generally measured by the Hach Drel 2000 methods which proved to be sufficiently accurate for the study and to detect the important trends and fluctuations of water masses. Those methods were suitable for frequent sampling and for use in remote stations and onboard medium sized boats without laboratory facilities. Regular accuracy checks were carried out. NH_4-N and NO_3-N were measured using the Nessler and cadmium reduction methods respectively (precision: 0.01 mg l^{-1}). NO_2-N was measured with the diazotization method (precision: 0.001 mg l^{-1}). The total phosphorus method was not always satisfactory (high variability) and the results should be considered as preliminary. The determination of phosphate was done on unfiltered water during the first year of sampling (1993–94) due to the lack of filtration apparatus. They corresponded to total reactive phosphorus (TRP). TP and TRP were measured with acid persulphate and ascorbic acid methods, respectively (precision: 0.01 mg l^{-1}). Median values were graphically compared using the “box and whiskers” representation (Tuckey, 1977).

Results

Temperature

Yearly median temperature of the 0–100 m water column at Bujumbura/Uvira (25.8 °C) was close to that at Kigoma (25.7 °C), but higher than at Mpulungu (24.5 °C). However, variation during the year was higher in Mpulungu. The comparisons between temperature means using the least significant difference method (LSD) (Sokal and Rohlf, 1995) showed that there were no significant differences in temperature during the year between Bujumbura/Uvira and Kigoma, but between these two stations and Mpulungu there was a significant difference ($p<0.001$) during the dry season due to upwelling of “cold” water at the latter (average of 24.4 °C in surface waters during the dry season). During the wet season, the mean thermocline depth at regular sampling sites was 49.7, 53.4 and 41.0 m at Bujumbura/Uvira, Kigoma and Mpulungu, respectively (Figure 2a). During the dry season, the thermocline was deeper at Bujumbura/Uvira and Kigoma, 65.0 and 75.6 m, but not present at the southern end due to upwelling and mixing by convection. The greatest variation in the mean thermocline depth was observed during the wet season at Mpulungu. The thermocline deepened from October to June at Bujumbura/ Uvira and from November to June at Kigoma. The sinking of the thermocline in the north was particularly well marked after April because of the accumulation of warmer water resulting from southerly winds (Figure 3). At Mpulungu, the thermocline was deepest between December 1993 and March 1994 and then became shallower to disappear finally during the upwelling (June, 1994). The range of variation of thermocline oscillations was about 10–15m at Bujumbura/ Uvira and Kigoma and 20–25 m at Mpulungu.

Transparency

Median transparency was lower at Bujumbura/Uvira (8.7 m, range 5.0–15.4 m) than at Kigoma (12.8 m, range 8.1–23.5 m) and Mpulungu (11.9 m, range 7.0–20.5 m). During the year, water temperature and transparency showed a positive correlation, particularly in Kigoma ($r^2 = 0.56$, $N = 29$) and Mpulungu ($r^2 = 0.53$, $N = 33$). Transparency may vary considerably on a daily basis. Variations in transparency (up to 5 m) were noted in a few hours in the south (e.g. on 17 September, 18 November and 16 December, 1994).

Turbidity

Median of turbidity from 0 to 100 m was similar at Bujumbura/Uvira and Mpulungu, 0.32 and 0.33 NTU, respectively, but lower at Kigoma, 0.25 NTU. Turbidity decreased with depth at each station (Figure 2a). However, in some months, turbidity increased in deeper water near the thermocline (Figures 4a–c). During the wet season, a turbidity layer developed near the thermocline at Bujumbura/Uvira.

Dissolved oxygen

Dissolved oxygen was present down to ca. 80 m at Bujumbura/Uvira and ca. 200 m at Mpulungu.

Some measurements of dissolved oxygen concentrations down to 300 m were made at each station. For example, at Mpulungu on 7 June, 1994, 2.1 mg l^{-1} were recorded at 1200 h and 1.4 mg l^{-1} at 1800 h at 300 m. Some temporary incursions of DO were possible in lower depths due to turbulence.

Conductivity

Median conductivity (0–100 m) was 659 at Bujumbura/ Uvira, 654 at Kigoma and 662 µS cm^{-1} at Mpulungu. Conductivity was more variable at Bujumbura/ Uvira than in the other stations (values generally between 580 and 730 µS cm^{-1} have been recorded). Conductivity increases with depth in each station (Figure 2a). Important differences were noted at the end of the dry season and at the beginning of the wet season (Figures 4a, b). At Bujumbura/Uvira, minimum of values of conductivity were recorded in September at 40 m. In October, conductivity of 700 µS cm^{-1}, normally detected at ca. 300 m, was measured at all depths >50 m. On 19 October 1993, conductivity at the surface reached 686 µS cm^{-1}, a value normally found at ca. 200 m. At Kigoma, a reduction in conductivity at 40–60 m was observed in September. At Mpulungu, ‘pulses’ of deep, more conductive water were observed during the year. These corresponded with the changes in thermocline depth. Variation in conductivity showed an ‘absorbed oscillation’ shape (Figures 4a, b). This was particularly clear at Bujumbura/ Uvira. The amplitude of the variation decreased towards the end of the sampling year. Similar but less significant changes were recorded at Kigoma. The changes of conductivity were relevant as they could be used as indicators of metalimnion movements.

pH

Median pH (0–100 m) was generally similar at each station, (ca. 8.9). pH often ranged between 9.0 at the surface and 8.7 at 300 m. Higher variation was noted at Bujumbura/Uvira

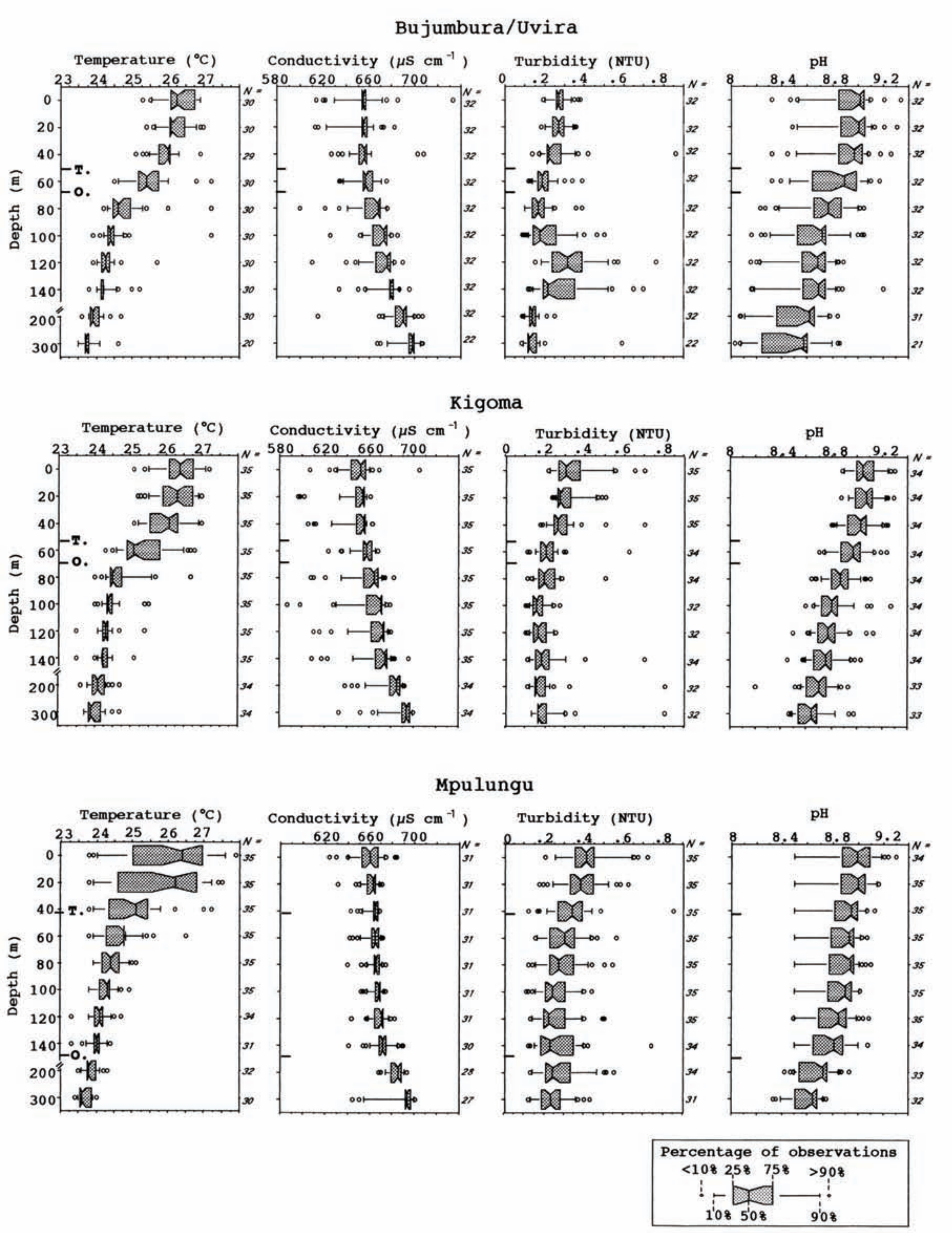

Figure 2a. Medians and percentiles of temperature, conductivity and pH. Samplings were made at intensive sampling stations. Depth of thermocline (T) and oxicline (O), calculated as the planes of strongest variation, are indicated, samples size is indicated in italic.

than at the other stations. Variation in pH was greatest in September–December. Upward pulses of deep water were recorded at site B from isopleths of low pH rising from depths >300 m to 80–100 m at Bujumbura/Uvira from September to December, to 60 to 80 m at Kigoma in December and to 140–200 m at Mpulungu from September to November (Plisnier et al., 1996). A second pulse of deep water with lower pH values was recorded in March at Kigoma and in March–April at Bujumbura/ Uvira.

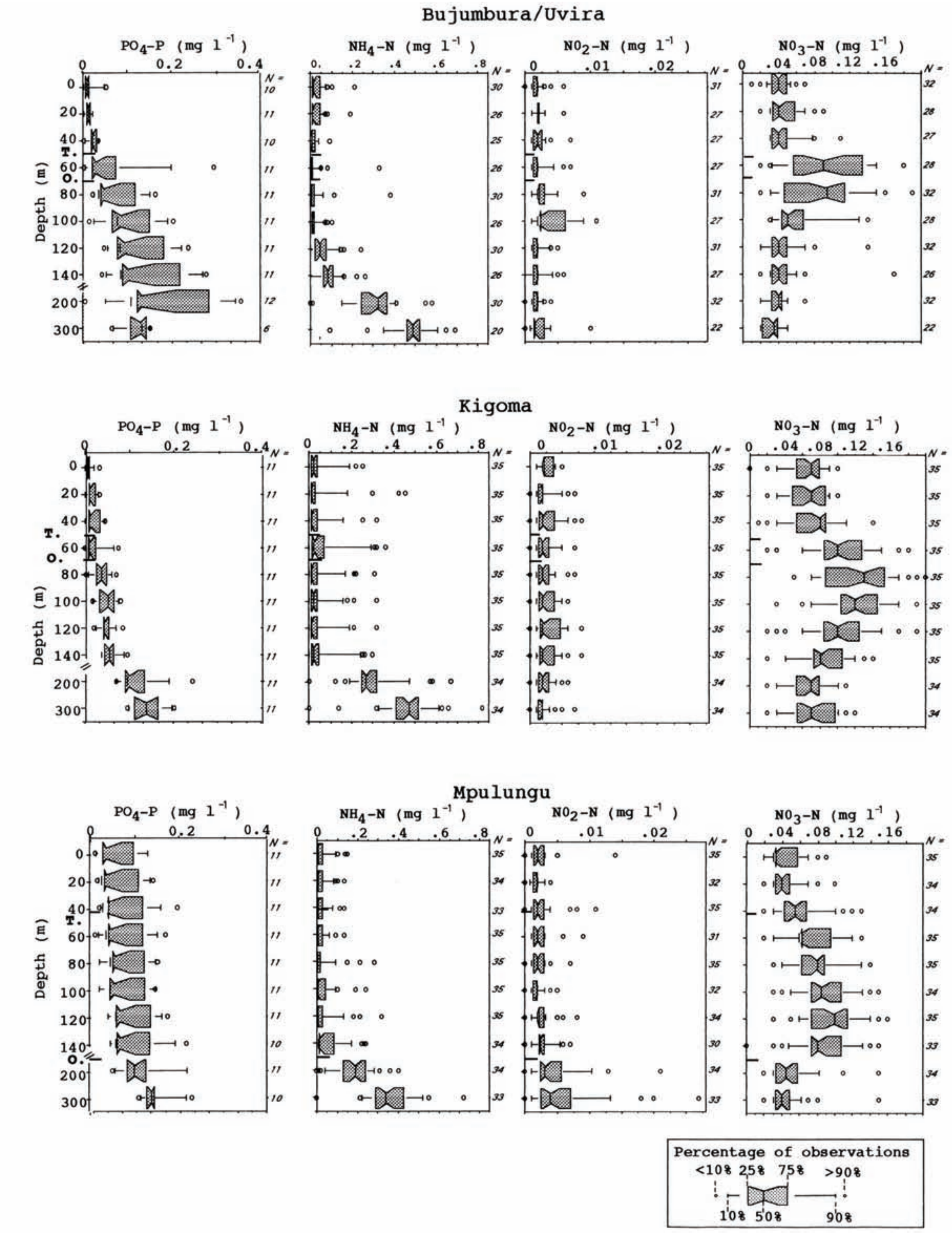

Figure 2b. Medians and percentiles of phosphate, ammonia, nitrites and nitrates. Samplings were made at intensive sampling stations. Depth of thermocline (T) and oxicline (O), calculated as the planes of strongest variation, are indicated, samples size is indicated in italic.

It corresponded to the upward movement of the thermocline at this time. At both ends of the lake, pH oscillations lessened over the year (Figures 4a–c).

Phosphorus

Concentrations of total phosphorus in near surface water were ca.16 µg l^{-1} (TRP in PO_4-P). A clear increase in concentration was observed (5–10 times) at 100 m depth at Bujumbura/Uvira and 200 m depth at Kigoma and Mpulungu (Figure 2b). During the upwelling period in the south, the concentrations of total phosphorus almost tripled in the epilimnion (mean of 104 µg l^{-1} P) in the upper 0–100 water column compared to 40 µg l^{-1} during the wet season. Pulses of high phosphate concentrations caused by internal waves raising the rich deeper layers were observed at each station (Figures 4a–c).

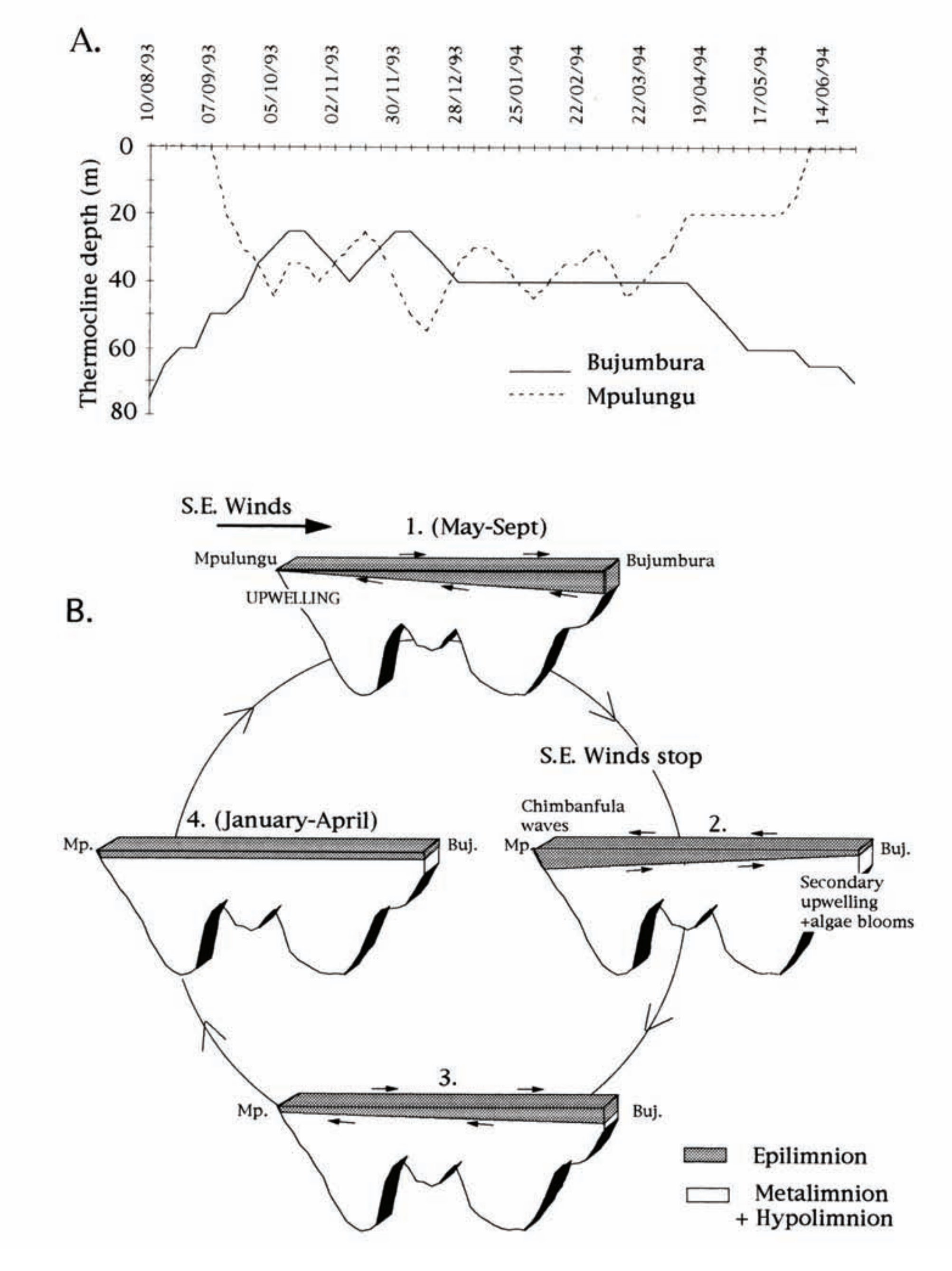

Figure 3. (A) Monthly means in thermocline depth at routine sampling stations (see Figure 1). (B) Schematic profile of water layers during an annual cycle. States 2 and 3 alternate before reaching stage 4. Internal waves are indicated.

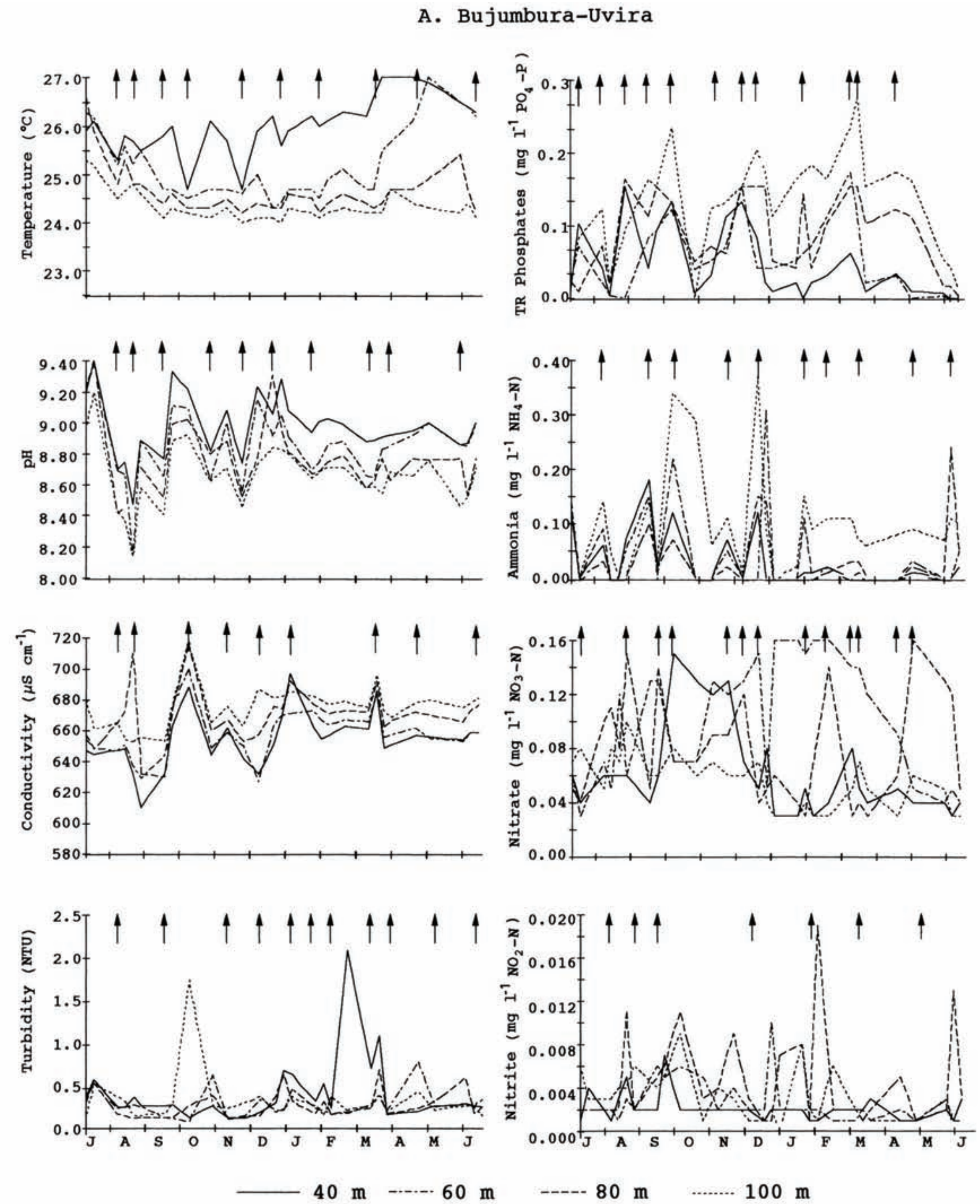

Figure 4a. Time series of temperature, pH, conductivity, turbidity, total reactive phosphorus, ammonia, nitrates and nitrites at the routine site of Bujumbura/Uvira in 1993-94 (4 depths drawn). Internal waves inferred from matching high values of conductivity, TRP, ammonia and nitrate and low values of temperature, turbidity, pH and nitrite are marked by arrows.

Nitrogen

Nitrate had a maximum in concentration of ca. 0.10 mg l^{-1} NO_3-N at 60–80 m in the north and 100– 140 m in the south (Figure 2b). The nitrate rich layer was related to the thermocline and oxycline depths at each station. The layer was particularly well defined when the lake became calm after January–February. Below the nitrate layer a nitrite layer was sometimes detected such as at 80 m at Bujumbura/Uvira (0.005 mg l^{-1} NO_2-N). At this station, higher values of nitrites (0.012 mg l^{-1} NO_2-N) were also observed in the epilimnion during the mixing period in October and November. This was probably linked with the well defined thermocline near

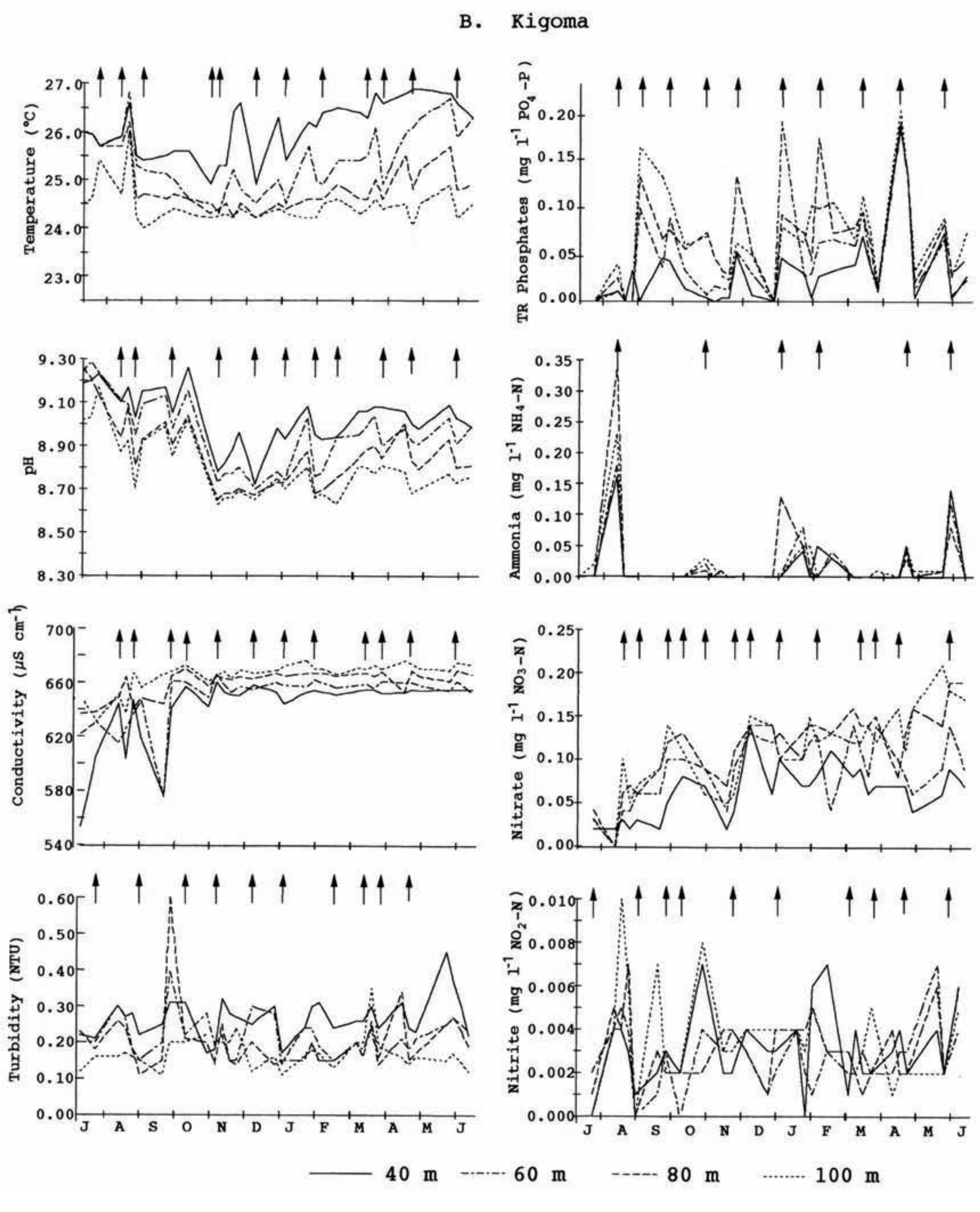

Figure 4b. Time series of temperature, pH, conductivity, turbidity, total reactive phosphorus, ammonia, nitrates and nitrites at the routine site of Kigoma in 1993-94 (4 depths drawn). Internal waves inferred from matching high values of conductivity, TRP, ammonia and nitrate and low values of temperature, turbidity, pH and nitrite are marked by arrows.

Bujumbura/Uvira and a strong vertical gradient of dissolved oxygen affecting nitrification and denitrification processes. Below the oxycline, high concentrations of ammonia were measured. At Bujumbura/Uvira, mean concentrations of ammonia were 0.05 mg l^{-1} NH_4-N at the surface water and >0.40 mg l^{-1} NH_4-N at 300 m (Figure 2b). Mixing may have brought significant concentrations to the surface (once > 0.20 mg l^{-1} NH_4-N) but decomposition was probably also involved. High ammonia concentrations were recorded more often at Bujumbura/Uvira, probably because of the shallow thermocline depth there. Ammonia was often low or not detected in Mpulungu probably because of deeper epilimnion in the south.

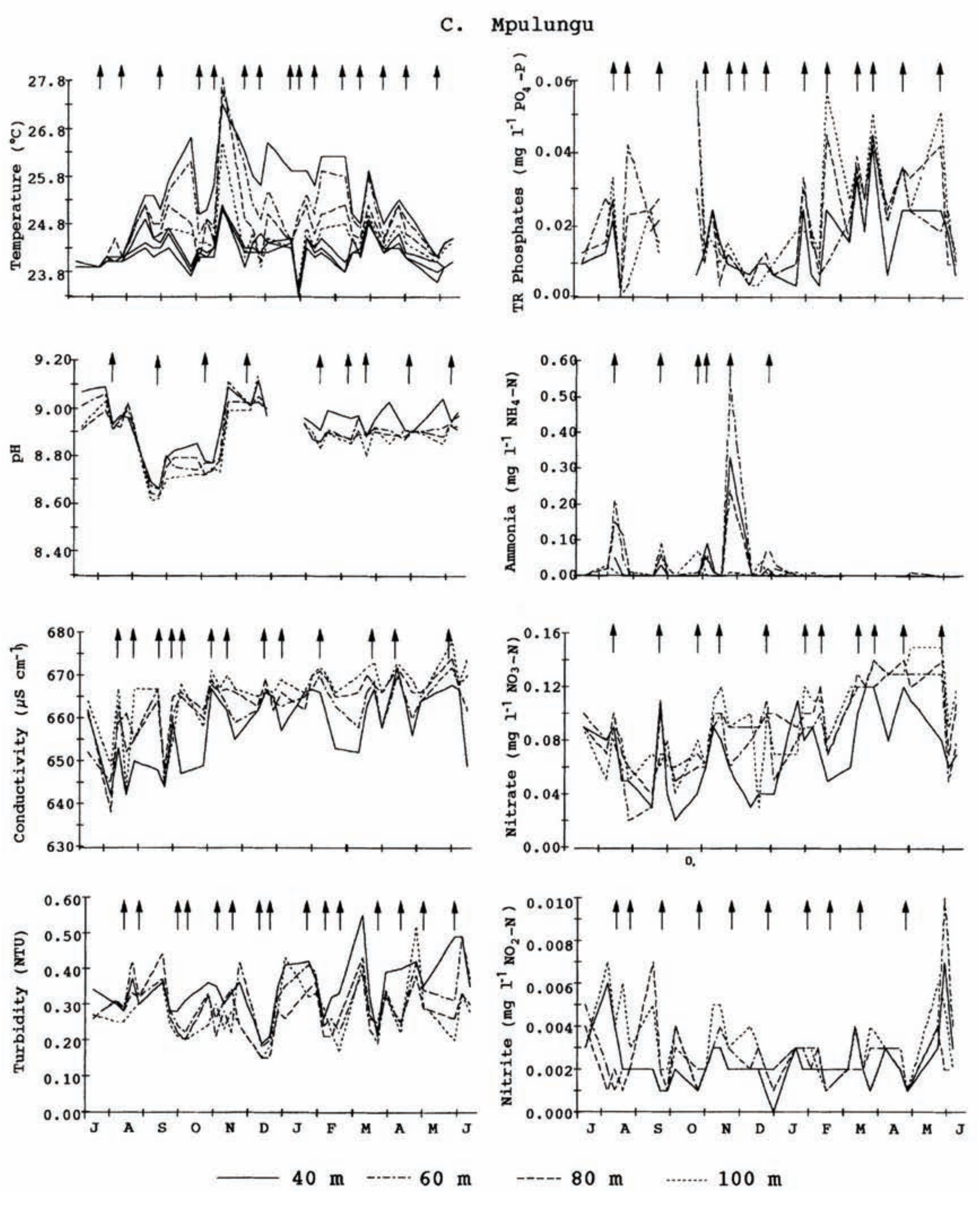

Figure 4c. Time series of temperature, pH, conductivity, turbidity, total reactive phosphorus, ammonia, nitrates and nitrites at the routine site of Mpulungu in 1993-94 (4 depths drawn). Internal waves inferred from matching high values of conductivity, TRP, ammonia and nitrate and low values of temperature, turbidity, pH and nitrite are marked by arrows.

Discussion

The annual limnological cycle

In May–June, south east winds drive warm epilimnion water towards the north of the lake (Figure 5). This results in a tilting of the epilimnion. The volume of warm water accumulated in the north depends on the strength of the wind. Thermocline depth is a good indicator of the volume of warm water amassed at the north of the lake. The warm water accumulation in the north is mainly a surface process and water flows to south as deep currents causing upwelling along the southern coast. Upwelling was inferred from the measurement of colder

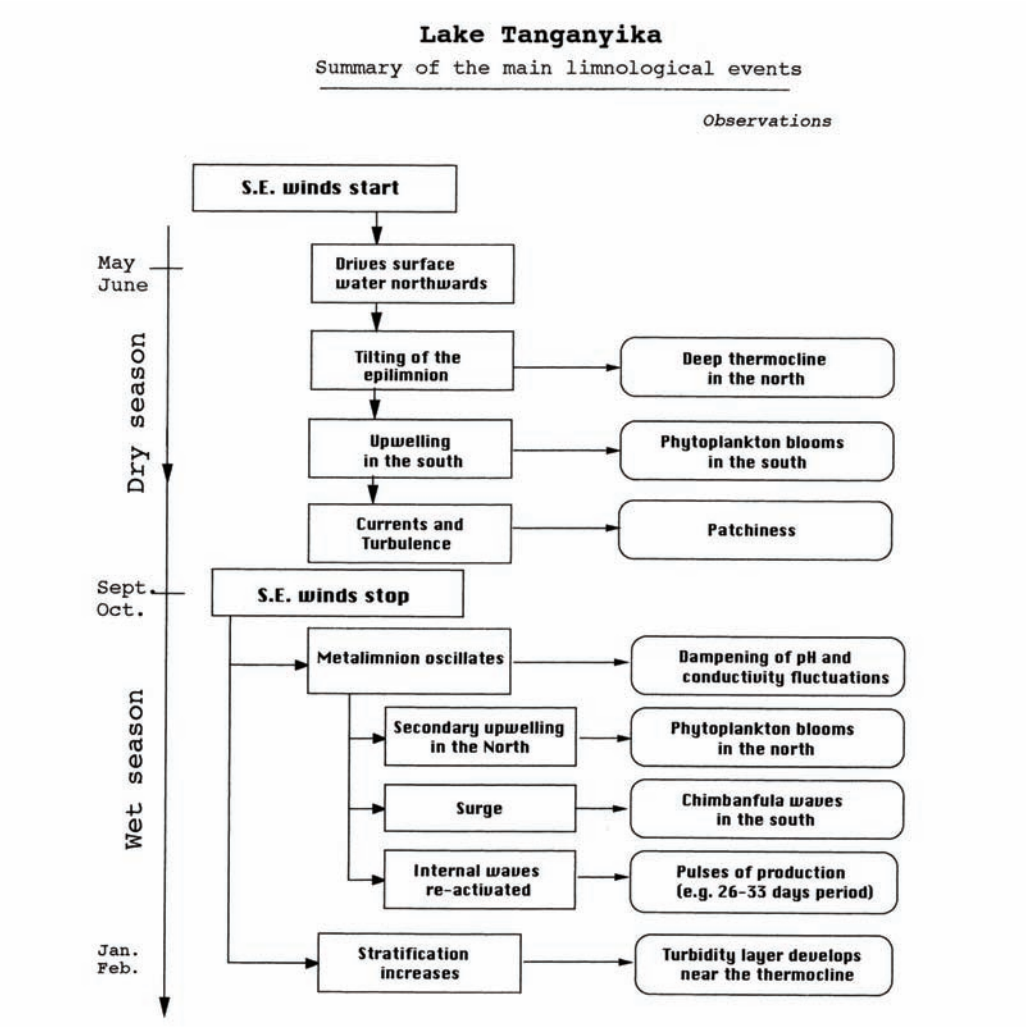

Figure 5. Seasonal hydrodynamic cycle of Lake Tanganyika and its consequences.

and nutrient rich water that averaged 24.4 °C at the surface during the dry season (compared to 27.2 °C during the wet season) at Mpulungu.

The upwelling corresponded with high wind speeds (3 h mean 4–7 m s^{-1}) and with the minimum air temperature for the year (3 h mean 23.0 °C) resulting also in the cooling of the surface water. Cooling from the deep, return currents and from lake-atmosphere interactions resulted in very weak stratification. During upwelling, mixing of water near Mpulungu increased and higher concentrations of N and P (normally abundant below the thermocline) were measured in the epilimnion. Average water transparency decreased to 8–10 m (12–18 m during the wet season). Higher phytoplankton biomass resulting from upwelling in the south was observed by Beauchamp (1939) and Coulter (1968). In 1993–94, mixing during upwelling was observed to be particularly conspicuous when deep internal waves showed an ‘apex’. During a daily cycle, mixing increased particularly in the early morning when strong winds and low air temperature coincided. During the dry season, turbulence was extensive and vortices and exchange of water from both sides of the thermocline were detected to at least 200 m. Coulter (1968) suggested that the amplitude of internal waves in the upper 150 m implied that turbulent mixing, due to internal waves, extended well below 150 m.

After the dry season, in September, 1993, the 23.75 to 24.00 °C isotherm was not detected in the south again in the upper 90 m (up to May, 1994). The upwelling probably ended between 10 and 21 September, 1993 when the 24.00 to 24.50 °C isotherms disappeared from the surface and a permanent thermocline was formed. The south-east winds ceased at the end of the dry season (September), and the metalimnion ‘fell back’ towards a horizontal plane but continued to oscillate over several months. This period was characterised by increased water movements. The changes in pH and conductivity provided an excellent way to examine the movements of the metalimnion (Figures 4a–c). Yearly variations in the pH at 40 m ranged between 8.47 and 9.40 at Bujumbura/Uvira, 8.72 and 9.26 at Kigoma and 8.66 to 9.12 at Mpulungu. Deep water characterised by lower pH (relative to the surface) affected the pH in surface waters at the end of the dry season. The nutrient rich deep water probably strongly influenced primary production when it was brought near the surface. Consumption of $HCO3^-$ during photosynthesis results in higher pH values. This could explain the fluctuations of pH measured in the lake. During the wet season, pH changes were reduced to reach more stable values in February at each station. pH did not change as rapidly as other parameters probably due to the high buffering capacity of Lake Tanganyika. There is no data on primary production variability during an annual cycle and detailed causes of pH variability still need to be investigated. After the cessation of the wind, upward movement of deep layers of water in the north probably corresponded to “secondary upwelling” (= upward movements of water due to oscillations of water masses toward equilibrium). Significant fluctuations of some parameters (e.g. conductivity) suggest the existence of a secondary upwelling in October-November in the north of the lake. Transparency near Bujumbura/ Uvira was particularly low in October (8.4 m) and November 1993 (7.1 m). Phytoplankton blooms have previously been detected at this time of the year in the north (Symoens, 1955a,b; Dubois, 1958; Hecky and Kling, 1981) which suggests the yearly occurrence of the secondary upwelling. This northern bloom often coincided with the onset of the rain that was held mainly responsible for a higher nutrient input. However, while the rains probably play some role in phytoplankton blooms, it is suggested that secondary upwelling at that time should be held mainly responsible for bringing nutrients towards the surface. This would explain the typical delay between high algae production in the south (main upwelling) followed a few weeks later by increased productivity in the north (secondary upwelling). It is suggested that the upwelling detected in the north of Lake Malawi in October 1993, from satellite images of the lake surface temperature (Wooster et al., 1993) may be similar to secondary upwelling in Lake Tanganyika. In October, strong surface waves were observed near the shores of Mpulungu and seem to correspond to a surge at the beginning of the metalimnion oscillations during that period. These waves are observed every year at the end of the dry season. They are locally called ‘Chimbanfula’. This means ‘digging for the rains’ because they occur at the beginning of the wet season. Some Zambian fishermen report that ‘Chimbanfula’ waves can be associated with fish-kills and plankton blooms. In September, 1993, a fish-kill of *Boulengerochromis microlepis* was observed. Corpses were seen floating in many areas near Mpulungu. ‘Chimbanfula’ waves may be related to travelling waves and oscillations of the metalimnion after the S.E. winds ceased. The surge is probably an important phenomenon for the re-activation of the internal waves. This supports Coulter’s (1991) suggestion that oscillations are accompanied by water movements that take the form of a, large amplitude, progressive wave which gradually transforms into a standing wave. He suggested that such a surge could cause a ‘local severe mixing’.

The presence of internal waves, during the whole year, at all the stations of LTR, was inferred from fluctuations of temperature, pH, conductivity, turbidity, total phosphorus, phosphates, ammonia, nitrates and nitrites (Figures 4a–c). In the present study, an average of 11 waves for all the parameters at each station was identified. They corresponded to a period of 33 days. Some parameters such as nitrates in the north and phosphates in the south had up to 13 peaks during the year (average period was 28 days). Some peaks were probably missed because of the relatively low frequency of sampling (2–3 regular samples per month). Arrows in Figures 4a–c indicate matching waves with several parameters. The apex of a wave is noted from the low temperature, pH, turbidity, nitrite and high values of conductivity, phosphates, ammonia and nitrate. There seemed to be no period when waves were absent for any of the parameters at any station. Even during the upwelling in the south, the persisting waves of the preceding year 1992–93 were detected between 200 and 300 m deep which supports the theory of Coulter (1991) suggesting that internal waves could persist much longer than one season. Pulses generated by internal waves were reflected in nutrient concentrations in the water column. The long period waves showed a vertical displacement of nutrient concentrations of ca. 20 m in the water column. Regular pulses of phytoplankton production probably followed the rhythmic movements of internal waves because deep eutrophic water was able to reach the biotic and photic zones which usually showed oligotrophic characteristics. The ‘nutrient waves’ should also have influenced organisms that were adapted to take advantage of favourable but episodic conditions. As the lake became more stable, particularly, from February to May, turbidity increased (especially during the pulses linked to internal waves) near the thermocline at Bujumbura/Uvira. Plankton and bacteria probably cause the greatest variability in turbidity in the pelagic area. The pelagic area appears not significantly influenced by river inflows in Lake Tanganyika as these waters are generally colder and may sink below the thermocline. A deep-living community of organisms linked to nutrients and reduced matter brought up by the internal waves may have developed particularly when the lake was calm near the thermocline. In Lake Kivu, the stable chemocline at 60 m allowed a layer of chemosynthetic bacteria to form there (Haberyan and Hecky, 1987). This bacterial ‘plate’ was nourished by the reduced compounds moving up from deep waters. A bacterial ‘plate’ may also exist in Lake Tanganyika, particularly when the lake is calm.

Pulses and patchiness in water composition

Lake Tanganyika is not homogeneous and stable during an annual cycle. Patchiness has been observed in several studies on autotrophic (algae blooms) as well as heterotrophic organisms (zooplankton) (Vuorinen and Kurki, 1994; Bosma, pers. comm.). The patchy distribution of *Stolothrissa tanganicae* has been reported by Collart (De Bont, 1972). Patchiness could possibly be divided into random and non random patchiness. Random patchiness is mainly due to turbulence. An extensive patchiness in the chemical water characteristics of Lake Tanganyika was observed during 24 h experiments (Plisnier, in preparation). Very variable transparency on a short time scale (hours) might result from patchiness in nutrients linked to to internal waves and turbulence. It could also be affected by solar radiation and photo-inhibition, vertical migration, grazing and/or movements of water. Changes in physical and chemical variables showed some rhythmic changes induced by internal waves with a defined period (apparently 28–33 days). Pulsed production and non random patchiness might result from this. Hecky and Fee (1981) found that Lake Tanganyika phytoplankton had the highest growth rate of those examined in tropical lakes. It is possible that fast growing algae populations, adapted to fluctuating environmental conditions, are able to capitalise upon these ‘nutrient waves’.

Conclusions

A limnological cycle has been proposed in a sequence of events detailed in Figure 5. Internal waves have been observed for all the parameters studied at all three stations around the lake throughout the year. They are a very important aspect of the lake’s limnology and could play a considerable role in the ‘non-random patchiness’ and the production pattern of the ecosystem. A regular pulse of primary production is likely to follow the rhythmic movements of internal waves bringing deep eutrophic water toward the photic zone. These ‘nutrient waves’ could also have acted as a major environmental factor in the selection of organisms by favouring the occurrence of fast growing organisms adapted to highly variable fluctuating conditions. Non-random patchiness could be linked on a large scale with internal waves, upwelling and main currents. On a shorter time and geographical scale random patchiness probably resulted from turbulence. Vortices have been often observed in the water column at each station.

Elucidation of patchiness in limnological variables is vital to the understanding of patchiness in organisms. Simultaneous sampling through multidisciplinary lake wide cruises is a pre-requisite. Parts of non-random patchiness (internal waves) may however be best studied through very frequent sampling at a few fixed stations. An annual cycle of sampling shows that productivity of Lake Tanganyika, like in the sea and probably like in other large deep tropical lakes, depends to a large extent on the regeneration of nutrients from the water column. Nutrient rich waters were observed below the thermocline. Their access to the upper photic and oxic layer is highly dependent on several hydrodynamic events that arise annually in a sequence driven by the climatic cycle.

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Chapter 3

Comparison of thermal stratification, light attenuation and chlorophyll-*a* dynamics between the ends of Lake Tanganyika

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Abstract

Thermal structure, light attenuation and chlorophyll-*a* dynamics within the upper 100 m at the northern and southern ends of Lake Tanganyika were measured from August 1995 to July 1996. Pronounced variability of thermal structure in time, depth and region could be observed. During the dry windy season (June-September), the water column in the south was largely isothermal down to 100 m, while in the north stratification was detectable. Subsequently in October, cessation of winds coincided with a re-establishment and strengthening of thermal stratification in the south and a distinct rise of a weakened thermocline in the north was accompanied by an increase in epilimnetic concentrations of dissolved solids.
The depth of photic zone was highly variable with the average position of 1 % of incident PAR found between 20 -70 m, sometimes showing vertical shifts of 25 m a week. Weekly observations showed that concentrations of chlorophyll-*a* were rather similar at both ends of the lake. At both stations, periods of unstable or absent thermal stratification were accompanied by increased concentrations of chlorophyll-*a*, although in the north chlorophyll-*a* also peaked during periods of deep thermal stratification and low rates of mixing. Concentrations of chlorophyll-*a* did not show significant relationship with the available amount of underwater available PAR (I_m between 11-173 $\mu Em^{-2}s^{-1}$).
We suggest that in Lake Tanganyika chlorophyll-*a* maxima can occur whenever growth rates exceed spatial mixing rates i.e., if mixing is less than a critical turbulence. Our observations underscore the consequences of hydrodynamic aspects on biological productivity either by securing internal nutrients or by controlling the timing and magnitude of phytoplankton biomass production.

Keywords: Tropical lakes; PAR; Mixing; Deep chlorophyll; Thermal stability

Résumé

D'Août 1995 à Juin 1996, la dynamique de la structure thermique, atténuation de la lumière et la dynamique de la chlorophylle des 100 premiers m ont été mesurées aux extrémités Nord et Sud du lac Tanganyika. Des variations prononcées de la structure thermique en fonction du temps, de la profondeur et du lieu ont pu être observées. Au cours de la saison sèche (Juin-Septembre), la colonne d'eau au Sud était largement isotherme jusqu'à 100 m alors la stratification était observée Nord. Par conséquent, l'arrêt des vents en octobre coïncidant avec le rétablissement et renforcement de la stratification thermale au Sud et, au Nord à une distincte remontée de la faible thermocline, était accompagné d'une augmentation dans l'épilimnion de la concentration des solides dissous.
La profondeur de la zone euphotique variait beaucoup avec en moyenne 1 % du PAR (radiation photosynthétiquement active) incident trouvé entre 20-70 m, montrant à certains moments des changements verticaux de 25 m par semaine. Des observations hebdomadaires ont montré que les concentrations de la chlorophylle a sont plutôt similaires aux deux extrémités du lac. Dans ces deux stations, des périodes d'instabilité ou d'absence de stratification thermique étaient accompagnées d'une augmentation de la concentration de la chlorophylle a alors qu'au Nord, elle présentait aussi des pics en des périodes de stratification thermale profonde et de faible degré de brassage. Les concentrations de la chlorophylle a ne montraient pas de corrélation significative avec la quantité disponible de PAR dans l'eau (I_m compris entre 11-173 $\mu Em^{-2}s^{-1}$).
Nous supposons qu'au lac Tanganyika le maxima de la chlorophylle a peut avoir lieu lorsque le taux de croissance dépasse celui du brassage p.ex., si le brassage est inférieur à la turbulence critique. Nos observations mettent l'accent sur les conséquences des aspects hydrodynamiques sur la productivité biologique en assurant les nutriments internes ou en contrôlant le temps et le degré de production de la biomasse planctonique.

Mots clés: lacs tropicaux; la radiation photosynthétiquement active (PAR); Brassage; Chlorophylle des fonds; Stabilité thermique

Introduction

Tropical Lake Tanganyika occupies a deep, elongated and steep-sided trough of the western branch of the East African rift valley (Fig. 1). The lake is unique in terms of its dimensions (volume of ca. 19000km^3), age (> 10^7 years) and faunal diversity (e.g., ca. 300 fish species). It is also known for its productive pelagic fishery (Roest, 1992; Coenen et al., 1998), which has recently been estimated to yield 55-66 kg ha^{-1}yr^{-1} (Mölsä et al., 1999).

Lake Tanganyika has been classified meromictic (Horne and Goldman, 1994) and although permanently oligotrophic in appearance, periodic phytoplankton blooms occur (Dubois, 1958; Hecky and Kling, 1981; Coulter, 1991; Salonen et al., 1999).

Since the work of Beauchamp (1939 and 1940) and Kufferrath (1952) it has been known that in Lake Tanganyika relatively strong vertical gradients in concentrations of nutrients and dissolved oxygen approximate a persistent thermocline which divides clear, impoverished surface water layers from reservoirs of nutrients resident within the anoxic hypolimnion.

Recent results from Lake Tanganyika have shown that breakdown of water column stratification and upsurge of hypolimnetic waters are mainly due to wind induced events like upwelling and internal seiches (Kotilainen et al., 1995; Huttula, 1997). These events, with associated turbulence and mixing, cause a decrease in the stability between water layers facilitating nutrient upwelling (Coulter, 1988; Crul, 1993; Edmond et al., 1993; Langenberg, 1996, Plisnier et al., 1999).

Knowledge on the aquatic properties of the upper waters of Lake Tanganyika has expanded in recent years and several researchers have implied that periods of enhanced phytoplankton growth in Lake Tanganyika and other large tropical lakes, such as Lake Victoria and Lake Malawi, are principally determined by the strength of vertical stratification of the water column and the upward flux of nutrients (Talling and Talling, 1965; Talling, 1966; Hecky and Kling, 1981; Coulter 1991; Hecky and Bugenyi, 1992; Bootsma, 1993b; Patterson and Kachinjika 1993). However, in Lake Tanganyika, most assumptions on the functioning of the processes linking water column stability with phytoplankton dynamics are based on observations characterized by poor temporal and spatial coverage (Moss, 1969; Degens et al., 1971; Ferro, 1975; Hecky and Fee 1981; Hecky and Kling, 1987; Coulter 1991). Furthermore, measurements on the vertical distribution of photosynthetically active radiance (PAR), an essential factor affecting phytoplankton dynamics, are scarce.

This study attempts to understand the linkages between chlorophyll-*a* dynamics, thermal stratification and light attenuation in Lake Tanganyika. We compared the pelagic zones of the northern and southern ends of the lake, because such areas generally seem to respond stronger to hydrodynamic events than mid-lake regions (Coulter, 1963 and 1968; Langenberg, 1996). Furthermore, these regions are known to hold a considerable and well-developed industrial fishery, which might imply increased productivity.

Material and Methods

Sampling was carried out from August 1995 until July 1996 at the ends of Lake Tanganyika near Bujumbura (Burundi) and Mpulungu (Zambia) (Figure 1). Both sampling stations were located > 4 km from the shore with depths >120 m. We used GPS positioning and regularly sampled stations 3-5 times a month. In general, at both stations, sampling took place every Tuesday at ca. 0900 hrs. (GMT+2).

Temperature (accuracy ± 0.1 °C) was measured by a digital probe (Yellow Springs Instruments Co., USA) and bottle thermometers (VEL Co.) up to 100 m at 10 m intervals. Water density was calculated according to Hutchinson (1957). Thermal water column stability (N^2 in s^{-2}; where N represents the Brunt-Vaisälä buoyancy frequency) was calculated according to the equation:

$$N^2 = \frac{-\mathrm{g}}{\bar{\rho}} \frac{d\rho}{dz} \tag{1}$$

Where $\bar{\rho}$ (kg l^{-1}) is the mean water density, g (m s^{-2}) is the gravitational acceleration constant and *d*ρ/*d*z is the density gradient over depth interval z (m). Chlorophyll-*a* concentration were determined using a modified spectrophotometric procedure (ISO, 1992)

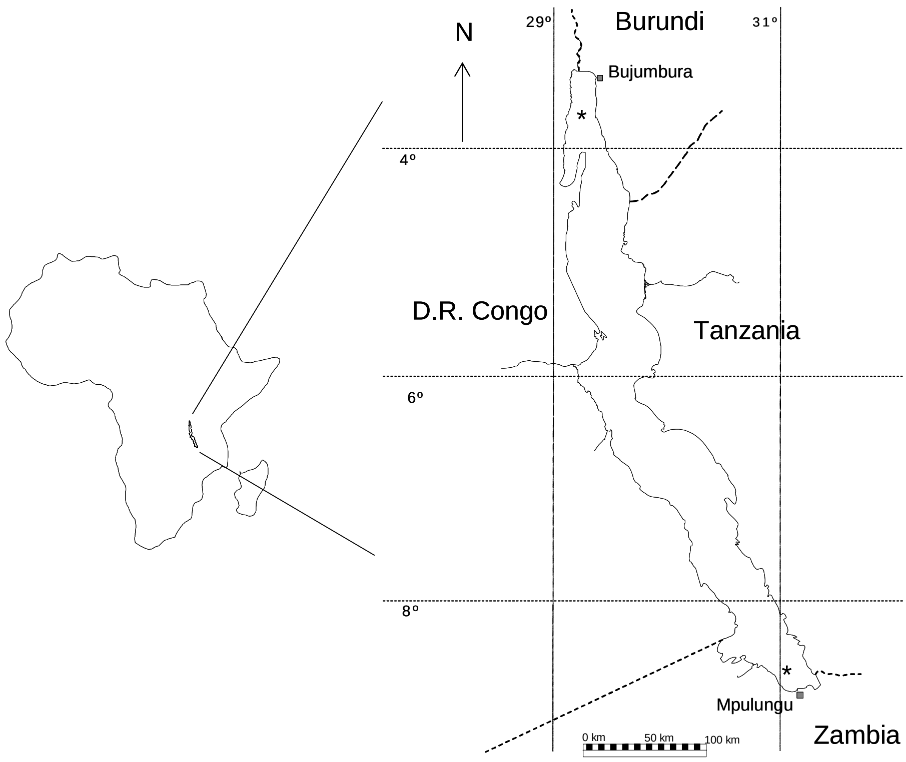

Figure 1. Geographical position and map of Lake Tanganyika. Sampling stations north and south are indicated by asterisk.

with 'cold' ethanol extraction and phaeopigment correction. In vivo fluorescence of chlorophyll-*a* was measured using a Turner Designs 10-AU-005 field fluorometer (with CS-5-60 excitation filter of 340-500 nm, CS-2-64 emission filter >665 nm, daylight white lamp and a red sensitive photomultiplier; further details in Salonen et al., 1999). In vivo fluorescence correlated with extracted chlorophyll-*a* (N=370, R^2=0.9) and this regression was used to replace some gaps in chlorophyll-*a* determinations. The depth profiles of concentrations of chlorophyll-*a* were used to calculate contour plots (we used a 'point-kriging' gridding method found in Surfer 7, Golden Software Inc.). Mean daily incoming photon flux densities were recorded by light sensors from automatic weather stations based at Bujumbura harbour and the meteorological buoy off Mpulungu. The sensors were cross-calibrated by a Li-Cor quantum sensor, to give mean daily incident radiance (I_0 in $\mu Em^{-2}s^{-1}$ of PAR: 400-700 nm). In situ PAR measurements were made at 10 m intervals up to ca. 50 m of depth and were used (Li-Cor quantum sensors LI-193-SA and LI-188 in combination with data logger LI-1100) to calculate attenuation coefficients (K) by a least square linear regression from the slopes of transformed irradiance versus depth values.

The attenuation coefficients were used to calculate the integral amount of PAR available in the epilimnion. The amount of PAR (I_m) to which a freely circulating algal cell would be exposed in a probably well-mixed epilimnion can be defined as:

$$I_m = \frac{1}{Z_m} \int_0^{Z_m} I_0 e^{-kz} dz \qquad (2)$$

where I_0 represents daily, mean incident PAR ($\mu Em^{-2}s^{-1}$) during 24 hrs. before sampling. Mixing depth (Zm, m) was set to the midpoint of that 10 m interval at which maximum stratification occurs (i.e., maximum N^2). The underwater light attenuation coefficients of all PAR versus depth profiles were used to calculate the photic zone depth (Z_{eu}), which was defined as the depth where the under water light has decreased to 1% of incident surface light (Kirk, 1983). Conductivity (K_{25} in μScm^{-1}) and turbidity (NTU) were measured by HACH equipment at 10 m intervals (HACH Co. USA; respectively conductivity/TDS meter model 4460 and nephelometer model 2100A). To characterise epilimnetic waters of Lake

Tanganyika throughout the study period, mean values for temperature, turbidity and conductivity were calculated for the upper 50 m of depth.

Results

Thermal stratification.
Throughout this study, the vertical water column structure at the northern and southern ends of Lake Tanganyika exhibited different seasonal patterns (Figure 2). Temperatures ranged between 25.2-27.2 °C (mean = 26.3 °C) at the north station and between 24.1-27.4°C (mean = 26.1^{o}C) at the south station (Figure 2) and correlated at both stations to Z_m ($r \geq 0.47$, $n = 44$, $p < 0.005$). At the north station, the thermal structure always showed some degree of stratification within the upper 100 m. Here, mixing depth ranged between 25-95 m (mean = 65 m). High values (>80 m), were more common during August-July and low values (25-65 m) during October - November (Figure 2).

At the south station the mixing depth varied between 25-85 m (mean = 55 m) in October-June, whereas during other times the upper 100 m was isothermal at temperatures of ca. 24.4 ^{o}C (not shown).

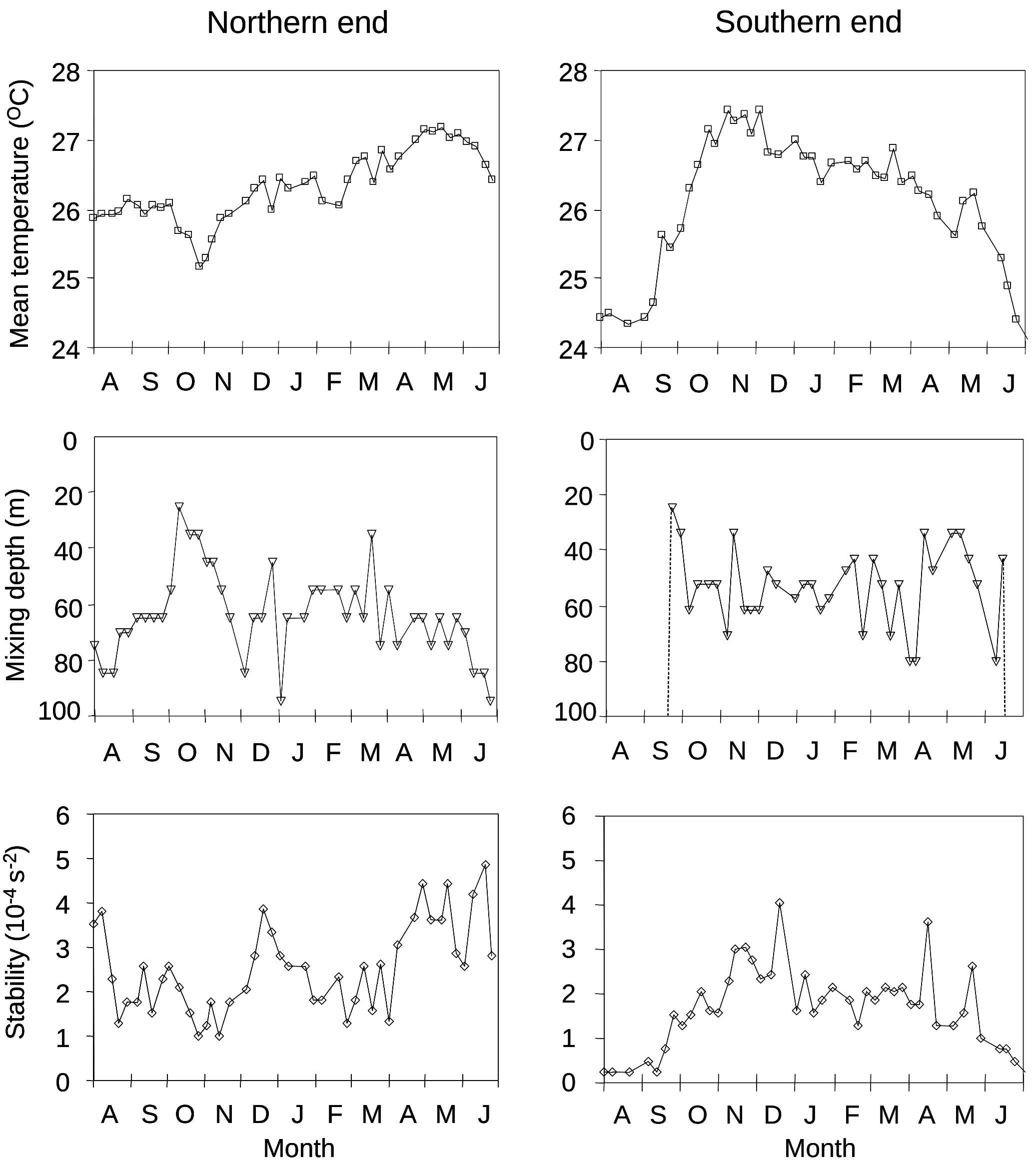

Figure 2. Seasonal dynamics of mean temperature (0-50 m), mixing depth and maximum thermal stability (0-100 m) at northern (left) and southern ends (right) of Lake Tanganyika.

After the re-establishment of thermal stratification at the end of September, the mean temperature of the upper 50 m increased by ca. 2°C to a maximum of 27.4 °C and subsequently decreased approximately linearly with time until June, the onset of a new deep mixing event. At the north station, thermal stability (N^2) ranged between 1.0 and 4.9 $10^{-4}s^{-2}$ (mean = 2.5 $10^{-4}s^{-2}$) and at the south station between 0.2 and 4.1 $10^{-4}s^{-2}$ (mean = 1.8 $10^{-4}s^{-2}$). At the north station, the evolution of N^2 in time showed that low values for N^2 were found in October-November and in February-April with minimum values for N^2 (ca. 1.0 $10^{-4}s^{-2}$) in October-November, a period also characterised by minimum temperatures and mixing depths. Highest values for N^2 were encountered from May to July (> 4 $10^{-4}s^{-2}$). At both stations, changes in N^2 correlated with changes in Zm. However, the correlation was positive at the north station ($r = 0.53$, $n = 45$, $p < 0.005$), but negative at the south station ($r = -0.63$, $n = 44$, $p < 0.005$).

Water quality.
At both stations, mean turbidity values ranged between ca. 0.3 and 1.4 NTU (mean 0.6 NTU). From August to October and from May to July, turbidity fluctuated between 0.6-0.3 NTU, whereas during other months values were generally higher showing larger variations in time. Fluctuations were more frequent at the north than at the south station (Figure 3) where turbidity was correlated to temperature ($r = 0.5$, $n = 44$, $p < 0.005$). Although, mean values for conductivity were of the same order of magnitude (ca. 660 µScm^{-1}, Figure 3) at each station, seasonal trends differed. At the south station, conductivities were low at the onset and generally increased throughout the study period. At the north station, maximum values were observed from the second half of September to December. At the north station, changes in conductivity were following changes in the thermal properties of the water column and inversely correlated respectively with Z_m, N^2 and temperature ($r \leq -0.5$, $N = 45$, $p < 0.005$).

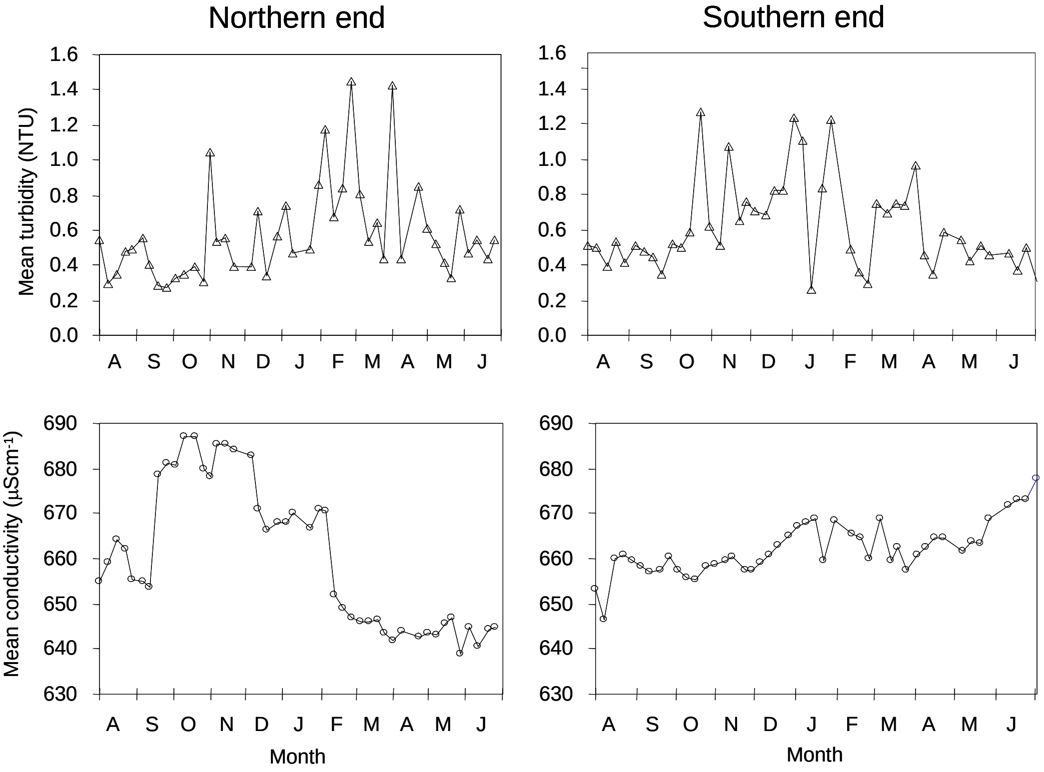

Figure 3. Seasonal succession of conductivity and turbidity in the 0-50 m water column at the northern (left) and southern ends (right) of Lake Tanganyika.

Light.
Weekly means of I_0 (Figure 4) were on average lower at the north station than at the south station (469 and 512 µEm^{-2}s^{-1}, respectively) and varied more with ranges 336-629 and 419-

628 µEm^{-2}s^{-1}, respectively. At the south station, incident PAR (I_0) seemed to be less variable and two maxima around October and March could be resolved.

The depth of the photic zone (Z_{eu}) was highly variable throughout the study period (Figure 4). At the north station, Z_{eu} ranged between 21–69 m (mean = 36 and SD. = 13 m) and between 19–71 m (mean = 41 and SD = 10 m) at the south station. At both stations, fluctuations of Z_{eu} of 25 m wk^{-1} were not uncommon. At the south station, lowest Z_{eu} was found during an *Anabaena* spp. bloom in October. At the north station, Z_{eu} was inversely correlated to turbidity (r = -0.60, N = 45, p < 0.005).

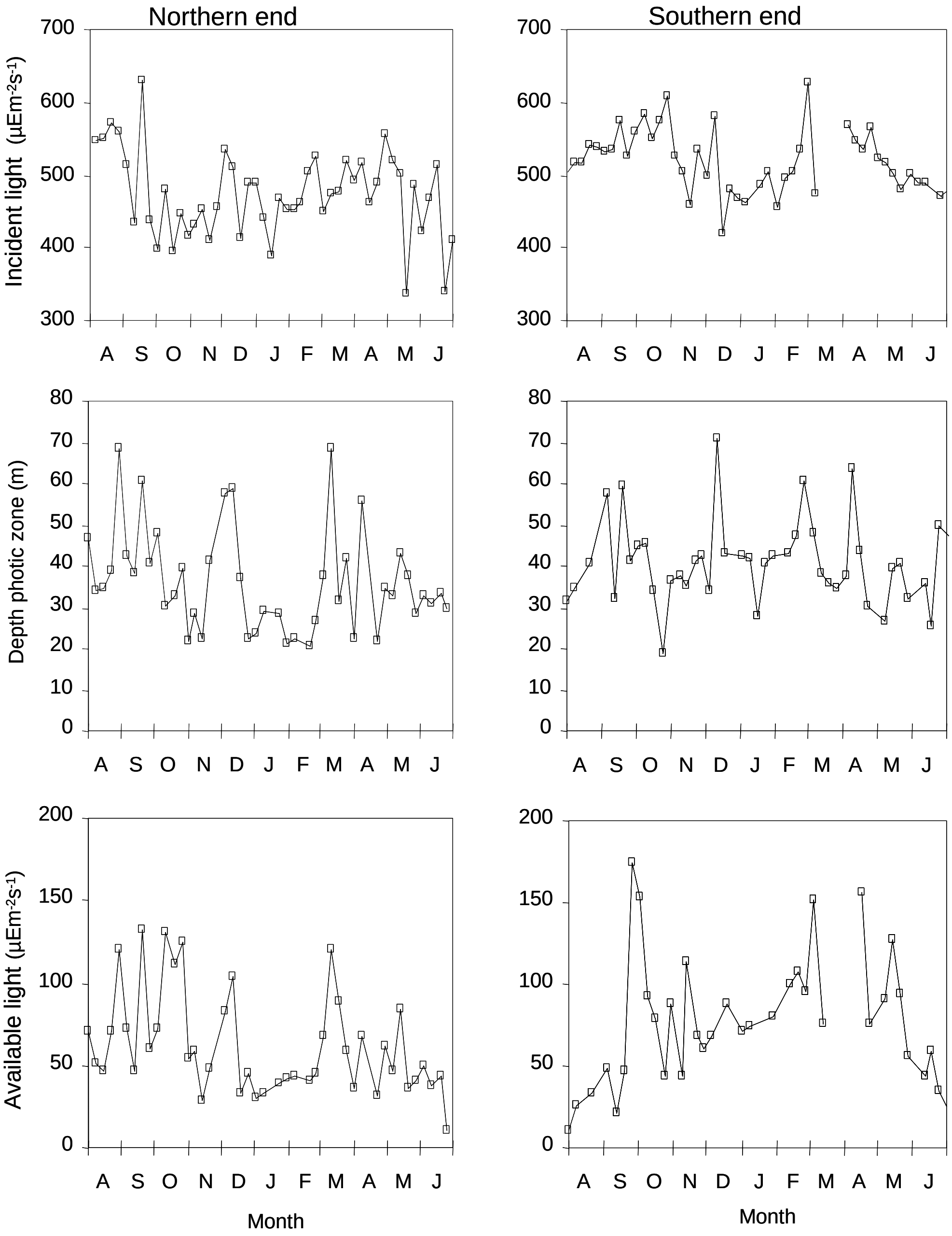

Figure 4. Seasonal dynamics of incident and underwater available light as well as depth of photic zone at northern (left) and southern ends (right) of Lake Tanganyika.

At both stations, quantities of available epilimnetic PAR (I_m) were found to be highly variable but were on average higher in the south (Figure 4). I_m ranged between 11-132 µEm^{-2}s^{-1} (mean 61 µEm^{-2}s^{-1}) at the north station and between 11-173 µEm^{-2}s^{-1} (mean = 73 µEm^{-2}s^{-1}) at the south station.

Only between December and March, variation seemed to be low at both stations. In the south, similar to incident PAR, I_m seemed to be highest around September-October and March. At the north station, I_m was inversely correlated to Z_m ($r = -0.5$, $N = 44$, $p < 0.005$) and positively to Z_{eu} ($r = 0.5$, $N = 45$, $P < 0.01$).

In order to calculate I_m at the south station during periods of upwelling, that is, absence of clear stratification down to 100 m, we estimated depth of temperature discontinuity (replacing Z_m in equation 2) from temperature-depth profiles recorded in close vicinity of sampling point at the south station but down to 150-200 m depth (Huttula, 1997). Low values (11-46 $\mu Em^{-2}s^{-1}$) were found during periods of upwelling (August–September and from June onwards). High values were encountered at the end of September and the beginning of October and were also found at times from March until May. At the south station, irrespective the particular *Anabaena* spp. bloom event during October, I_m was inversely correlated to Z_m ($r = -0.7$, $n = 44$, $p < 0.005$).

Chlorophyll-a.

At both stations, higher values of chlorophyll-*a* concentrations were generally encountered in the upper 50 m water column. Nevertheless, at the north station in May-June and the south station in August-October, chlorophyll-*a* maxima were found in deeper water.

At the north station, areal chlorophyll-*a* values in the upper 100 m (Figure 5) ranged between 58 and 306 mg m^{-2} (mean = 126 and SD. = 54 mg m^{-2}). Higher values were found during the October-December and May-June periods (maximum of 306 mg m^{-2} in December), whereas chlorophyll-*a* gradually decreased in January towards a minimum of 58 mg m^{-2} in April). Chlorophyll-*a* in the upper 50 m was inversely correlated to temperature ($r = -0.4$, $n = 45$, $P < 0.01$), and positively to conductivity ($r = 0.6$, $n = 45$, $P < 0.005$).

At the south station, areal chlorophyll-*a* values, which ranged between 22 and 480 mg m^{-2} (mean = 109, and SD = 71 mg m^{-2}), were higher during periods of upwelling than during periods when the water column was stratified and were inversely correlated with N^2, I_m and temperature ($r \leq -0.5$, $n = 44$, $p < 0.005$).

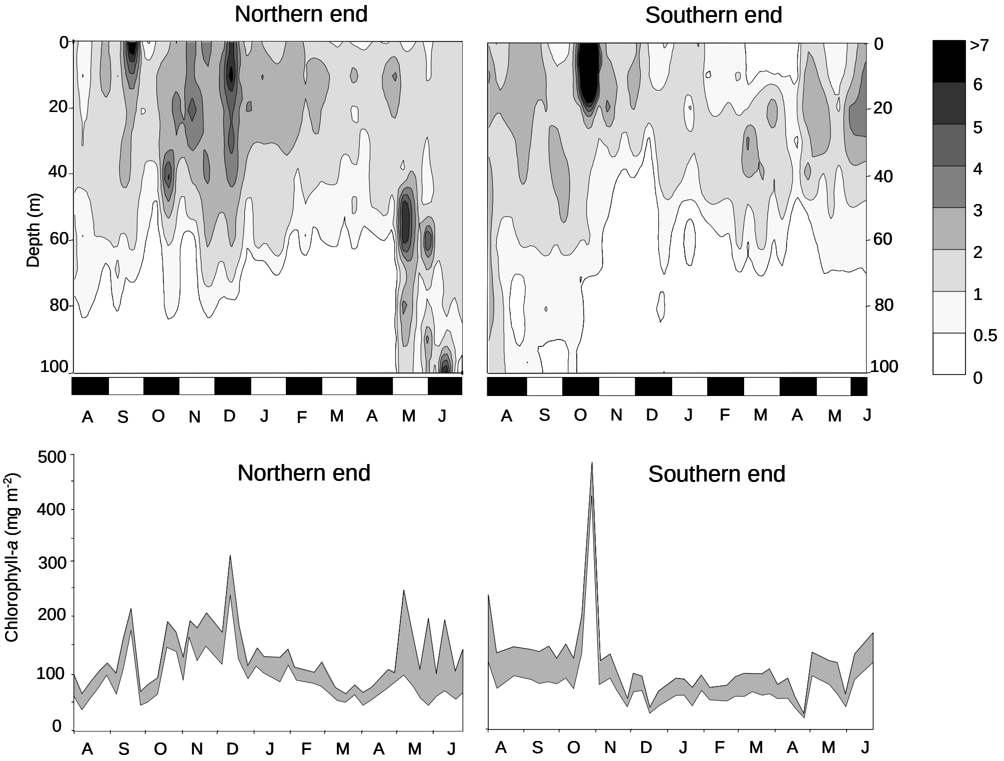

Figure 5. Seasonal course in the vertical distribution (top panel) and areal concentrations of chlorophyll-a in 0-50 m (white fill) and 0-100 m (shaded plus white fill) water columns at northern (left) and southern ends (right) of Lake Tanganyika. Legend in top panel indicates chlorophyll-a concentrations ($\mu g\ l^{-1}$).

Generally, the ratio of chlorophyll-*a* integrated over 0-100 m to that over 0-50 m (see also Figure 5) was ca. 1.5. At the north station, values above 2 (indicating more chlorophyll-*a* below 50 m) were encountered during May and June (maximum 4.2 in May). While at the south station, higher values were encountered during periods of upwelling (ca. 2 in August).

Discussion and conclusion.

The vertical thermal structures of the upper water layers at the north and south end of Lake Tanganyika were highly variable in time and depth. During the dry, windy season (June-September), when strong mixing occurs, the north end was characterised by a strong and deep thermocline, while at the south end rather opposite conditions (e.g., weak or absent thermocline) characterised a strong upwelling event. With the onset of the wet, warm season (October-May), thermal stratification re-established and strengthened itself in the south, while the north showed a temporary 25 m rise of a weakened thermocline. Thereafter, water column stability generally increased in the north, while in the south, a general weakening, accompanied by large fluctuations in thermocline depth, was noted towards the onset of a new windy season. During the study, the upper waters at the north end of the lake remained thermally stratified, while the south end of the lake became largely isothermal during the dry windy season.

The influence of the annual hydrodynamic cycle on the physical structure of Lake Tanganyika has been reported by Coulter (1991), Crul, (1993), Kotilainen et al. (1995), Huttula, (1997) and Plisnier et al. (1999). They show that at the beginning of the dry season (May-August), prolonged southerly winds drive surface waters north, resulting in upwelling of deeper waters at the southern end of the lake and accumulation of warm surface waters in the north. Cessation of the winds (September-October) allows the density imbalance to return to equilibrium, initiating a surge that plays a role in reactivating an internal seiche. Generally, our findings agree and point to a strong coupling between the annual cycle of meteorological conditions on the lake and the properties of the water column. Moreover, this study showed thermal stratification, water column stability and temperature to fluctuate regularly and drastically on time scales shorter than one week. This variability is hard to explain and patterns of seiches, surges and mixing might not simply relate to meteorological parameters measured on the lake. Presumably, synchronicity of prevailing wind patterns and seiching frequency plays an important role in dictating the overall behaviour and strength of internal movements of the water density layers and therefore the vertical thermal structure of Lake Tanganyika.

Lake Tanganyika's waters are known for being very transparent. Measurements carried out by Hecky (in Coulter, 1991) on the underwater light climate showed the photic zone on several occasions to be relatively stable, reaching down to ca. 28 m of depth. However, this study found that the photic zone reached deeper (mean depth ca. 40 m, ranging between ca. 20–70 m), varying strongly in time (ΔZeu of ca. 25 m wk^{-1} were not uncommon, see Figure 4). To explain fluctuations in light attenuation in Lake Tanganyika, the main absorption and scattering processes of the water itself and the combined effect of its constituent components (e.g., phytoplankton, detrital particles and dissolved substances) should be considered. Simple relations between different components affecting water clarity are generally not found due to the complexity of the process mechanisms involved (Kirk, 1983). Nevertheless, in similar oligotrophic waters, a positive correlation can usually be found between chlorophyll concentration and light attenuation coefficients (Kirk, 1983). Except for the algal bloom event encountered in the south, we found no correlation between light attenuation and chlorophyll concentration. In the north, however, the turbidity of the epilimnion decreased light penetration. The correlation was strongest during March and April, and probably indicates the influence of suspended and dissolved solids from riverine origin, as discharges from inflowing Rusizi river were then at their maximum (Langenberg et al., unpublished data). The period 1995-1996 belonged to a sequence of very dry years (Verburg et al., 1998) and decreasing influence of inflow and run-off might explain the differences in water transparency found between the results of this study and earlier published work.

Despite Lake Tanganyika's clarity, it does not automatically follow that its productive layer is well illuminated. We found that epilimnetic available PAR can fluctuate on time scales shorter than a week mainly because of the highly variable position of the thermocline. If we assume that algae mix throughout the epilimnion, then they may receive, on average, much lower quantity of PAR than at the surface. Thus available PAR might be an important factor in regulating algal biomass, according to Sverdrup's (1953) critical depth concept (e.g., the upper-mixed water layer is shallower than some critical depth so that favourable light conditions assure that photosynthesis at least equals phytoplankton losses and thus the phytoplankton population is maintained).

Only during August and September in the north, depth of photic zone and available PAR correlated positively to concentrations of chlorophyll-*a*. Thus during that time of the year, PAR might become insufficient to sustain higher amounts of chlorophyll-*a*. However, throughout most of the year, no correlation between available light and quantities of chlorophyll-*a* within the epilimnion was found, and algal communities seemed to be well adapted to low quantities of PAR (I_m < 50 µEm^{-2}s^{-1}), even at depths below the light compensation point. Therefore, the critical depth in Lake Tanganyika is likely deeper than expected earlier. This is in agreement with the phytoplankton primary production incubation experiments carried out by Sarvala et al., (1999). They concluded from the relatively flat responses of photosynthesis versus irradiance that Tanganyika phytoplankton is capable of efficient photosynthesis at low irradiance levels.

In Lake Tanganyika, overall concentrations of chlorophyll-*a* were low (ca. 1-1.5 µg l^{-1}). Elevated concentrations of chlorophyll-*a* (> 2 µg l^{-1}) could be found during, or directly following, periods characterized by a rise or breakdown of the thermocline, most probably responding to increased availability of nutrients (Langenberg et al., unpublished data). Although we did not monitor nutrients during this study, the increased conductivity values in the north during upward thermocline movement indicate entrainment of nutrient-rich hypolimnetic waters. In the south, we did not detect a distinct loading of dissolved solids from deeper waters. A weak evidence of nutrient loading in a supposed strong upwelling area was also found in Lake Malawi (Patterson and Kachinjika, 1995). In Lake Tanganyika, the vertical distribution of dissolved oxygen probably plays an important role. In the north, the oxycline and thermocline are generally located close to each other (< 100 m; Langenberg, 1996), while in southern regions the oxycline tends to reach much greater depths (up to 200-300 m; Degens et al., 1971, Coulter 1991). Chemoautotrophic and heterotrophic activities (e.g., denitrification processes) can take place deeper, impoverishing rising water layers from free nutrients before they can be traced in the upper 100 m. (Bootsma, 1993; Edmond et al., 1993; Hecky and Kling, 1981). The hypolimnetic water quality is similar throughout Lake Tanganyika (Degens et al., 1971). Therefore, differences between nutrient loading in the north and south probably reflect differences of biological activity in the trophogenic zone rather than different nutrient concentrations of the hypolimnion. The presence of deep chlorophyll in the south coincided with the upwelling period and can be explained by the linkages between chlorophyll-*a* concentration, dissipating water column stratification and deep mixing (Hecky and Kling, 1981; Coulter 1991; Patterson and Kachinjika 1993). However, the presence of deep chlorophyll in the north occurred during a period characterised by a piling-up of warm, epilimnetic waters by southerly winds (Langenberg, 1996), that intensified stratification. Furthermore, seiche activity is small at such times (Plisnier et al., 1999), that is, internal nutrient availability is limited to the area around the thermocline. Therefore, in Lake Tanganyika, the formation of a relatively shallow mixed layer and a weak vertical stratification of the upper waters are not the only prerequisites for phytoplankton biomass to maintain itself or increase. During periods of maximum, deep stratification and low light conditions as well, phytoplankton could peak within the epilimnion. The latter could merely be the result of a lack of critical turbulence as postulated by Huisman et al. (1999). Their concept is based on the notion that phytoplankton biomass can peak if turbulent mixing is less than a critical turbulence value (i.e., growth rates exceed spatial mixing), irrespective of water column stratification. Our findings support this view and imply that different mechanisms in Lake Tanganyika determine phytoplankton maximums at different times. Our study underscores the importance of hydrodynamic conditions in influencing biological productivity in large lakes such as Lake Tanganyika. This influence is exerted either in securing internal nutrient loading or by controlling the spatial distribution of phytoplankton biomass.

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Chapter 4

Phytoplankton in Lake Tanganyika – vertical and horizontal distribution of in vivo fluorescence

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Abstract

Determinations of chlorophyll-*a* and in vivo fluorescence of photosynthetic pigments were used to study vertical and horizontal distribution of phytoplankton in Lake Tanganyika (East Africa). Blue excited fluorescence (IVF_b) was an approximate predictor of chlorophyll-*a* at different depths and locations. Green excited fluorescence (IVF_g), which reflects phycoerythrin in cyanobacteria, explained chlorophyll-*a* variation equally well, and in combination with IVF_b the degree of explanation was improved to 87% (n = 90). Particularly during the shallow stratification in March–May, the maxima of chlorophyll-*a*, IVF_b and IVF_g were located within the thermocline. Such distribution may have resulted from the high penetration of UV light, often accentuated by very shallow daytime thermal stratification, leading to inhibition of phytoplankton near the surface. Because the decrease of chlorophyll-*a* specific IVF_b was less striking towards the surface, the decrease of IVF_b was not caused by light inhibition only. In October–November, epilimnetic IVF_b and chlorophyll-*a* values seemed to be consistently higher than in April– May and often showed remarkable patchiness. The sometimes very dense phytoplankton blooms (Anabaena sp., Cyanobacteria) observed in the central and southern parts of the lake, suggest that local upwelling or mixing events may be important for the development of phytoplankton in Lake Tanganyika.

Keywords: Lake Tanganyika, fluorescence, phytoplankton bloom

Résumé

Les distributions verticales et horizontales du phytoplancton du lac Tanganyika (Afrique Orientale) furent étudiées par des mensurations de chlorophylle a et la fluorescence in vivo de pigments photosynthétiques. La fluorescence bleue provoquée (IVFb) reflète approximativement la présence localisée de chlorophylle a à différentes profondeurs. La fluorescence verte provoquée (IVFg), traduisant les phycoérythrines des cyanobactéries, explique également bien les variations observées en chlorophylle a; ensemble, ces deux formes de fluorescence expliquent 87% de la variation observée (n=90). Surtout durant la stratification peu profonde de mars à mai, les maximums de chlorophylle a, IVFb et IVFg furent localisées à l'intérieur de la thermocline. Une telle distribution pourrait résulter de la grande pénétration de la lumière UV, souvent accentuée par une stratification thermique très peu profonde durant la journée inhibant la présence de phytoplancton près de la surface. La moindre vers la surface de la diminution de l'IVFb, caractéristique de chlorophylle a, ne fut pas causée par l'inhibition par la lumière. En octobre-novembre, les valeurs de l'IVFb épilimnétique et de la chlorophylle a paraissent être systématiquement plus élevées qu'en avril-mai, souvent démontrant des inégalités spatiales remarquables. Les floraisons parfois très denses de phytoplancton (Anabaena sp., Cyanobactéries) observées dans la région centrale et le sud du lac suggèrent une importance des remontées des eaux profondes et du mixage localisé pour le développement du phytoplancton.

Mots clés: Lac Tanganyika; Fluorescence; Floraison de phytoplancton

Introduction

Chlorophyll-*a* is the primary photosynthetic pigment in phytoplankton and hence its concentration has traditionally been used for the estimation of phytoplankton biomass in lakes and oceans. The fluorescence properties of living cells, with chlorophyll bound to specific proteins organized on thylakoid membranes, have led to the development of instrumental methods which can be used directly in the field and are suitable for rapid monitoring of large water bodies (Lorenzen, 1966). However, in vivo fluorescence is affected by many factors and is hence not straightforwardly related with chlorophyll-*a*, biomass or primary productivity of phytoplankton (Falkowski and Kiefer, 1985). In vivo fluorescence per chlorophyll-*a* varies due to species composition of phytoplankton (Heaney, 1978; Vincent, 1983) and photoadaptation may particularly affect the results of vertical profiles (SooHoo et al., 1986). Further, nutrient adaptation (Kiefer, 1973) and photoinhibition (Vincent et al., 1984) may influence in vivo fluorescence of chlorophyll-*a*. The measurement of fluorescence is also affected by instrumentation and only slightly different equipment may reflect different physiological characteristics (Cullen, 1988). Despite its limitations, in vivo fluorescence is widely used as a practical tool for overall evaluation of phytoplankton distributions in lakes and oceans. In large lakes, such as the 650-km long Tanganyika, for practical reasons the number of routine sampling points is limited, and hence any easily available rapid method for estimating the spatial distribution of phytoplankton is valuable. In this study, we used in vivo fluorescence of photosynthetic pigments as a tool to get large-scale information of horizontal and vertical distribution of phytoplankton in Lake Tanganyika (for the description of the lake see Coulter, 1991 and articles in this issue).

Methods

The samples were taken with a Limnos tube sampler during two sampling periods off Kigoma (in April and December 1994) and four cruises of R/V ‘Tanganyika Explorer’ (October 1995, April–May and November 1996, and March–April 1998). Water was led directly from the sampler to the black inlet tube of fluoromètre or it was taken into 2 l polyethylene bottles, which were then emptied, to the fluorometer through a funnel. In April 1994, we used a standard transparent water sampler, but later the sampler was darkened with black plastic sheet or samples were stored in darkness ca. half an hour before determinations to avoid possible effects of too bright light. During the cruise in April–May 1995, horizontal surface samples were also taken with a black plastic scoop from the surface of the lake at the rear of the moving R/V ‘Tanganyika Explorer’. Due to the mixing by the vessel, these samples probably represented a water column down to ca. 2-m depth. Most determinations were made with the same Turner 10-*a*U-005 field fluoromètre (with a CS5-60 excitation filter, 2-64 emission filter, daylight white lamp and a red sensitive photomultiplier). In 1994, another fluorometer of the same model was used and those results were converted roughly comparable with the others using respective chlorophyll-*a* vs. fluorescence regressions. In 1998, we also used a second fluorometer with a green excitation (544 nm/10 nm bandpass) filter set (with emission filter 577 nm/10 nm) to detect fluorescence of phycoerythrin of cyanobacteria. For the determination of chlorophyll-*a*, 1 or 2 l of water was filtered on Whatman GF/C or GF/F glass fibre filters. Chlorophyll-*a* was extracted with 96% ethanol and it was measured with Hitachi F-4000 fluorometer (excitation 420 nm, emission 660 nm). Pure chlorophyll-*a* (Sigma Chemical Co) was used for the calibration. The relationship between relative in vivo fluorescence and extracted chlorophyll-*a* was determined during the cruises of December 1994, April–May 1995 and March–April 1998. Visual observations of phytoplankton filtered on black polycarbonate filters were made on board the research vessel with a Nikon Optiphot epifluorescence microscope using 200- or 1000-times magnification. Vertical distributions of temperature and oxygen were measured at most sampling stations with CTD. Spectral light intensities in water were measured with a Macam SR-991 spectroradiometer equipped with a 4-m quartz light cable and 2 л light collector. Secchi disk transparency was measured using the white upper lid of the Limnos sampler. So-called functional regression was used in the comparison between fluorescence and chlorophyll-*a*, because the values of both variables include measurement error.

Results

The regression between the blue excited in vivo fluorescence (IVF_b) and chlorophyll-*a* in samples collected from different depths all over the lake was clear, but the scatter of the results (Figure 1) was rather high so that chlorophyll variation was only satisfactorily explained ($r^2 = 0.619$, n = 222).

The readings of green excited in vivo fluorescence (IVF_g), which were measured only in part of the samples in 1998, were an order of magnitude lower than those of IVF_b. In spite of the consequently lower precision in this data set, particularly near the surface and below 50 m, IVF_g explained chlorophyll-*a* variation equally well ($r^2 = 0.776$; n = 90) as IVF_b ($r^2 = 0.775$; n = 90). The functional regressions calculated from the results of different depths suggested that there were no marked differences in this relationship between the depths (Figure 2). Contrary to the regression of chlorophyll-*a* with IVF_b, the intercept of the respective regression with IVF_g was clearly different from zero (Figure 3). Multiple regression calculated using both IVF_b

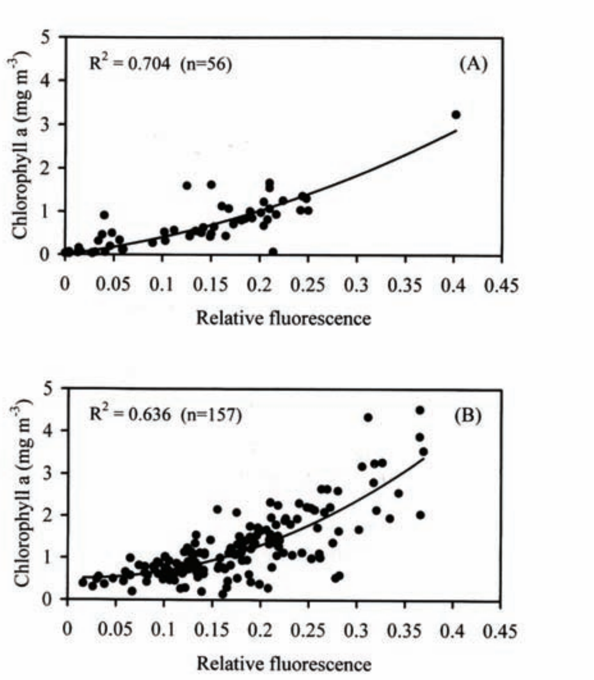

Figure 1. Relationship (with polynomial regression line) between extracted chlorophyll and blue excited in vivo fluorescence in Lake Tanganyika. (A) Samples (n=56) from different depths and locations during the April–May cruise in 1995; (B) Samples (n=157) taken from different depths and locations between Kigoma and Mpulungu in March–April 1998.

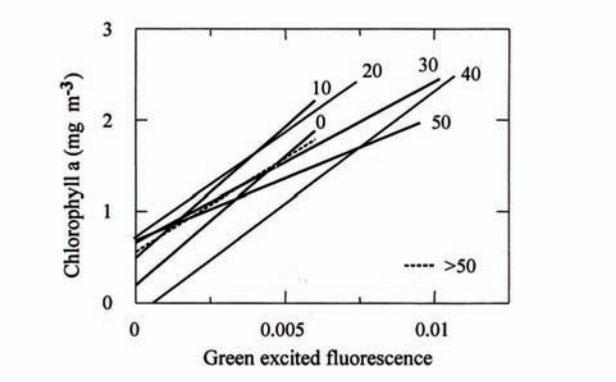

Figure 2. Functional regression lines between chlorophyll-*a* and green excited in vivo fluorescence at different depths (in meters) of Lake Tanganyika in March–April 1998. The number of observations for each line was 10–11. The lines are based on the material shown in Figure 3.

and IVF$_g$ explained a markedly higher proportion of the variation in chlorophyll-*a* ($r^2 = 0.869$; n =90). In the middle of April 1994 off Bujumbura (Burundi) and Kigoma (Tanzania), the IVF$_b$ of Lake Phytoplankton was very low (corresponding to less than 0.5 mg m^{-3} chlorophyll-*a*) and often showed remarkable changes during the day (Figure 4). Early in the morning, IVF$_b$ was more or less uniform in the epilimnion, but decreased rapidly with increasing light intensity and sometimes reached an undetectable level down to the depths of 5–10 m before noon. The decrease in IVF$_b$ was not limited only to the uppermost surface water layers, but even at 50–60 m depth it seemed to decrease ca. 50%.

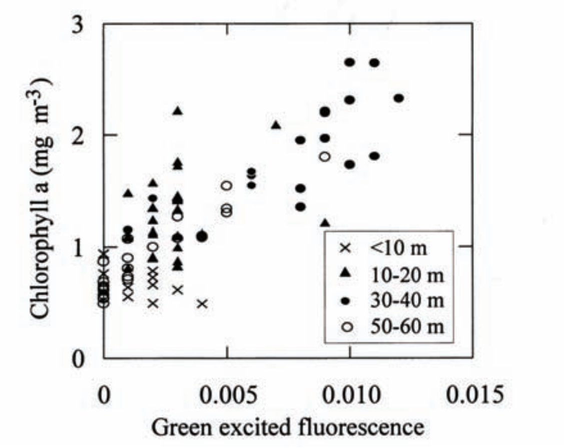

Figure 3. The relationship between chlorophyll-*a* and green excited in vivo fluorescence at different depths of Lake Tanganyika off Kigoma in March–April 1998.

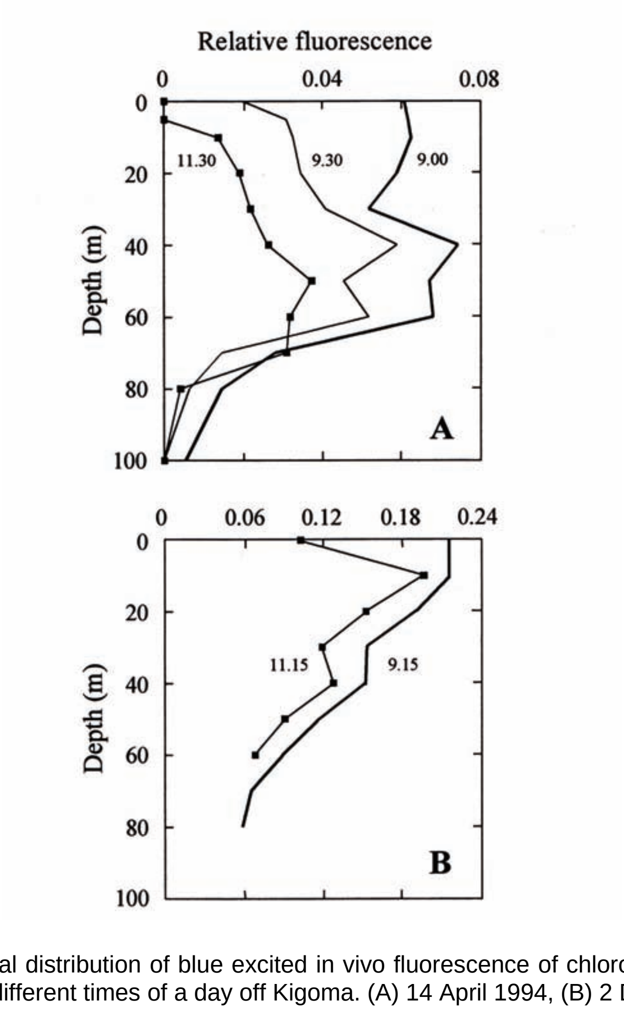

Figure 4. Vertical distribution of blue excited in vivo fluorescence of chlorophyll-*a* in Lake Tanganyika at different times of a day off Kigoma. (A) 14 April 1994, (B) 2 December 1994.

During the whole-lake cruise in late April–early May 1995, the results from the lake surface also indicated decrease of IVF$_b$, but the minimum was observed markedly after noon (Figure 5), around 3 pm (Burundese and Zambian time which is near the local solar time). Thereafter, there seemed to be a rather rapid recovery already before sunset. To exclude the possibility that the observed decrease of IVF$_b$ was due to some other factor (e.g. different water masses), we incubated lake water on the deck of the vessel in an open container and monitored its IVF_b along with time.

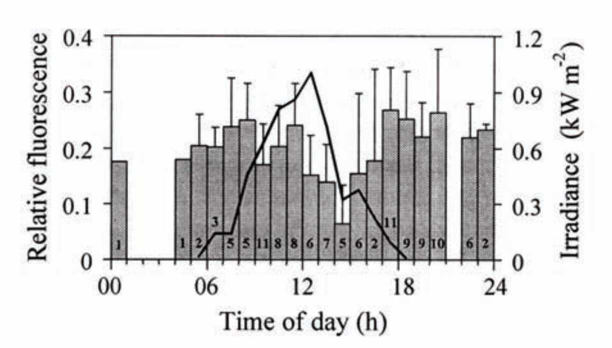

Figure 5. Dependence of surface water IVF_b in Lake Tanganyika from the time of day. The material was collected during the lake-wide cruise in April–May 1995. Vertical lines show standard deviation of the mean in each time interval and the number of observations is given at the bottom of each bar. Diel course of irradiance (solid line, hourly mean values) measured by the weather station of the research vessel is shown as a reference.

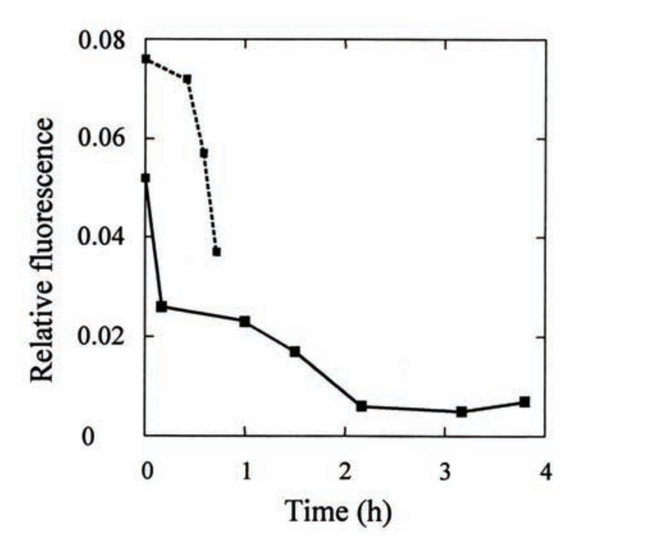

Figure 6. Decrease of IVFb in Tanganyika water taken from the depth of 1 m and kept in an open container under sunshine on the deck of the research vessel. Water samples were taken off Kigoma 14 April 1994 at 8.30 am (solid line) and 2 December 1994 at 2.00 pm (broken line). During the latter series the sky was cloudy at the beginning of the incubation.

The results showed a clear time dependent decrease of IVF_b within an hour (Figure 6), thus supporting the hypothesis that light mediated the observed decrease of IVF_b in our lake water samples. Because water of Lake Tanganyika is very clear, particularly green light reached rather high depths (Figure 7). In the beginning of April 1998 off Kigoma, 1% of UV-A (320–400 nm) radiation penetrated down to the depth of 5–15 m. Thus, considerable part of the epilimnion was affected by UV radiation. When the mixing depth of the epilimnion is high, phytoplankton is exposed only briefly to UV light.

However, during daytime it was not uncommon that the stratification of temperature in Lake Tanganyika was much shallower than the 1% penetration depth of UV-A radiation (Figures 8–9). In 1998 off Kigoma, the Secchi disk transparency was 13–16 m.

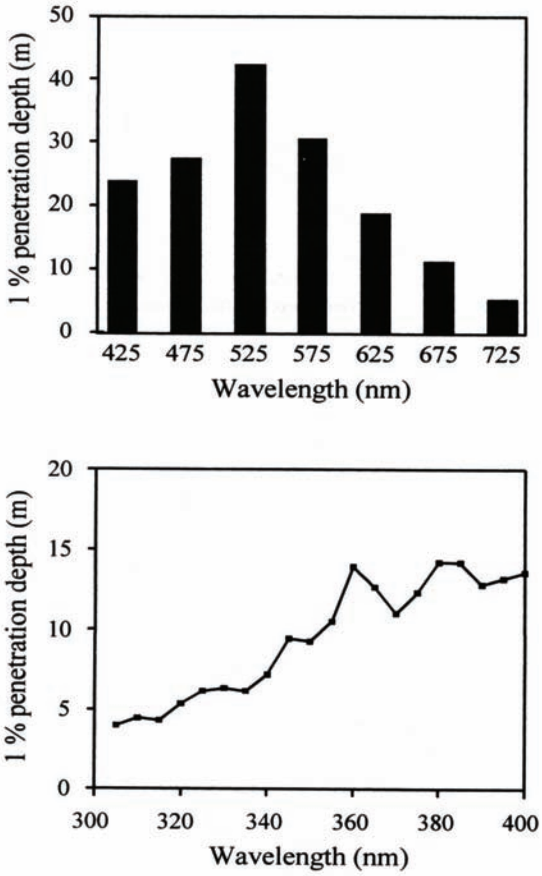

Figure 7. Spectral penetration (1%) of light in Lake Tanganyika in the beginning of April in 1998 off Kigoma. The results are based on the measurements done at 0.01 and 2-m depths. To reduce the variation, the results for visible light wavelengths are shown as integrated over 50 nm intervals.

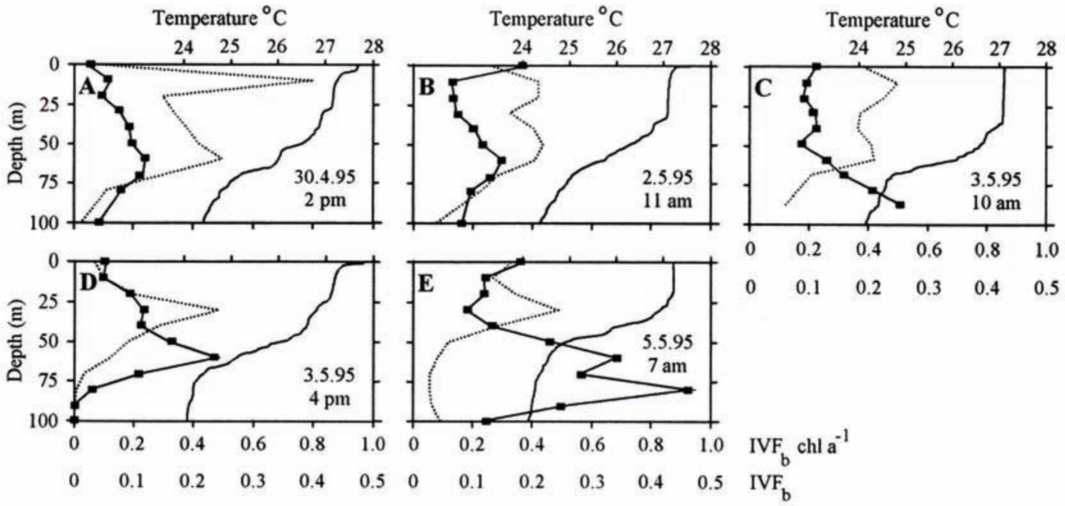

Figure 8. Vertical distributions of IVFb (dotted line), chlorophyll specific IVF$_b$ (solid line with filled squares) and temperature (solid line) in April–May 1995 in Lake Tanganyika. Panels A and B were obtained off Mpulungu and the others were distributed over the lake up to the neighbourhood of Bujumbura (panel E). (For more information of location, see Figure 12.)

In April–May 1995 (Figure 8) and March–April 1998 (Figure 9), both IVF$_b$ and chlorophyll-*a* were determined in most vertical series allowing the calculation of chlorophyll-*a* specific fluorescence. In both years, it showed a decreasing trend towards the surface where its variation was also highest (Figure 10). Although the number of observations was small, it is noticeable that the strongest decrease was consistently observed during the highest irradiance and the following afternoon hours (i.e. between 11 am and 5 pm). In 1998, the mean chlorophyll-*a* specific fluorescence in the 0–60 water column was only ca. 65% of that in 1995.

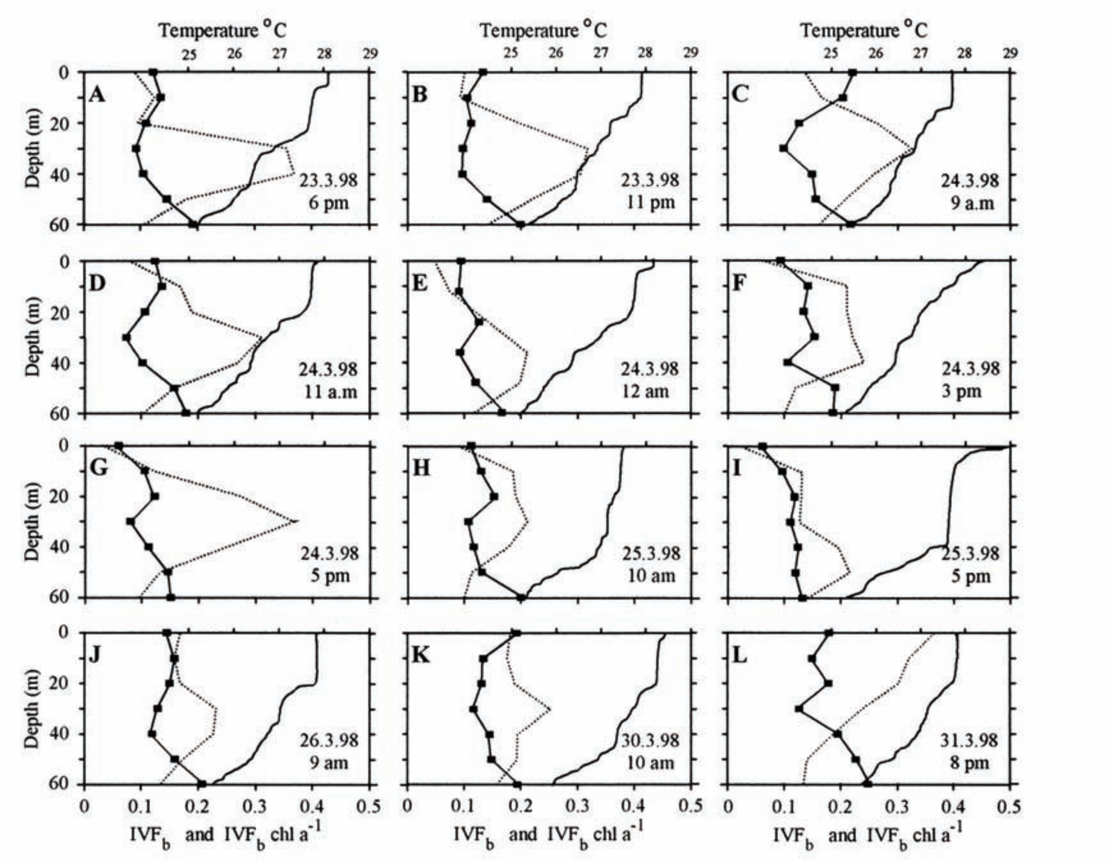

Figure 9. Vertical distributions of IVF$_b$ (dotted line), chlorophyll specific IVF$_b$ (solid line with filled squares) and temperature (solid line) in March–April 1998 in Lake Tanganyika. Panels A–G represent rather small area off Moba in the northern part of the southern basin. Panel H was obtained off Kalemie, I–K off Kigoma and L off the River Malagarasi delta. (For more information of location, see Figure 15.)

According to IVF$_b$, phytoplankton maximum often occurred in the epilimnion, but at the end of the wet season, in March–May, vertical series (Figures 4 and 12–15) generally indicated a metalimnetic maximum at 30–40 m. Similar, and possibly even sharper, maximum was also observed in IVF$_g$ in March–April 1998 (Figure 11). The ratio between IVF$_b$ and IVF$_g$ was consistently lowest in the metalimnion at 40 m. Taking into account the diel fluctuation of IVF$_b$ near the surface (Figure 5), the surveys in April–May 1995 (Figures 8 and 12) and in March–April 1998 (Figures 9 and 15) did not indicate marked differences in IVF$_b$ over the lake. However, taking into account the large size of the lake, the number of our measurements, although combined with visual observations, was in any case too small for reliable conclusions. Instead, in October– November (Figures 13–14) the results showed clear variability over the lake with occasionally high values in central or southern parts of the lake. Although our data were derived from only six expeditions, the readings of IVF$_b$ were consistently roughly two times higher in the beginning of the wet season in October–December compared to the end of the wet season in March–May.

Filamentous cyanobacteria were always abundant late in the year, but were almost absent in March–May.

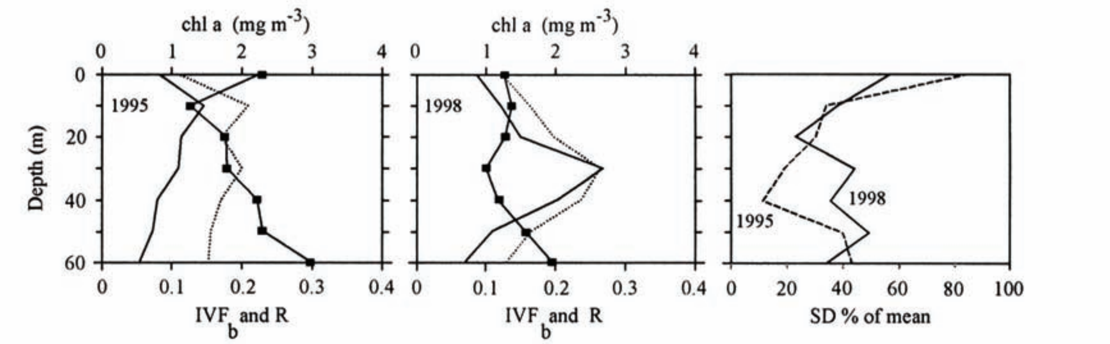

Figure 10. Mean vertical distributions of IVFb (dotted line), chlorophyll-*a* (solid line), chlorophyll-*a* specific IVF_b (R, solid line with squares, median values were used instead of mean to exclude the effect of few possibly abnormally extreme values; see Figure 8) and relative standard deviation of R (right panel) in April–May 1995 and March 1998. The figure is the summary of the results presented in Figures 8–9.

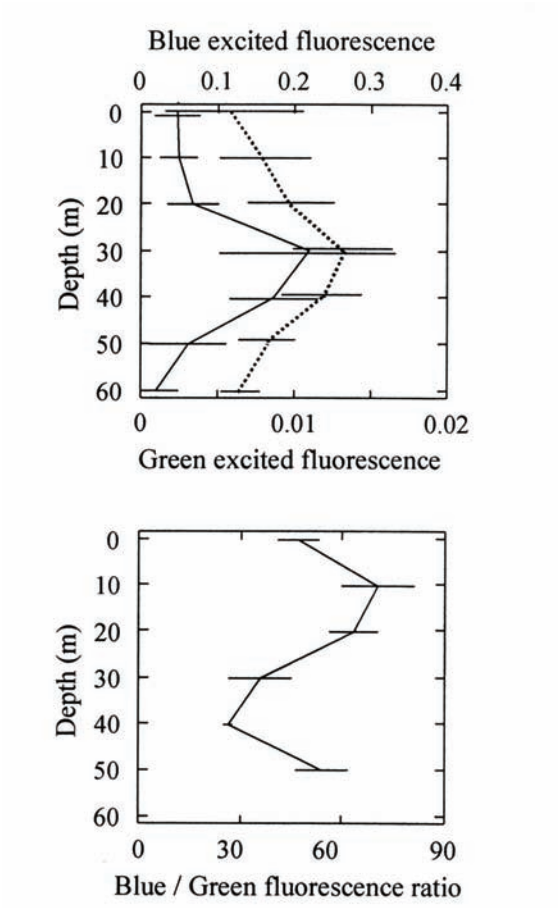

Figure 11. Vertical distribution of relative blue (solid line) and green (broken line) excited in vivo fluorescence and blue vs. green fluorescence ratio off Kigoma in March–April 1998. Standard deviations (n=10–11) for each depth are shown with horizontal bars.

Massive blooms of Anabaena sp. (Cyanobacteria) were observed in the southern part of the lake in 1995 and in the central part in 1996. In 1996, we observed a very special bloom of Anabaena sp. occurring as ca. 50m wide, but kilometres long, in a large scale, almost straight band (Figure 16). The highest algal accumulation floating on the surface was generally only some tens of centimetres wide and so dense that algal mass could be collected by bare hand. In a small scale, the surface band was meandering like old rivers. The laminated structure of the band was most clearly seen at the bends of the band. In our printed photographs, the band was made more visible by adjusting the colours by image processing software and consequently yellow colour was overemphasised.

The true colour of the band seen at the water surface was not dark green, but greyish. Because the orientation of the band was more or less perpendicular to the direction of weak wind and because there were no other parallel visible bands of algae in the neighbourhood, it could not have been caused by Langmuir circulation. There was also no foam present in the band. With epifluorescence and dissection microscopes, we found that it was neither formed around oil or any other similar substance, but it was only composed of Anabaena sp. cyanobacteria.

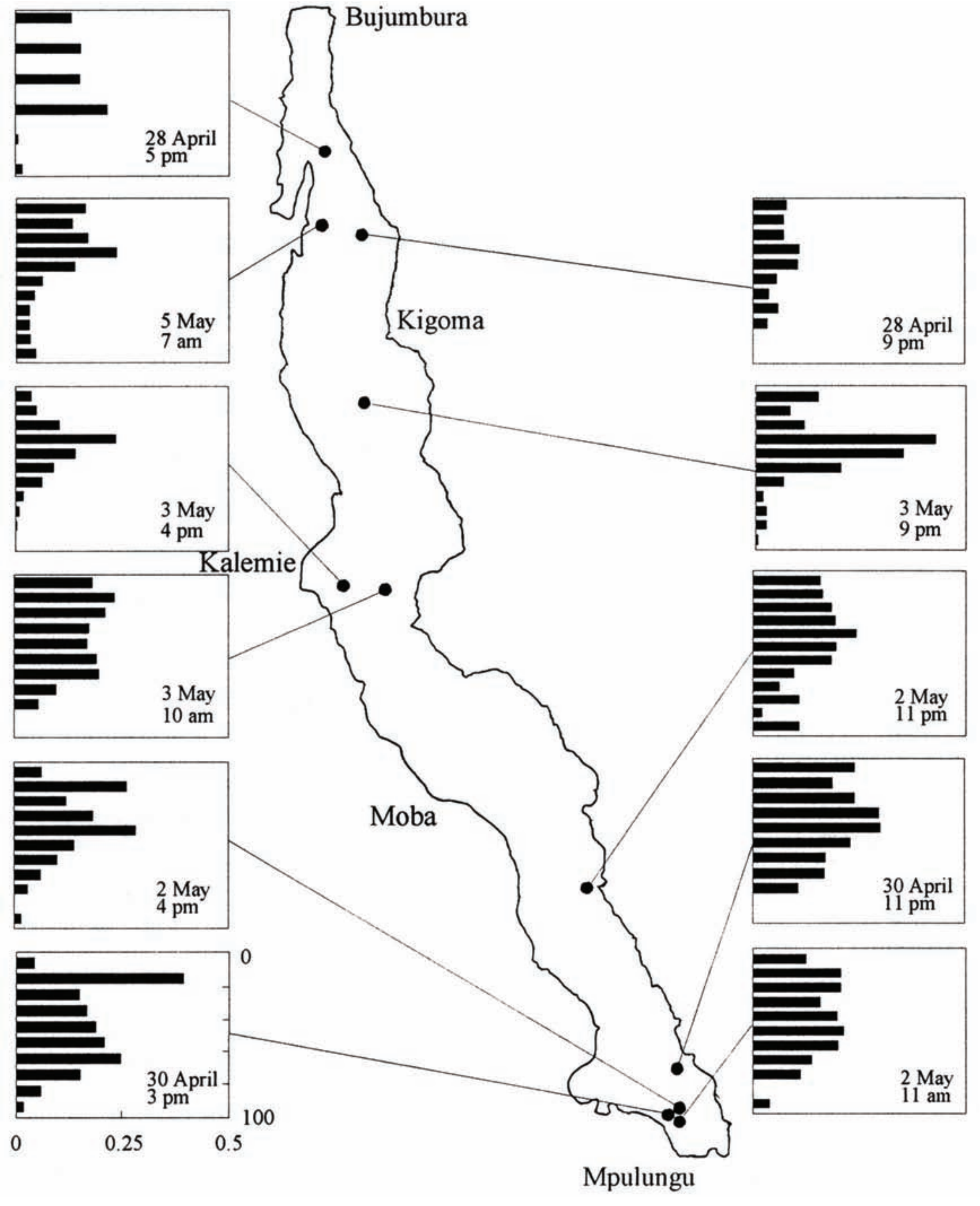

Figure 12. Vertical (0–100 m) distribution of in vivo fluorescence (scale 0–0.5 relative units) of chlorophyll a in different parts of LakeTanganyika in April–May 1995.

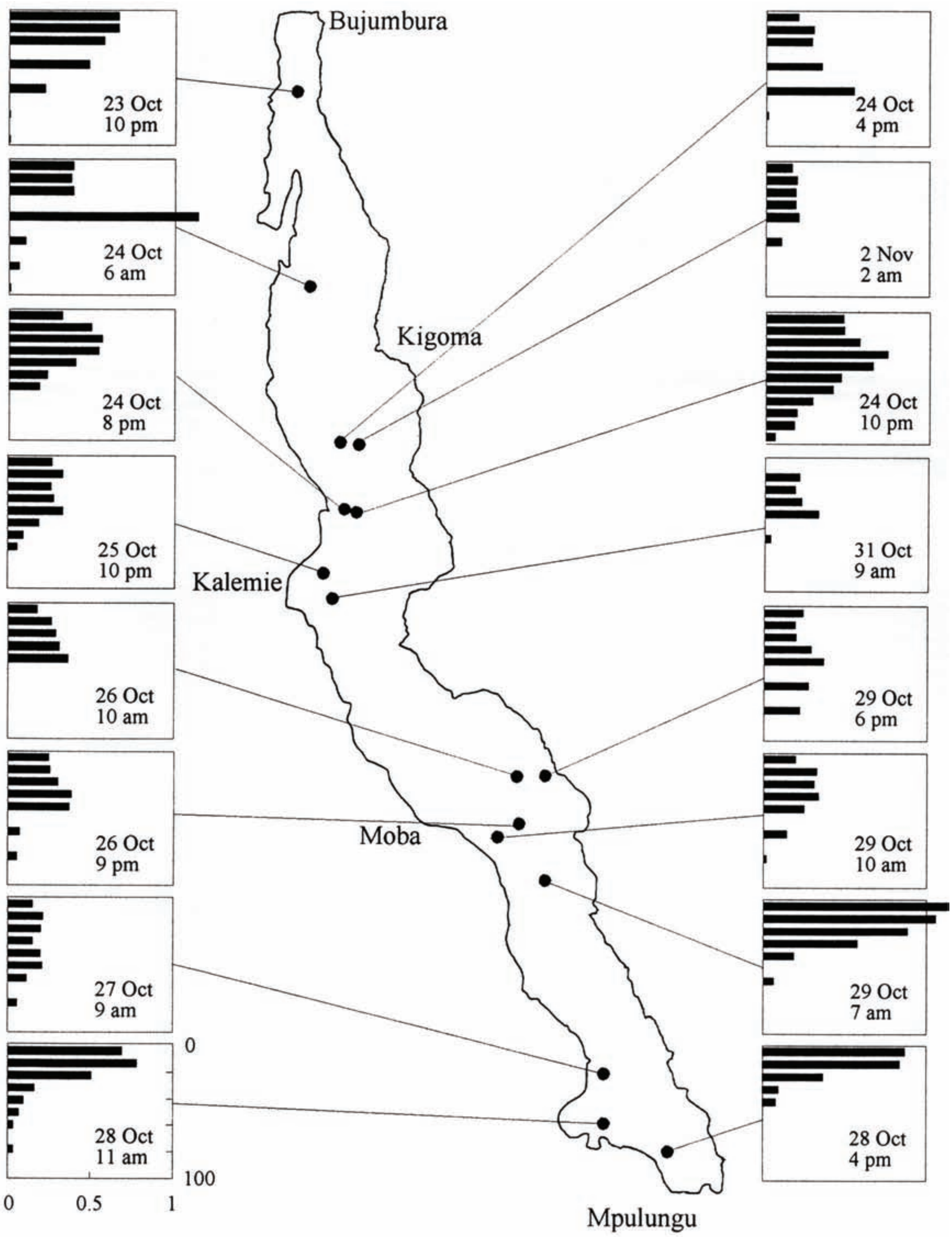

Figure 13. Vertical (0–100 m) distribution of in vivo fluorescence (scale 0–1 relative units) of chlorophyll a in different parts of Lake Tanganyika in October 1995.

Discussion

Due to the clear water of Lake Tanganyika, the background fluorescence (e.g. by humic substances) in the samples was very low making the sensitivity of IVF_b measurements high. Instead, the sensitivity of the measurement of IVF_g should be improved (e.g. by applying a light source with stronger output and optimising the bandpass of the filters) to make it a practical tool also when cyanobacteria are scarce in the uppermost water layers.

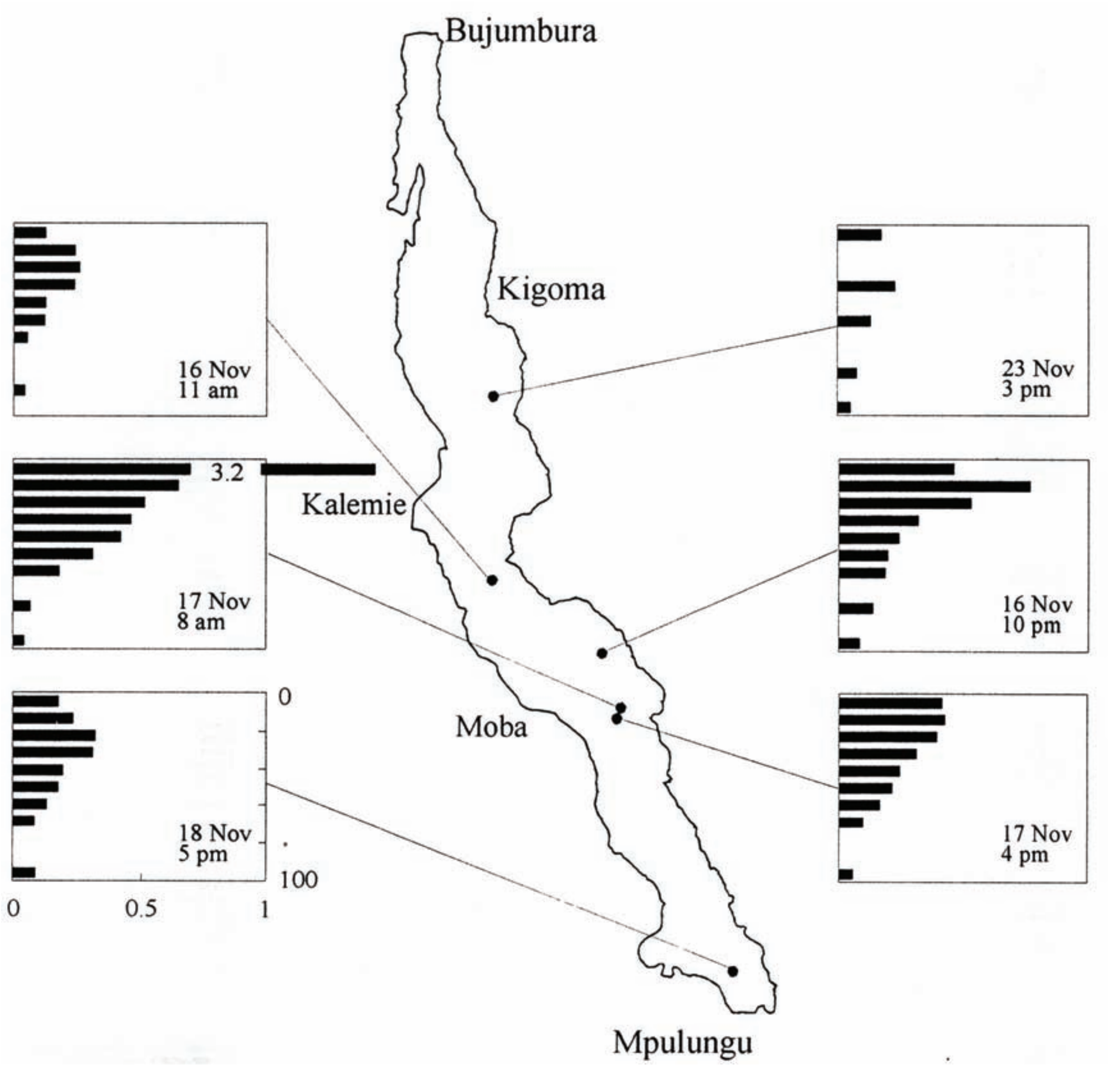

Figure 14. Vertical (0–100 m) distribution of in vivo fluorescence (scale 0–1 relative units) of chlorophyll a in different parts of Lake Tanganyika in November 1996.

In spite of the absence of interferences, the relationship between chlorophyll-*a* and IVF_b showed considerable scatter which may, among others, be explained by vertical and diel differences in light intensity, different light adaptation of algae and species composition (particularly the proportion of cyanobacteria). In Esthwaite Water, Heaney (1978) observed similar variation, which was, at least partly, dependent on the species composition of the phytoplankton assemblage. Filamentous cyanobacteria are often an important component of the phytoplankton assemblage of Lake Tanganyika (Hecky, 1991) and we also found picoplanktonic cyanobacteria always abundant (counted in most depth profiles of three cruises; Salonen, Moilanen and Nuottajärvi, unpubl.). However, since (as seen under an epifluorescence microscope) the latter fluoresced practically only under green excitation light, they likely contributed very little to IVF_b measured with the Turner fluorometer. The combination of both IVF_b and IVF_g measurements seems a promising approach for reducing the variance due to cyanobacteria in predicted chlorophyll-*a*. However, because in late year, filamentous cyanobacteria are most abundant and they may have much lower ratio between IVF_b and chlorophyll-*a* (Heaney, 1978), more information is particularly needed from such conditions. Further, the vertical distribution of IVF_g and the high intercept of the regression between IVF_g and chlorophyll-*a* suggest vertical differences in phytoplankton assemblage which should also be studied during all seasons to assess the usefulness of the multiple regression approach in Lake Tanganyika. Because of its low intensity in atmospheric radiation and low penetration in water, UV-B radiation may be quantitatively less damaging to water organisms than UV-*a*. The penetration of UV-A radiation down to ca. 10–15 m in Lake

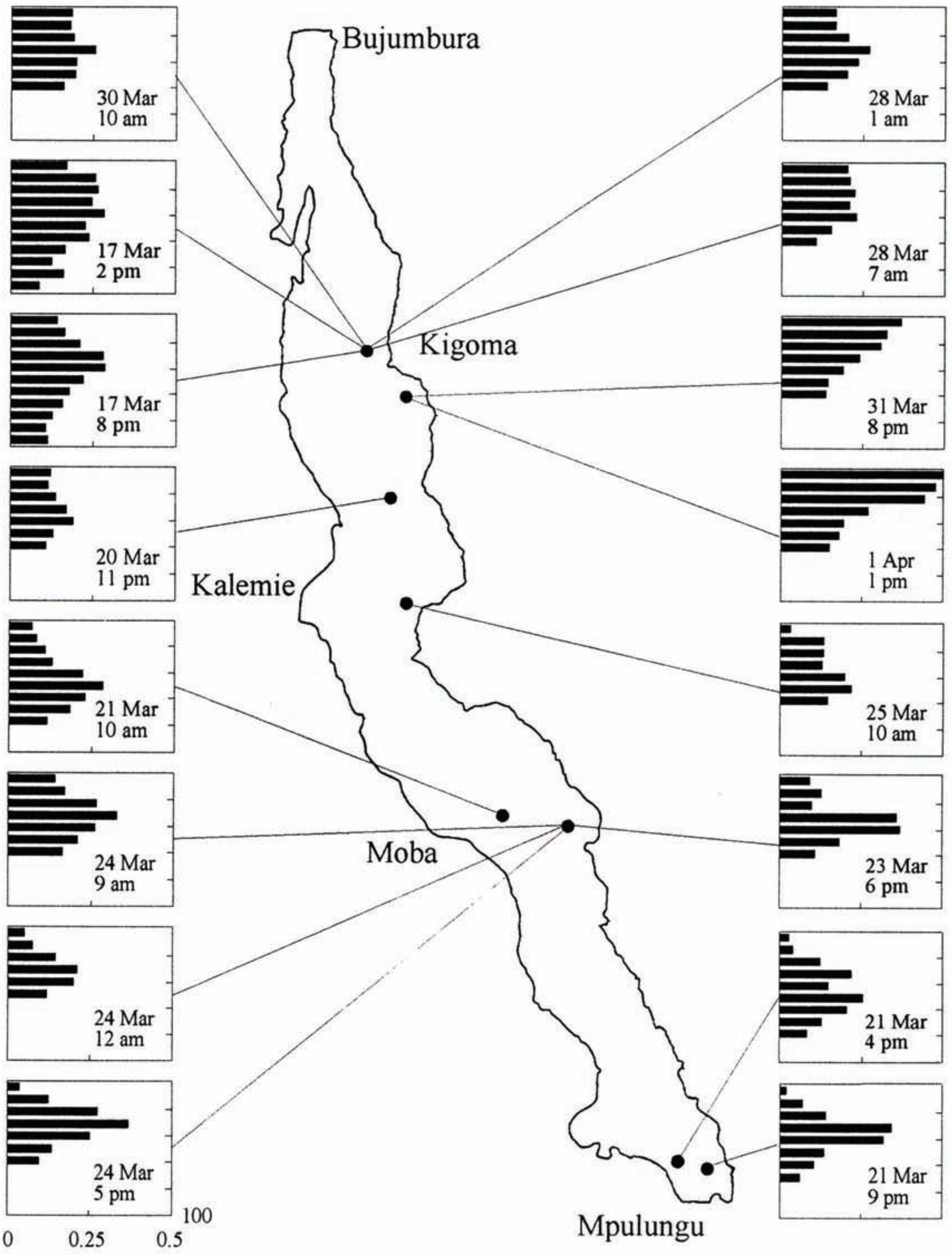

Figure 15. Vertical (0–100 m) distribution of in vivo fluorescence (scale 0–0.5 relative units) of chlorophyll a in different parts of Lake Tanganyika in March–April 1998.

Tanganyika (Figure 7) evidently explains that in the 0–10 m water column IVF_b could decrease to a fraction of the original within a few hours (Figures 4–6). During temporary daytime stratification, efficient mixing of water in Lake Tanganyika is often restricted to much shallower water column (Figures 8–9) than the penetration of UV-A radiation. Whether the daytime decrease in IVF_b was due to inhibition of IVF_b or cellular damage to phytoplankton cannot be known, because in the most striking cases in the field and experiments (Figure 6) no parallel determinations of IVF_b and chlorophyll-*a* were made. The much less striking decrease in chlorophyll-*a* specific IVF_b towards the surface than in IVF_b in the field samples in

April–May 1995 and March– April 1998 suggests that low surface IVF_b was not only caused by photoinhibition. The vertical distributions of phytoplankton (as indicated by chlorophyll-*a*) and/or species composition (as indicated by the ratio between IVF_b and IVF_g; Figure 11) also had marked contributions to the vertical distribution of IVF_b. The observed diel variation of IVF_b in the deep water of Lake Tanganyika in April 1994 may have been exaggerated, because the samples were taken with a standard acrylic plastic sampler, which passes UV light. Even a short exposure to strong visible and UV light (Cullen and Lesser, 1991) might have resulted in artificial decrease of IVF_b during sampling.

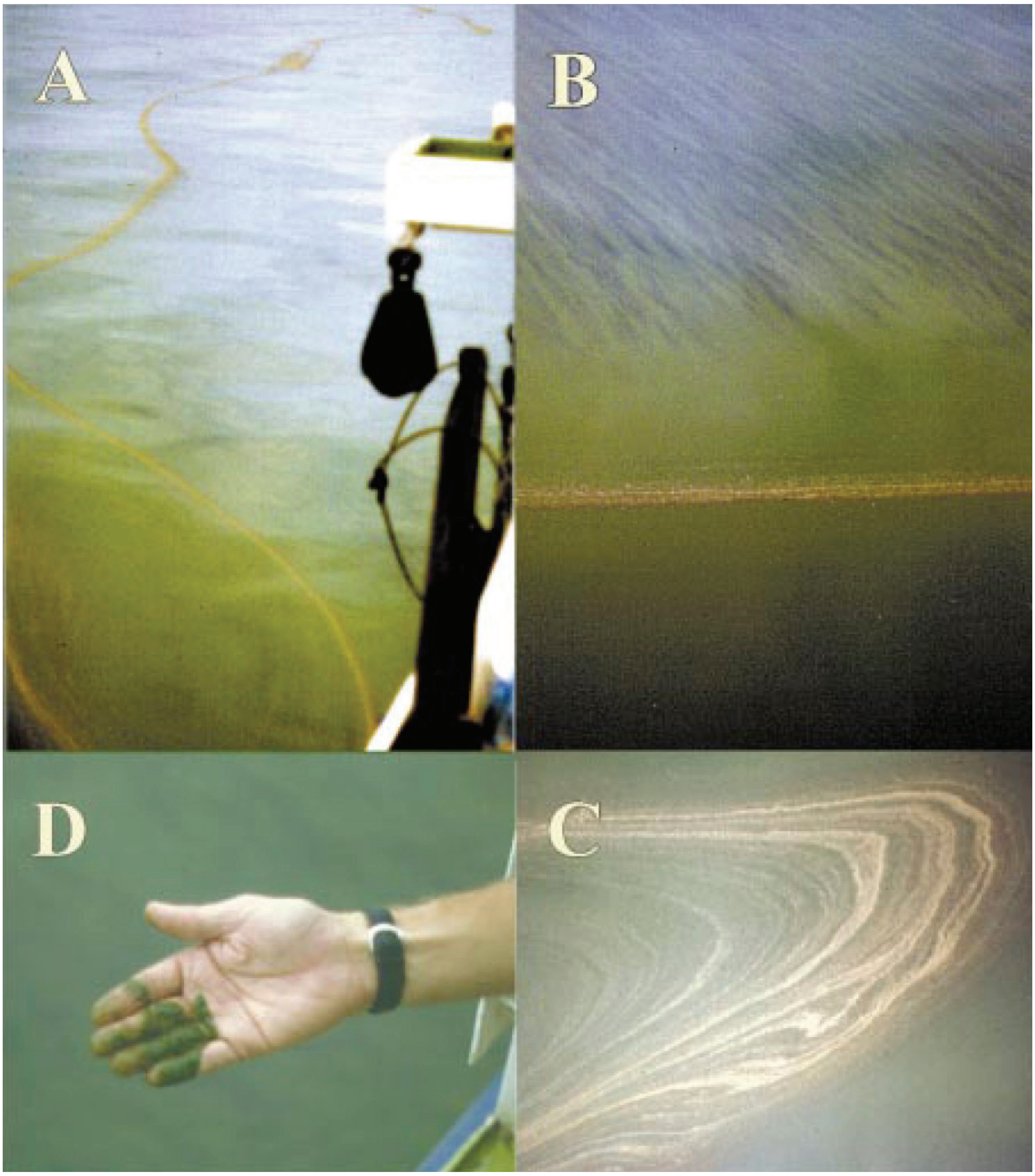

Figure 16. Details of the kilometres long straight band of Anabaena sp. (Cyanobacteria). All photographs were taken with the same objective from the deck of R/V ‘Tanganyika Explorer’. (A) Part of the band on the lake surface. (B) A closer detail showing the very rapid decrease of algal concentration with the distance from the surface band. (C) A detail of the surface band showing the ‘laminations’ of algae. (D) The surface band sampled by hand.

The rather similar changes in deep-water readings of IVFb also in December 1994, when a black sampler was used, suggest that the handling of samples did not alone explain the observed decrease in IVF_b during daytime. On the other hand, both in April and in December 1994, the diel changes in deep water may have been due to changing water masses. Because the 1% penetration depth of UV-A radiation was <15 m, the decrease of phytoplankton fluorescence in situ at the depth of 50–60 m could not be related to UV radiation, unless there was downwelling of surface water. Therefore, it is concluded that the reasons for the diel fluctuations in IVF_b in deep water layers of Lake Tanganyika still remain open.

In the high altitude Lake Titicaca, Vincent et al. (1984) found a 50% reduction of IVF_b within 5 minutes as a result of the inhibition of Photosystem II (PS II) reaction centres. Probably the same mechanism is also important in Lake Tanganyika although the lower elevation of the lake somewhat reduces the intensity of UV radiation. The recovery of the PS II in darkness may take 10–60 min (Heaney, 1978; Vincent et al., 1984; Falkowski and Kiefer, 1985). The sensitivity of IVF_b to visible light and ultraviolet radiation has been found to be particularly high during nutrient depletion (Cleveland and Perry, 1987; Cullen and Lesser, 1991; Lesser et al., 1994). Thus, combined stresses by nutrient limitation (Järvinen et al., 1999) and excessive light intensity (Kiefer, 1973) have likely contributed to the observed daytime decrease of IVF_b at the end of the wet season in April–May. These factors probably also contribute to the presence of metalimnetic maximum of fluorescence and chlorophyll-*a*. At the low light intensities prevailing in deep water, algal cells show higher levels of chlorophyll-*a* and fluorescence than at shallower depths. On the other hand, if hypolimnion is the dominant nutrient source, then nutrients seeping up to the epilimnion can be most efficiently trapped by organisms, which are nearest to the hypolimnion.

During the shallow stratification period there is enough light in the metalimnion (Figure 7), so that such strategy is likely. Hecky and Kling (1981) made the earliest lake-wide observations of chlorophyll-*a* in Lake Tanganyika during the same seasons as in our study. Similar to our observations, they generally found lower concentrations of chlorophyll-*a* in early May than in late October. In October, they found the highest concentrations in the middle part of the lake and lowest ones in the southern basin. Taking into account the unpredictable nature and restricted areal coverage of algal blooms following upwellings, our results are not contradictory with those of Hecky and Kling (1981). The seasonal development of phytoplankton seems also to differ between the basins (Langenberg, 1996). Among other East African Rift Valley lakes, Lake Malawi probably most closely resembles Lake Tanganyika (Hecky, 1991; Hecky et al., 1993). It has similar orientation and hence rather similar hydrodynamic patterns affected by trade winds. In Lake Malawi, the average chlorophyll-*a* approximated 1 mg m^{-3} (Patterson and Kachinjika, 1995), not far from what has been estimated for Tanganyika from IVF_b (the present study) or extracted chlorophyll measurements (Langenberg, 1996). The chlorophyll maximum (ca. 7 mg m^{-3}) in Lake Malawi was of the same order of magnitude as in Lake Tanganyika in late October 1995, but much less than one year later in Tanganyika (maximum tens of mg m^{-3}; i.e. off the scale of the fluorometer). Similar to the April–May situation in Tanganyika, the highest IVF_b (Patterson and Kachinjika, 1995) and chlorophyll-*a* (Degnbol and Mapila, 1982) in Lake Malawi were generally observed in deep water. Chlorophyll-*a* specific IVF_b (Patterson and Kachinjika, 1995) was, as in Lake Tanganyika, lower at the surface than in deeper water layers.

However, because the difference was similar during both day and night, this could not be ascribed to the influence of high surface irradiance. As in Lake Tanganyika (Hecky and Kling, 1981; Hecky, 1991), the proportion of *Anabaena* sp. was high in the southern part of Malawi where upwellings are most frequent (Patterson and Kachinjika, 1995). Patterson and Kachinjika (1995) ascribed higher phytoplankton primary production in one study year to higher degree of seiching. Likewise, upwellings and other mixing events could also have a major influence on the phytoplankton production in Tanganyika (e.g. Hecky, 1991; Edmond, 1993). Indeed, recent intensive hydrodynamic studies indicate that wind-driven currents initiate and maintain upwelling events not only in the southern end of Tanganyika as suggested earlier (Coulter and Spigel, 1991), but also at several locations along the eastern and western coasts (Huttula et al., 1997).

Similar blooms as observed in this study have frequently been reported in the literature and the blooming cyanobacterial species generally seem to belong to genus *Anabaena* (Symoens, 1956, 1958; Hecky, 1991). *Anabaena* blooms have been suggested to be a typical feature in the Rift Valley lakes during the late year epilimnetic warming period (Talling, 1966). This may be traced to the high pH (ca. 9; Coulter, 1994) in Lake Tanganyika and its associated low concentration of free carbon dioxide (CO_2) and/or to nitrogen depletion. *Anabaena* and some other cyanobacteria are more efficient at acquiring CO_2 than most other algae (e.g. Shapiro, 1997), and, therefore, may more likely form blooms in warm and alkaline tropical waters. Because of the important role of filamentous as well as picoplanktonic cyanobacteria in Lake Tanganyika, techniques based on their specific pigments, such as fluorescence of phycocyanin (e.g. Watras and Baker, 1988) or phycoerythrin, are likely useful for large scale studies of phytoplankton. In this study, we observed two types of *Anabaena* sp. blooms – one covering a broad area and one that was like a line. The extremely dense band-type *Anabaena* sp. bloom observed in November 1996 resembled the algal line found by Yoder et al. (1994) at the convergence of major sea currents in the equatorial Pacific at similar water temperature. In Lake Tanganyika the formation mechanism of Anabaena-band has likely been similar. This hypothesis is supported by the laminated structure of the surface band. Water sinking very sharply under the surface together with periodically different concentrations of algae or changing flow rate could have caused the observed longitudinal laminations. In the algal line in the equatorial Pacific, primary production was high and resulted in the accumulation of diatoms at the warm side of the front between two water masses. In Lake Tanganyika, the accumulation of algae may have been even stronger, because, due to gas vacuoles the buoyancy of *Anabaena* sp. is probably much higher than that of *Rhizosolenia* diatoms. Similar to the equatorial Pacific, the locally high primary production may have created the observed algal line in Lake Tanganyika. The magnitude, frequency and location of upwellings may contribute to the development of *Anabaena* blooms. Under good weather conditions combination of thermal and chlorophyll observations by satellites with adequate spatial resolution would allow tracing the physical origin, wax and wane of such blooms. Time series of satellite pictures could even allow derivation of minimum estimates of bloom primary production. Although the poor vertical resolution generally limits the usefulness of remote sensing in oligotrophic lakes, the presence of filamentous cyanobacteria near the surface make it a potential tool in evaluating the role of cyanobacteria in the energy and carbon flow of Lake Tanganyika. Taking into account the diel fluctuation of IVFb, the episodic nature of cyanobacterial blooms and the still low number of lake-wide surveys, our data did not indicate marked systematic differences in phytoplankton abundance over Lake Tanganyika. Phytoplankton seems to be exposed to unpredictable nutrient and light stresses, but sometimes there are also favourable episodes creating blooms. The highly dynamic and patchy conditions together with the large size of the lake make its production very difficult to assess. Therefore, the next step in the understanding of the production and dynamics of Lake Tanganyika might be to apply devices which together with fluorescence of different pigments could also measure some physiological activities of phytoplankton directly in the field.

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Chapter 5

Effect of wind induced water movements on nutrients, chlorophyll-a, and primary production in Lake Tanganyika

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Abstract

We determined the spatial and temporal distribution of major plant nutrients, dissolved oxygen, chlorophyll-a and primary production, at three deep-water locations in Lake Tanganyika to infer patterns of water displacements and to interpret the impact of wind-generated changes in nutrients on the timing and magnitude of phytoplankton production.

In the southern end of the lake, the onset of cooler, windier conditions during May–September caused stratification weakening, tilting of isotherms and upwelling of dissolved inorganic nitrogen and soluble reactive phosphorus from nutrient-rich deeper waters. These factors coincided with an increase in chlorophyll-a concentrations but not with clear evidence of increased primary production. An internal seiche at that time seemed associated with similar but less pronounced events at the other stations after cessation of the winds. We suggest that internal seiching can spread kinetic energy throughout the lake, triggering upward nutrient fluxes through mixing elsewhere. The response to water displacements in terms of nutrient supply to the epilimnion seems to be governed by differences in the strength of vertical temperature, and by nutrient and dissolved oxygen gradients. At the most northern station, these gradients were strongest and closest to each other and throughout the year primary production rates, phosphorus and chlorophyll-a concentrations in the euphotic zone appeared generally higher than at the other stations, probably also because of increased nutrient input from the Rusizi River.

We emphasise that the intra- and interannual differences between the strength of lake stratification and wind regime are of major importance in determining the extent of upwelling events upwind as well as internal seiching strength and duration. That consequently affects the extent of internal nutrient loading throughout the lake and ultimately plays an important role in the lake trophic status.

Keywords: Shear stress, Wedderburn, mixing cycles, upwelling

Résumé

Nous avons étudié dans trois sites des eaux profondes du lac Tanganyika, la distribution spatiale and temporelle des principaux nutriments des plantes, oxygène dissous, chlorophylle a et productivité primaire afin d’en déduire les différents modèles de déplacements d’eau et d’interpréter l’impact des changements en nutriments en fonction du temps et du taux de production du phytoplancton.

A l’extrémité Sud du lac, le début des périodes froides, avec beaucoup de vent de Mai à Septembre, entraîne un affaiblissement de la stratification, une inclinaison des isothermes et le jaillissement de l’azote inorganique dissous, de phosphore réactif soluble des couches d’eaux profondes et riches en nutriment. Ces facteurs ont coïncidé avec une augmentation de la concentration en chlorophylle a mais sans une claire évidence de l’augmentation de la productivité primaire. Une oscillation interne a semblé à ce moment être associée à d’autres phénomènes similaires mais peu prononcés dans les autres stations après la cessation des vents.

Nous suggérons que les oscillations internes peuvent propager de l’énergie cinétique à travers tout le lac, provoquant quelque part des flux ascendants des nutriments à travers le brassage. La réponse aux déplacements des eaux en terme d’apport en nutriment à l’épilimnion, semble dépendre des différences dans la force des gradients verticaux de température, des nutriments et de l’oxygène dissous à la station de l’extrémité Nord, ces gradients ont été plus importants et plus proches les uns des autres. Et au cours de l’année, les taux de productivité primaire, la concentration du phosphore et de la chlorophylle a dans la zone euphotique apparaissant comme étant généralement plus élevés que dans les autres stations. Ce qui serait probablement dû aussi à l’apport croissant en nutriment de la rivière Rusizi. Nous soulignons le fait que les différences intra et interannuelles entre l’ampleur de la stratification du lac et le régime des vents dans la détermination de la portée des phénomènes de jaillissement (upwelling) dûs à la remontée des vents aussi bien que la force et la durée des courants internes. Ce qui affecte par conséquent l’importance de la décharge interne des nutriments à travers le lac et, joue finalement un rôle important dans l’état trophique du lac.

Mots clés: Effort de cisaillement; Wedderburn; cycles de brassage; jaillissement (Upwelling); Nutriments; Productivité primaire

Introduction

Lake Tanganyika lies in the western branch of the East African Rift Valley system. The basin is relatively narrow and has a surface area of approx. 32600 km2. With a mean depth of ca. 570 m it is the second largest fresh water body in the world after Lake Baikal. The vertical thermal structure of the lake is described as being triphasic meromictic (Edmond et al., 1993; Spigel and Coulter, 1996; Huttula, 1997). Throughout most of the lake a persistent epilimnion varies in depth between 0–100 m covering a metalimnion varying in thickness but occasionally extending up to 250 m of depth. At greater depths the upper boundaries of the hypolimnion approximate to the lower levels of dissolved oxygen. Increasing amounts of plant nutrients are found with increasing depth, for example, concentrations of nutrients silicate, phosphorus and nitrogen compounds are higher in the metalimnion compared with the epilimnion, increasing further in the hypolimnion (Hecky et al., 1991; Plisnier, 1996). Since these stratification structures cover such great depths, complete vertical exchange does not occur and consequently the lake’s hypolimnion seems to remain a vast anoxic reservoir of nutrients largely isolated from the surface influences (Coulter and Spigel, 1991; Plisnier et al., 1999). Research on the known nutrient inputs crucial for the level of production showed that although external nutrient input (e.g., from inflowing waters and atmospheric deposition) appears significant (Hecky et al., 1991; Langenberg and Nyamushahu, 1997), it is believed that the replenishment of nutrients from deeper water layers through upward flow or turbulent transport will largely determine nutrient availability to phytoplankton in the upper waters (Hecky et al., 1991). Thus, physical mechanisms enhancing cross metalimnetic mixing and supply of nutrient-rich water to the epilimnion play decisive roles in determining lake productivity. During limited periods and in limited areas, metalimnetic nutrient transport upward through upwelling and seasonal mixing appears to take place. Such events occur especially at times of southerly trade winds (June–September) when there is a weakening and rise of the thermocline in southern areas of the lake (Coulter, 1988; Plisnier et al., 1999). Langenberg et al. (2002) provide evidence that phytoplankton biomass is higher then. During this time a substantialinternal seiche also occurs, a common response of water strata to episodic wind forcing (Mortimer, 1952). The persistent displacement of the strata generates shear flow and turbulence that contribute to mixing and dispersal (Imberger, 1994; Ostrovsky et al., 1996). Plisnier et al. (1999) provide indirect evidence of these periodic mixing events. From the manifestation of periodic chemical variation in water quality variables, including pH, conductivity and temperature, they also deduced it likely that in Lake Tanganyika an internal seiche continues to oscillate with decreasing amplitude for at least one year after the trade winds cease. In theory, a waning internal seiche loses kinetic energy mostly at lateral boundaries and around topographic features by a variety of phenomena, which have in common that they can bring about turbulent mixing (Imberger, 1994). Thus kinetic energy built up at a source tends to dissipate throughout the lake to other places via internal seiching. Prolonged wind forcing and upwelling take place in the south of Lake Tanganyika. Hydrodynamic and biologic data from Lake Tanganyika are too scarce and fragmentary to comprehend the importance of water displacements in introducing nutrient-rich hypolimnetic water into the epilimnion and affecting productivity. This paper uses new data on the spatial and temporal distribution of plant nutrients, dissolved oxygen, thermal structures, chlorophyll-a and primary production at three deepwater locations in Lake Tanganyika to infer patterns of vertical water displacements, and to better interpret the impact of wind-generated changes in the timing and magnitude of nutrient supply and phytoplankton production.

Methods

Sampling was carried out from August 1995 until July 1996 at pelagic stations (>120 m) near Bujumbura, Burundi (NB), Kigoma, Tanzania (MK) and Mpulungu, Zambia (SM) (Figure 1). We used GPS positioning and sampled the stations weekly at ca. 0900 hrs. (GMT+2). Temperature accuracy ± 0.1◦C) and dissolved oxygen were measured by digital probes (model 5795A, Yellow Springs Instruments, Inc., USA), temperature also by thermometers

(VEL Co., Belgium) fitted to sampling bottles (Limnos Ltd., Finland), to 100 m depth at 10 m intervals. Water samples from similar intervals were analysed for nutrients and chlorophyll-a. A HACH DR/2000 spectrophotometer (HACH Co., USA) was used to determine ammonia (Nessler), nitrate (Cd-Cu reduction), nitrite (Azo-dye formation) and soluble reactive phosphorus (SRP) (molybdate). Chlorophyll-a concentrations were determined using a modified spectrophotometric procedure with ‘cold’ ethanol extraction and phaeopigment correction (Salonen and Sarvala, 1995: a modified ISO procedure). Additionally, in vivo fluorescence of chlorophyll-a was measured using a Turner Designs 10-AU-005 field fluorometer (see also Salonen et al., 1999). Fluorescence correlated with extracted chlorophyll-a ($N = 370$, $R^2 = 0.9$, $p < 0.001$), and this regression was used to replace some gaps in chlorophyll-a extraction determinations. In situ phytoplankton primary production was assessed with the whole-water modification of the radiocarbon method (Schindler et al., 1972). Further treatment of the radio labelled samples and controls can be found in Sarvala et al. (1999). Meteorological data describing conditions on the lake were obtained from automatic recording meteorological stations and moored meteorological buoys (Aanderaa Inc., Norway) located in close vicinity of the lake sampling stations (Figure 1). Thermal stability structures within the upper 100 m (N^2 in s^{-2}) were calculated according to the equation:

$$N^2 = \frac{-g}{\bar{\rho}} \frac{d\rho}{dz} \qquad (1)$$

Where $\bar{\rho}$ (kg l-1) is the mean water density, g (m s^{-2}) is the gravitational acceleration constant and $d\rho/dz$ is the density gradient over depth interval z (m).

During September 1993 to August 1996, we calculated daily Wedderburn numbers (W) at Mpulungu station to describe wind generated mixing events. The non-dimensional Wedderburn number, as a balance between surface wind stress and the pressure gradient resulting from the slope of the interface, depends largely on the depth of the epilimnion, wind speed and the length of the lake (Imberger and Patterson, 1990, Patterson et al., 1984). In general, high values of W indicate low shear stress and marked thermal gradients; while low values characterise thermocline tilting, increased mixing and possibly upwelling at the windward side of a water body. Wedderburn number is given by:

$$W = (g' h^2) / (U_*^2 L)^{-1} \qquad (2)$$

where h is thermocline depth (m) at which $\Delta\rho/\Delta z$, was highest. For calculation purposes h was assumed to change linearly between sampling dates; U_* is the shear velocity of air (in m s^{-1}); L is the length of the lake in meters (ca. 673000 m); g is modified acceleration due to gravity at the thermocline calculated by:

$$g' = g(\rho_2 - \rho_1)/\rho \qquad (3)$$

where ρ_1 and ρ_2 are the densities of water for the epilimnion and hypolimnion respectively and ρ is a reference density of water given a value of $[(\rho_2 + \rho_1)/2]$. Water density was determined from vertical density profiles made by a hydrographic probe (CTD-12 plus, Applied Microsystems Ltd.) or was calculated from vertical temperature and conductivity profiles according to Chen and Millero (1977). U_* is calculated by:

$$U_*^2 = (\rho_{air}/\rho_{water}) C_d \cdot U^2 \qquad (4)$$

where U is wind speed (m s^{-1}), and drag coefficient C_d was given a value of 0.0013 (Imberger, 1979). The calculated density ratio of air to water (ρ_{air}/ρ_{water}) throughout the study was ca. 0.0012. Information on the intra- and interannual trends of vertical distribution of water density, thermal structures, dissolved oxygen and nutrients for the period of 1993–1996 at all stations and nutrient and oxygen series from 1993–1995 were used to replace a few data gaps for 1995–1996 at the Mpulungu and Kigoma stations. During this study only mean concentrations of DIN (dissolved inorganic nitrogen as NO_3-N, NO_2-N and NH_4-N), and integrated chlorophyll-a and integrated primary production rate over the upper 40 m were considered, since this depth approximated the yearly average depth of photic zone (Langenberg et al., 2002).

Wind data (daily means) were collected by lake- and land-based meteorological stations all in close vicinity of the limnological sampling stations. At Kigoma station, from December 1995 onward, no wind data from the meteorological lake station were available, but for December 1995 to July 1996 data from a land-based station were used.

The depth profiles of dissolved oxygen, temperature and thermal structures were used to create contour plots (we used a ‘point-kriging’ gridding method in Surfer 7, Golden Software Inc.).

Results

Wind patterns

Wind speeds were in general higher during the dry season (May–September) than in the wet season (October–April) (Figure 1). Respectively at NB, MK and SM, dry season means of 3.4 ± 0.6 m s^{-1}, 3.8 ± 0.3 m s^{-1} and 3.6 ± 1.0 m s^{-1} compared to wet season means of 2.8 ± 0.8 m s^{-1}, 3.5 ± 0.4 m s^{-1} and 2.4 ± 0.4ms^{-1}. At MK yearly mean wind speeds were less variable than at both the lake ends. Differences between wind speeds of the two seasons were highest at SM followed by NB and smallest at MK. Throughout the year, the largest variance in daily wind speeds was at SM with daily means varying between ca. 1–8 ms^{-1}, while mean speeds at NB and MK ranged between ca. 1.5–5 and 2–6.5 m s^{-1} respectively.

Thermal structure

During the dry season, the surfacing of isotherms and disappearance of thermal stratification (evidence for upwelling and strong mixing) at SM coincided with a general increase of isotherm depth, strengthening of thermal structures and warming of the surface waters at the more northern stations NB and MK (Figure 1). In October, thermal structures re-established at SM coinciding with an upward movement of isotherms at NB and to a lesser extent at MK as well (evidence for secondary upwelling). Contrary to the upwelling period at SM, stratification at NB and MK did not break down in the upper 100 m.

At all stations throughout the year, periodic fluctuations in isotherm depth were noticed most probably reflecting internal seiche movements superimposed on the major seasonal vertical movements. The fluctuations seemed to be larger and of shorter duration at NB than at the other stations. In general, fluctuations were marked at the thermocline at the two most northern stations but were evident for most isotherms throughout the upper 100 m at SM.

The seasonal dynamics of buoyancy frequency versus depth (Figure 1), indicative of strength and position of thermal stratification, showed the upper waters at NB to be characterised as homogenous with a developed thermocline. The overall homogeneity of the epilimnion and extent of thermocline development seemed to decrease towards the south. The upper waters at SM reached higher temperature during the wet season than the other stations, and the evenly distributed isotherms indicated a more linear decrease in temperature with depth. Seasonal dynamics at MK were comparable to NB but somewhat weaker stratification structures covered wider depths.

Dissolved oxygen

At NB, oxygen became rapidly depleted below the thermocline, while at the other stations oxygen was still detectable below the thermocline (Figure 1). At SM, during the dry windy season, dissolved oxygen was supplied to greater depths than at the other stations. Note the significant dissolved oxygen concentrations at the 24^{o}C isotherms then situated at around 100 m (Figure 1).

Throughout the year, long- and short-term changes in dissolved oxygen concentrations at different isotherms were found. In general, the downward movement and strengthening of the thermal structures coincided with a decrease of oxygen in the isotherms. Although, dissolved oxygen concentrations were observed to decrease throughout the whole water column on several occasions, the most noticeable depletion in dissolved oxygen concentrations over time was at the 25–25.5 ^{o}C isotherm at the lower boundaries of the thermocline. Depletion here may have been due to oxygen demanding processes when reducing compounds are brought in contact with oxidative waters. Throughout the rest of the year the relatively small

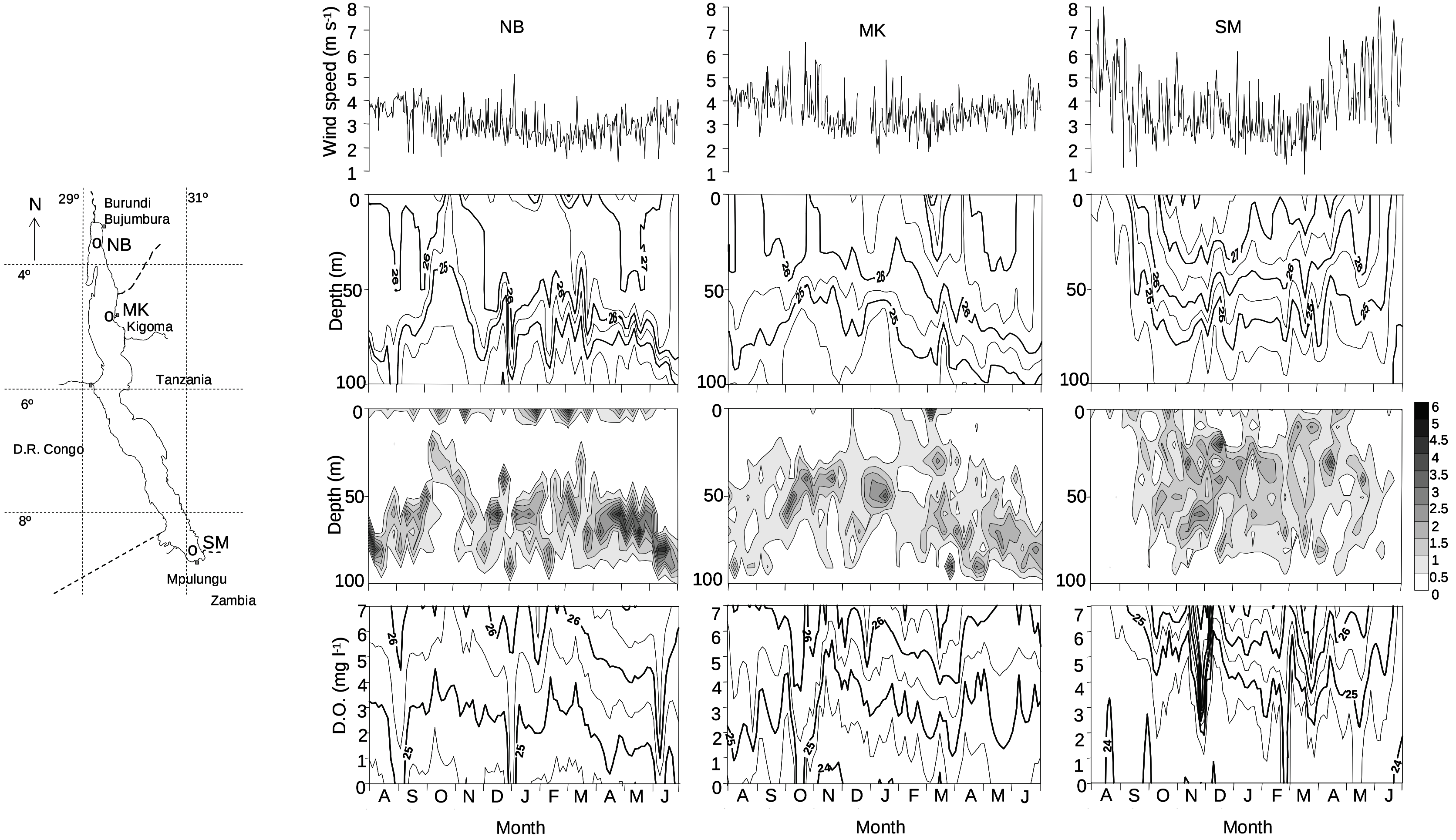

Figure 1. Respectively from top to bottom; the seasonal dynamics of mean daily wind speed, depth distribution of temperature, depth distribution of the squared buoyancy frequencies (N^2 values of scale bar $x10^{-4}$ s^{-2}) and dissolved oxygen concentrations (D.O.) of isotherms (ºC) at the three sampling stations NB (north, Bujumbura), MK (middle, Kigoma) and SM (south, Mpulungu).

variance of oxygen found associated with each isotherm indicated that dissolved oxygen co-varies fairly closely with isotherms.

During relatively calm and stratified conditions in November we observed lower oxygen concentrations at all depths at SM. This might indicate a net oxygen demand within the water column itself rather than being the result of an increased influx of reduced matter from deep, since this would be more noticeable in colder isotherms first.

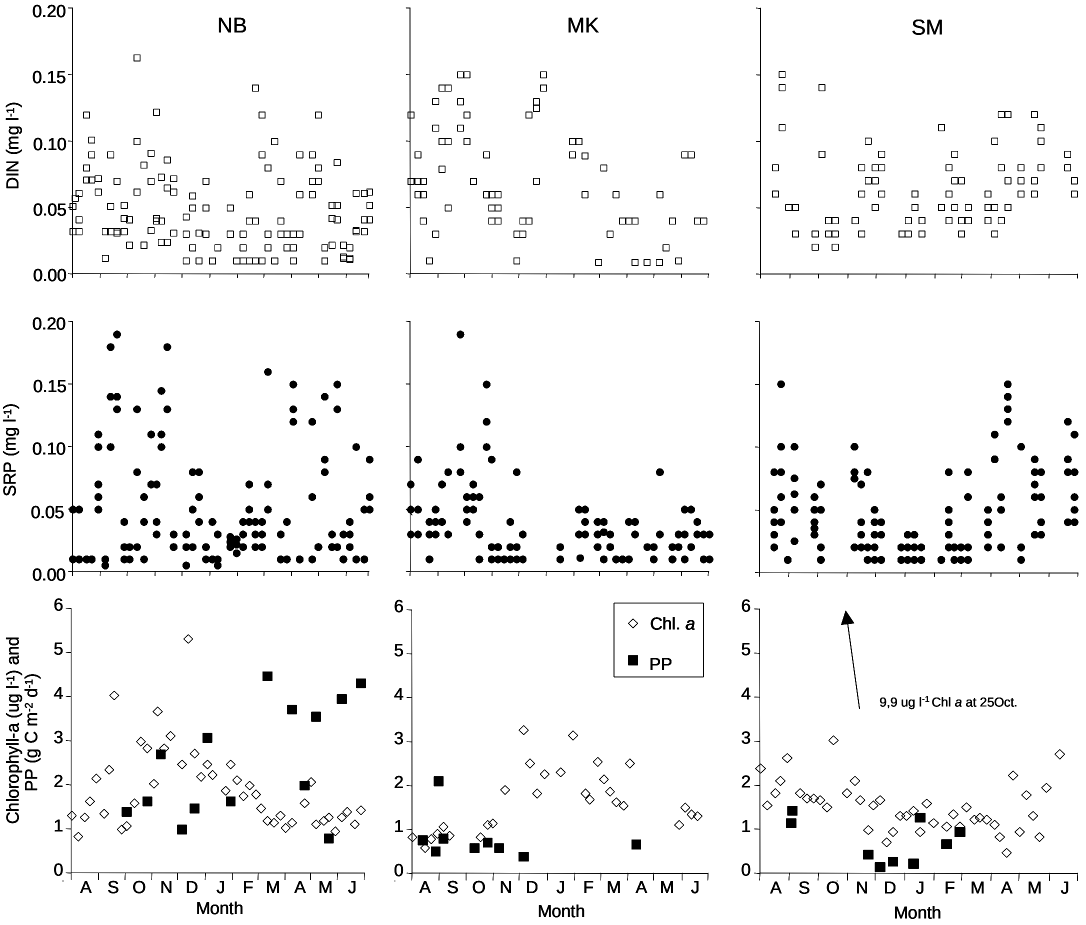

Figure 2. Respectively from top to bottom; the seasonal dynamics of dissolved inorganic nitrogen (DIN) and soluble reactive phosphate (SRP) , Chlorophyll-a concentrations and in situ primary production rates (PP) at the three sampling stations NB (North, Bujumbura), MK (middle, Kigoma) and SM (south, Mpulungu). Chlorophyll-a represent mean euphotic zone concentrations, nutrient concentrations at 4 depths (0, 10, 20 30 and 40 m), while PP rates are integrated over the euphotic zone.

Nutrients

Concentrations of dissolved inorganic nitrogen (DIN) and SRP in the euphotic zone (0–40 m) during the dry season were on average twice as high as in the wet season. At NB lowest concentrations were encountered through December and January (avg., 0.025 mg l^{-1}). Furthermore, the lower limits of SRP where higher during August and during October and November, the period of thermocline movement upward. At MK, higher SRP concentrations (> 0.05 mg l^{-1}) were found during August–November, and lower concentrations during December–June (< 0.05 mg l^{-1}; avg., 0.025 mg l^{-1}). The peak of DIN was around September and December–January (> 0.10 mg l^{-1}) whereas for the rest of the year they averaged ca. 0.05 mg l^{-1}. Concentrations of nutrients at NB fluctuated more and reached throughout most of the year higher average values than at MK and SM, possibly indicating stronger influx of nutrients from the Rusizi river as well as the city Bujumbura. At SM, DIN and SRP concentrations were lowest during January (respectively 0.05 and 0.02 mg l−1).

Chlorophyll-a and primary production

At SM, chlorophyll-a concentrations of <1.5 μg l^{-1} characterised the euphotic zone during the wet season, increasing to ca. 2–3 μg l^{-1} in the dry season (Figure 2). At NB the highest values were found in October and November (ca. 3 μg l^{-1}), but decreased thereafter and remained rather stable at ca. 1–1.5 μg l^{-1} throughout the dry season. At MK a similar yearly trend was observed although concentrations were lower than at NB and chlorophyll-a peaked 2 months later (December and January). Primary production rates showed that values for SM and MK were mostly < 1 g C m^{-2} d^{-1}, while the values at NB varied more and reached higher values (up to 4.5 g C m^{-2} d^{-1}). At NB higher rates were found during the dry windy season (> 3 g C m^{-2} d^{-1}).

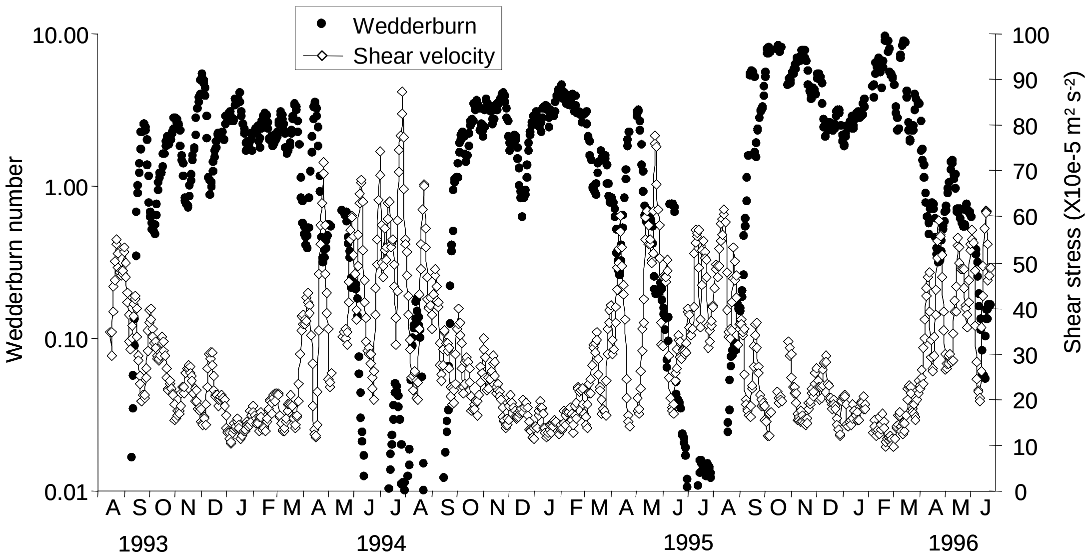

Figure 3. Weekly running means of the Wedderburn number (W) and shear stress for station SM (South, Mpulungu).

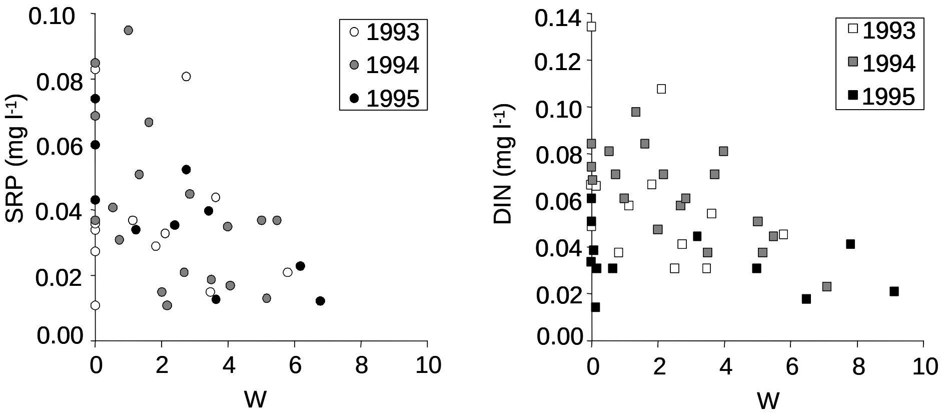

Figure 4. Mean concentrations of soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) for euphotic zone at station SM (South, Mpulungu) of sampling years 1993-95 in relation to the Wedderburn number (W).

Wedderburn numbers

The yearly recurring trends in shear velocities and Wedderburn number (W) at SM were indicative of their strong coupling (Figure 3). During the dry windy season, high shear velocities and low Wedderburn numbers (< 1) indicated periods when strong mixing would be expected, while higher numbers coincided with low wind stress and well-established thermal stratification during the wet season. Wedderburn numbers during the wet season of 1995–1996 were higher than the two previous years ($n = 27$, $p < 0.01$), and shear velocities fell from the second half of dry season 1995 up to July 1996.

Mean W for 93–94, 94–95 and 94–95 wet season were respectively 2.7 ± 1.5. 3.0 ± 1.3 and 5.5 ± 2.4. Inverse relations were found between the mean concentrations of SRP and DIN in the euphotic zone and Wedderburn numbers (Figure 4). Concentrations in the euphotic zone generally increased with decreasing Wedderburn numbers.

Discussion and conclusion

Seasonality in the physical structures of the water column in Lake Tanganyika seemed largely dominated by the annual cycle of monsoon winds. A cooler dry period (June–August) with strong winds cooled surface waters through a combination of increased evaporative cooling (Verburg et al., 1998) and upwelling at the south. Northward-driven surface waters accumulated at the windward end of the lake and intensified density structures at greater depths. When wind energy no longer forced downwelling in the north (September–October), a rise of weakened gradients (secondary upwelling) and the reestablishment of stratification in the south indicated the return to a season of more stable density stratification in which isotherms oscillated regularly in an apparent internal seiche. Compared to the lake’s ends, the physical dynamics in the middle (MK) were characterised by intermediate conditions. Seasonal isotherm movements similar to NB were observed but they were in general smaller and comprised weaker density gradients at shallower depths. The seasonal oscillations of thermal structures in the upper water layers along the north-south axis as a whole around a central positioned node might explain why the vertical physical structures away from the ends and thus closer to the node may show overall less response to hydrodynamical forcing (Allanson, 1990).

Furthermore, factors like basin morphometry and wind may also affect seiches locally. The station at MK is characterised by a steeply shelving bottom and a wind regime with a strong east-west component, while the NB and SM stations are characterised by more gently sloped bottoms and south-north winds (Coulter and Spigel, 1991; Kotilainen et al., 1995). Shelving bottoms may exaggerate seiching and associated mixing events as found by Ivey and Nokes (1989), Garrett et al. (1993) and MacIntyre et al. (1999). Stations MK and SM have in common that yearly net wind force is moving surface waters away from the station while NB is at the downward end of the lake (Verburg et al., 1998). The marked extension or stretching of the metalimnion structures at MK and SM can be explained by that phenomenon.

Long and short term fluctuations in the oxygen temperature relationship were observed. Throughout the year, the oxygen content of water of similar temperature related to the position and strength of the thermocline. During periods of shallow and weak gradients (upwelling), isotherms generally had higher oxygen content. Surfacing isotherms are likely to be more easily replenished by oxygen from the surface compared to those situated deeper in the water column which are also more susceptible to oxygen demanding processes especially at levels where reducing constituents are mixed into the epilimnion due to water movements at the interface. Furthermore, short-term drops in oxygen at the lower boundaries of well-established thermoclines were observed (e.g., the 25 ^{o}C isotherm during September, January and June at NB and during October at MK). Rapid depletion may occur due to oxidation-reduction processes where epilimnetic waters mix with actively reducing matter from below the thermocline. Oxygen may in this case be distinctly depleted compared to near surface concentrations. Cross-thermocline mixing probably occurs throughout the year but our data showed that they were only detectable during periods where temperature and oxygen gradients were strong and situated at similar depths. At MK and SM, in contrast to NB, oxygen occurred below the thermocline and as a consequence oxidation-reduction processes must take place there. Therefore, seiche-related water movements, generally best defined at thermocline level, may at these stations not necessarily result in nutrient replenishment of the epilimnion because nutriclines are at greater depths.

Wind induced turbulence determines to what extent oxygen is locally mixed into the epilimnion. Nevertheless, high wind speeds at MK (on average they are higher than at NB) did not necessarily lead to a better aerated epilimnion at all times. At NB, distinct oxygen depletions, due to mixing with hypolimnion water, occurred at the lower boundaries of the thermocline distant from surface influences, whereas at MK oxygen depletions occurred throughout the epilimnion during October when thermal structures moved upward. Most probably, local differences in wind direction at NB and MK and therefore net transport of aerated surface waters and consequential the upward movement of reducing constituents will, next to surface replenishment, determine the epilimnetic oxygen concentrations. Wind-induced seiching in Lake Tanganyika is noticeable throughout the year (Huttula, 1997), and although resultant mixing would be expected to cause nutrient intrusions into the epilimnion year-round this was not obvious from our data. The rapid uptake of dissolved nutrients by phytoplankton, significant denitrification activity at the oxic-anoxic boundary, and dilution over thermal structures covering large depths will reduce concentrations in the euphotic zone close to the detection level. Nevertheless, when upward nutrient flux was large enough nutrients were mixed into the epilimnion becoming detectable even within the euphotic zone. Clearest nutrient upwelling was observed at SM, during the dry windy season, where concentrations of DIN and SRP as well as chlorophyll-a increased. Our observations furthermore indicate that the largest upward movement of the thermal structures at NB (October) was related to elevated concentrations of nutrients and chlorophyll-a. At MK strongest upward movement of the thermocline also took place during October. Although increased euphotic concentrations of DIN and SRP due to this upwelling event were observed here, chlorophyll-a concentrations remained relatively low. Contrary to NB, the nutrient upwelling in October at MK coincided with a sharp decrease of dissolved oxygen throughout the epilimnion. Substantial cross-thermocline transport of anoxic water containing significant amounts of H_2S and NH_3 might have created conditions where phytoplankton growth is not favourable. It is believed that similar events may attribute to the occasional occurrence of fish kills as well (Plisnier et al., 1999). Phytoplankton at MK seemed to respond to a smaller upwelling event during December– January. The decrease in euphotic SRP then can be explained by DIN stimulation of algal growth causing rapid uptake of SRP. Occasionally, elevated DIN and SRP concentrations could not be satisfactorily explained by strong seiching or upwelling events. The intensified seiche activity of gradients in the shallowest sub basin of Lake Tanganyika combined with the input of river Rusizi might explain why on average the highest nutrient concentrations of DIN and SRP as well as primary production rates were observed at NB. Increased influx of nutrients due to upwelling did, however, not lead to increased production rates. At NB, primary production was highest during the dry season when thermal structures intensified and deepened (downwelling). Possibly, rates may have been affected by entrainment of hypolimnetic water or ameliorated underwater light conditions. Langenberg et al. (2002) showed that at NB the underwater available photosynthetically active radiance (PAR) was largely determined by the depth of the mixed layer. At NB, epilimnetic available PAR fluctuated strongly around a value ca. 100 $\mu Em^{-2}s^{-1}$ during strong upwelling and remained fairly constant at ca. 50 $\mu Em^{-2}s^{-1}$ during the dry season. The low primary production rates at SM during a strong upwelling event may be due to very low values of under water PAR as a result of deep mixing ($< 50\ \mu Em^{-2}s^{-1}$). However, a thorough assessment of the phytoplankton production rates at all stations can not be made due to insufficient data. Wedderburn numbers are useful in providing an immediate description of how the physical and biological variables responded to meteorological or hydrological forcing. During the dry windy season, low numbers (< 0.5) indicated shear velocities to be large enough to move surface waters in the direction of the prevailing winds, breaking down thermal stratification, causing isotherm tilting (April) and eventually upwelling of nutrients at windward side of the lake (May–September).

The observed inverse relation between Wedderburn numbers and mean euphotic concentrations of DIN and SRP shows that higher concentrations of nutrients may become detectable in the euphotic zone (e.g., DIN in Figure 4) during windier years. Our observations showed that higher rates of nutrient supply at SM supported higher phytoplankton biomass. Throughout the rest of the year higher Wedderburn numbers showed the water column to be less susceptible to wind-induced instability.

Differences in yearly recurring trends in Wedderburn numbers were observed. Throughout the period 1995–1996 higher Wedderburn numbers indicated an overall increase in thermal stability probably as a result of decreasing shear velocities. The period 1995–1996 had lower wind speeds (Huttula, 1997). Lower wind strength and associated evaporation cooling can bring about surface warming causing stronger thermal gradients. Episodic wind forcing determined the extent of the upwelling process in the south and formation of internal seiching, which in turn, was associated with significant down- and upwelling events elsewhere in the lake. We observed that seiching created mixing across the thermocline year-round but when the wave motion has a large enough amplitude it may come close to the surface, merge with the upper waters and lead to similar results as wind-induced upwelling. Hence, after relaxation of the winds in the south, the resulting upwellings (October–January) in northern waters seemed to have amplitude strong enough to affect the development of the phytoplankton. Variation in wind energy between years may thus considerably affect of the extent of up- and downwelling events as well as seiching. We might assume that if the lake-wide tilting of thermal structures in a certain year is not large enough because of weak winds, upwelling events upwind will be smaller in terms of nutrient influx. Consequently, seiching and upwelling events downwind might not be intense enough to reach a critical depth where gradients might erode and lead to significant nutrient replenishment promoting phytoplankton. In such years, phytoplankton in extensive pelagic areas might remain restricted by important nutrient fluxes and areas of production might be confined to the shallow parts in the most southern part of the lake as well at the lake's periphery where most seiche energy is dissipated through turbulent mixing (Imberger, 1994; MacIntyre et al., 1999; Fer et al., 2002). However, it is too simplistic to consider solely a strong positive correlation between wind strength and internal nutrient loading at all times. Our results indicated that when sufficient wind energy is applied to the lake it deepens and strengthens stratification structures and, depending on the locality, might also supply oxygen to sub-thermocline waters consequently pushing nutriclines downward, away from the productive zone.

We hypothesise the relation between wind energy and internal loading to be strongest following a relatively calm period during which oxygen penetration has been less, allowing metalimnetic waters to 'recharge' themselves with nutrients 'fallen' from the productive zone or from the anoxic hypolimnetic waters.

This study showed the strong coupling between physical processes and nutrient dynamics in the pelagic waters of Lake Tanganyika. However, to make more progress in understanding the importance of this mechanism in governing the phytoplankton productivity more data is needed.

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Chapter 6

Heterogeneity in physical, chemical and plankton community structures

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Abstract

From 28 August to 6 September 1995 we monitored the lake-wide physical, chemical and biological properties of the pelagic waters in Lake Tanganyika. The aim of this study was to examine the spatial environmental variability and its relation with fluctuations in plankton abundance and community assembly.

Trade winds had triggered an overall downward tilt of the isotherms, accumulation of warm surface waters and intensified stratification towards the north and on the other hand upwelling, increased mixing combined with decreased stratification towards the south. Dissolved oxygen, turbidity, conductivity, phosphorus and chlorophyll-a were higher whereas temperature and pH were lower in southern than in northern waters. We observed a transition zone (6 to 7 ^{o}S) where vertical water column structures changed from northern to southern conditions. This did not include the river Rusizi affected regions north of 4 ^{o}S.

High spatial heterogeneity in nutrient supply and degree of mixing had a strong impact on the plankton community. While the northern environments appeared to be based on reduced internal nutrient loading, lower phytoplankton biomass and smaller sized zooplankton with an important role of Cyclopoids, the mixed environments in the south seemed to be based on increased phosphorus availability and larger sized zooplankton dominated by Calanoid grazers.

We emphasise that wind-driven formation of a gradual change in physical and chemical properties of the productive zones along the north-south axis of Lake Tanganyika is of importance in regionally determining nutrient flows and consequently affecting plankton community structures and composition and therefore food web structure and functioning.

Keywords: Upwelling, Chlorophyll-a, primary production, zooplankton, stratification, Tanganyika

Résumé

Du 28 Août au 6 Septembre 1995, nous avons vérifié sur toute l'étendue du Lac Tanganyika les propriétés physiques, chimiques et biologiques de ses eaux pélagiques. Cette étude a pour but d'examiner les variations spatiales des facteurs environnementaux et leurs relations avec les fluctuations dans l'abondance en plancton et l'assemblage des communautés (biologiques).

Les vents alizés ont d'une part provoqué sur toute la longueur du lac une inclinaison des isothermes, l'accumulation des eaux superficielles chaudes et ont approfondi la stratification vers le Nord ; d'autre part, le jaillissement (upwelling), le brassage croissant combiné à la décroissance de la stratification vers le sud. Les valeurs de l'oxygène dissous, turbidité, conductivité, phosphore et chlorophylle a ont été plus élevées dans les eaux du Sud que celles du Nord là où la température et le pH présentaient des valeurs inférieures. Une zone de transition a été observée (du 6 au 7 ^{o}S) là où les structures verticales de la colonne d'eau changeaient du nord au sud. Ceci n'inclut pas les zones affectées par la rivière Rusizi au Nord du 4 ^{o}S.

Une importante distribution spatiale hétérogène en nutriment ainsi que le degré de brassage ont un grand impact sur la communauté planctonique. Alors que les milieux environnementaux du Nord semblent être fondés sur un apport interne réduit de nutriment, une faible biomasse phytoplanctonique et des zooplanctons de très petites tailles avec prépondérance des Cyclopoïdes, les milieux environnementaux du Sud ont semblé quant à eux, être fondés sur la disponibilité accrue du phosphore et des zooplanctons de grande taille dominés par les brouteurs Calanoïdes.

Nous avons mis l'accent sur le fait que la formation des vents ayant généré un changement graduel des propriétés physiques et chimiques de production tout long de l'axe Nord – Sud du lac Tanganyika revêt une importance quant à la détermination régionale des flux des nutriments et par conséquent affecte les structures et la composition communauté planctonique et ainsi, la structure et le fonctionnement de la chaîne alimentaire.

Mots clés: jaillissement (Upwelling), Chlorophylle a, productivité primaire, zooplancton, stratification, Tanganyika

Introduction

Lake Tanganyika, a large, deep, clear lake occupies one of the East African rift valleys. Its biological and geochemical features are well known and with an estimated volume of 18,940 km^3 it holds ca. 15 % of the world's fresh lake water. Combined with a relatively high fish production of ca. 60 kg $ha^{-1}yr^{-1}$ (Mölsä et al., 1999) the lake represents an extremely valuable resource providing cheap protein, transport, drinking water and irrigation that form the basis of life for millions of riparian people.

Despite its importance it is only since a few decades that knowledge on Tanganyika's system structure and functioning has expanded and been put into context of the lake's productivity (Coulter, 1963; Sarvala et al., 1999). Research has shown that concentrations of nutrients and planktonic organisms in Lake Tanganyika are often highly variable in time and place (Hecky and Kling, 1981; Edmond et al., 1993; Craig, 1997; Kurki et al., 1999). This variability may be due to biological processes like growth and grazing, but it may also be caused by physical processes (Plisnier et al., 1999; Langenberg et al., 2002).

Biochemical and hydrological processes active upon the lake waters have resulted in a predominantly three-layer thermal structure. In similar meromictic lakes, thermal stratification influences mixing and is a controlling parameter for the distribution of dissolved and suspended matter.

Several scientists have implied that periods of enhanced phytoplankton growth in the productive zones of Lake Tanganyika seemed principally determined by the position and strength of vertical stratification structures of the water column (Talling, 1966; Hecky and Kling, 1981; Hecky et al., 1991; Langenberg et al, 2002). Basin-scale forcing by the yearly wind patterns has been of particular interest because of its dominant role in setting thermal structures in motion, which is believed to generate seiche-related mixing and transport of nutrient-rich water from below the wind-mixed layer upward securing biological production (Coulter, 1991; Plisnier et al., 1999).

Nevertheless, in Lake Tanganyika, most assumptions on the functioning of the processes linking water column stability with plankton dynamics are based on observations characterised by poor temporal and spatial coverage (Coulter, 1991). Furthermore, the lake's enormity, the general lack of reliable infrastructure and general safety in the region are probably still the main reasons why up to now most limnological studies have been carried out in close vicinity of a handful of more developed towns. Consequently, basic limnological information for the larger part of the lake is very scanty.

This general lack of information on the structure and functioning of this unique ecosystem underscores the need to investigate the basis for biological production supporting the pelagic fish resources. Motivated by these considerations, the regional Lake Tanganyika Research project (Lindqvist et al., 1999) was formulated and carried out during 1992-1998. The project's limnological component, as part of the Scientific Sampling Programme (SSP), was primarily concerned with describing the main physical processes in Lake Tanganyika and how these affect factors such as chlorophyll-a, nutrient chemistry and fluxes, temperature distribution and light penetration which in turn control primary production in the lake.

Multiple year sampling studies at fixed stations as well as lake-wide cruises have been carried out. Some of the results on the measurements made at the fixed stations have been released (see Lindqvist et al., 1999). In addition, here we present data of the first lake-wide cruise that took place from 28 August to 6 September 1995.

The objective of this study was to examine to what extent wind induced forcing affect the physical structures, chemistry and biological properties of the pelagic ecosystem throughout the lake during the upwelling season. We present new data on the spatial distribution of physical and chemical characteristics, plant nutrients, primary production, chlorophyll-a, light attenuation as well as zooplankton community structures.

Methods

A total of 38 horizontal and 17 vertical samplings were carried out onboard R/V Tanganyika Explorer from 28 August to 6 September 1995 (Figure 1). During a vertical sampling, the following variables were measured: water transparency (Secchi disc), water temperature, underwater PAR (photosynthetically active radiance), primary production, relative fluorescence,

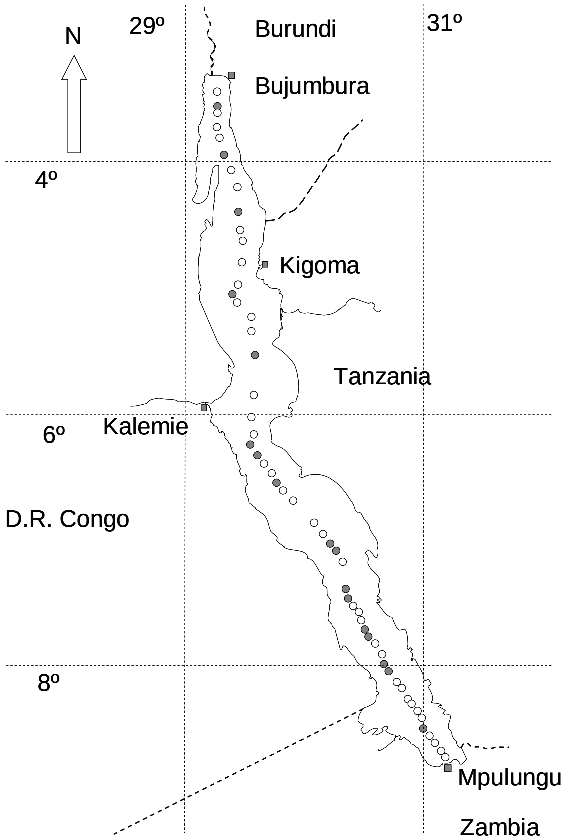


Figure 1. Map of Lake Tanganyika showing vertical sampling sites (full) and horizontal sites (open) during the limnological cruise from 28 August-6 September 1995.

dissolved oxygen, conductivity, pH, turbidity and nutrients (PO_4-P, NH_4-N, NO_3-N, NO_2-N and SiO_2-Si). All measurements were carried out on water samples collected down to 100 m depth at 10 m intervals except for primary production, nutrients and underwater PAR. During a horizontal sampling, normally when R/V Tanganyika Explorer was cruising between two vertical sampling stations, we determined temperature, conductivity, pH, turbidity and relative fluorescence of mixed water samples from the upper 5 m taken at the stern of the vessel.

Temperature (accuracy ± 0.1 °C) and dissolved oxygen (DO in mg l^{-1}) were measured by digital probes (model 5795A, Yellow Springs Instruments, Inc. USA) with additional temperature measurements with thermometers (VEL Co., Belgium) fitted to sampling bottles (Limnos Ltd., Finland). In situ PAR measurements (using Li-Cor quantum sensors LI-193-SA and LI-188 in combination with data logger LI-1100) were made at 10 m intervals up to ca. 50 m of depth and were used to calculate attenuation coefficients by a least square linear regression from the transformed irradiance versus depth values. Conductivity, pH and turbidity were measured with HACH equipment (HACH Co. USA; conductivity/TDS meter model 44600, pH/temperature combination meter model 43800 and a portable nephelometer). Nutrient concentrations were determined onboard in duplicates of mixed water samples of the upper 60 m of water. A HACH DR/2000 spectrophotometer (HACH Co. USA) was used to determine ammonia (Nessler), nitrate (Cd-Cu reduction), nitrite (Azo-dye formation) and soluble reactive phosphorus (molybdate).

In vivo fluorescence of chlorophyll-a was measured using a Turner Designs 10-AU-005 field fluorometer adjusted according to Salonen et al. (1999). Earlier research (Langenberg et al., 2002) showed that in vivo fluorescence correlated well with extracted chlorophyll-a (N = 370, R^2 = 0.9). This regression was used to transform values for fluorescence into chlorophyll-a concentrations.

Phytoplankton primary production was determined by 4h in situ radiocarbon incubations carried out up to a depth of 60 m at 10 m intervals. We used a whole-water modification of the radiocarbon method (Schindler et al., 1972). Further treatment of the radio labelled samples and controls can be found in Sarvala et al. (1999).

At the start and end of each vertical sampling, additional measurements on conductivity, temperature and density were measured with a hydrographic probe (CTD-12 plus, Micro systems Ltd) down to 300 m depth at 10 cm intervals.

Thermal stability indicative for stratification structures within the upper 100 m (N^2 in s^{-2}) was calculated according to the equation: $N^2 = -g.\Delta\rho / \rho_m.\Delta z$, where g is acceleration due to gravity (9.8 m s^{-2}), ρ_m (kg l^{-1}) is the mean density and $\Delta\rho / \Delta z$ is the density gradient over depth interval z (m). Thermocline depth was set at depth at which $\Delta\rho / \Delta z$ was highest. Water density was determined from vertical density profiles made by a hydrographic probe every vertical sampling (CTD-12 plus, Microsystems Ltd.) or calculated from vertical temperature and conductivity profiles according to Chen and Millero (1977).

Zooplankton samples were collected during vertical sampling by taking a vertical haul from 100 m depth with a plankton net of 100 µm mesh, mouth diameter of 25 cm and a hauling speed less than 0.5 m s^{-1}. Three replicate hauls were taken and treated separately. The samples were preserved in 4 % formaldehyde. Subsamples of 1 ml were taken from a well-mixed whole sample with an automatic pipette of 4 mm mouth diameter and allowed to settle in a counting chamber. The procedure was repeated until at least 100 specimens of the micro- and mesozooplankton (nauplii, copepodid and adult stages of Copepoda) were counted. Sampling, sub-sampling and counting were carried out according to Vuorinen (1993) and Kurki (1993). Individuals of the Calanoid species *Tropodiaptomus simplex* were identified to the species level while Cyclopoids were counted as one group and divided into small and large size classes, “small” ones referring to copepodids and adults of *Tropocyclops tenellus*, *Microcyclops cunningtoni* and big ones to *Mesocyclops aequatorialis aequatorialis*. Counting was restricted to these four species because they comprise the majority of the pelagic mesozooplankton in Lake Tanganyika (Coulter, 1991).

Carbon-length regressions of the main crustacean zooplankton species established by Sarvala et al. (1999) were used to derive mean carbon values needed to calculate standing biomasses. For standing biomass calculations the carbon masses taken were as follows: adult Calanoid = 2.95 and 2.01 µg C ind.$^{-1}$ (respectively for female and male), Calanoid copepodid = 0.77 µg C ind.$^{-1}$, small cyclopoid copepodid = 0.10 µg C ind.$^{-1}$, small adult cyclopoid = 0.18 µg C ind.$^{-1}$, big cyclopoid copepodid = 0.53 µg C ind.$^{-1}$, big adult cyclopoid = 2.28 and 1.00 µg C ind.$^{-1}$ (respectively for female and male).

As most nauplii passed through the 100 µm mesh, the results presented deal only with post-naupliar stages. Jellyfish (*Limnocnida tanganyicae*), decapod shrimps and a ciliate genus *Vorticella* were also counted.

The depth profiles of the main variables were used to create contour plots (we used a ‘point-kriging’ gridding method found in Surfer 7, Golden Software Inc.).

Results

Horizontal sampling

Mean surface temperature decreased near linearly with increasing latitude (Figure 2). Temperatures dropped from 26-26.5 °C in the northern regions to 25-25.5 °C in southern regions ($p<0.0001$, n=55). Close to the southern end of the lake temperatures of ca. 24.5 °C were measured.

Conductivity increased towards the south from ca. 668 to 677 µS cm^{-1} ($p<0.0001$, n=54), while pH decreased from ca. 9.05 in the north to values below 8.85 in the south ($p<0.01$, n=54). Turbidity values varied between 0.20 and 0.32 NTU in the northern regions and increased towards the south ($p<0.01$, n=54), reaching values up to ca. 0.50 NTU south of 8 °S.

Chlorophyll-a concentrations ranging from 0.5-1 µg l^{-1} were most common throughout the lake’s surface waters but tended to increase towards the south ($p<0.0001$, n=54). Concentrations increased south of the 7 °S latitude to 1.0-2.2 µg l^{-1} while the sharpest increase was measured in the southernmost regions (up to 3.7 µg l^{-1} close to Mpulungu).

Mean SiO_2 concentrations in the upper 60 m of depth ranged between 0.9-1.5 mg l^{-1}. They tended to be relatively lower at the lake’s ends where concentrations < 1.2 mg l^{-1} were found compared to relatively higher values in the mid regions of the lake (Figure 2).

Concentrations of dissolved inorganic nitrogen (DIN) showed no clear pattern with latitude and concentrations ranged from 0.03-0.09 mg l^{-1}. Soluble reactive phosphorus (SRP) concentrations were low in the north (0.00-0.02 mg l^{-1}) but increased south of the 6 ^{o}S to concentrations ranging from ca. 0.02-0.17 mg l^{-1}.

Largest fluctuations in temperature, conductivity and pH were found between 6 and 7 ^{o}S latitude.

Inter-correlation was high amongst the measured variables (Table 1). In general, during this period, lower temperatures and pH characterised the surface waters in the southern regions while conductivity, chlorophyll-a and turbidity were higher than in the northern regions. Furthermore, Secchi disc depth correlated negatively with chlorophyll-a and positively with concentrations of SiO_2.

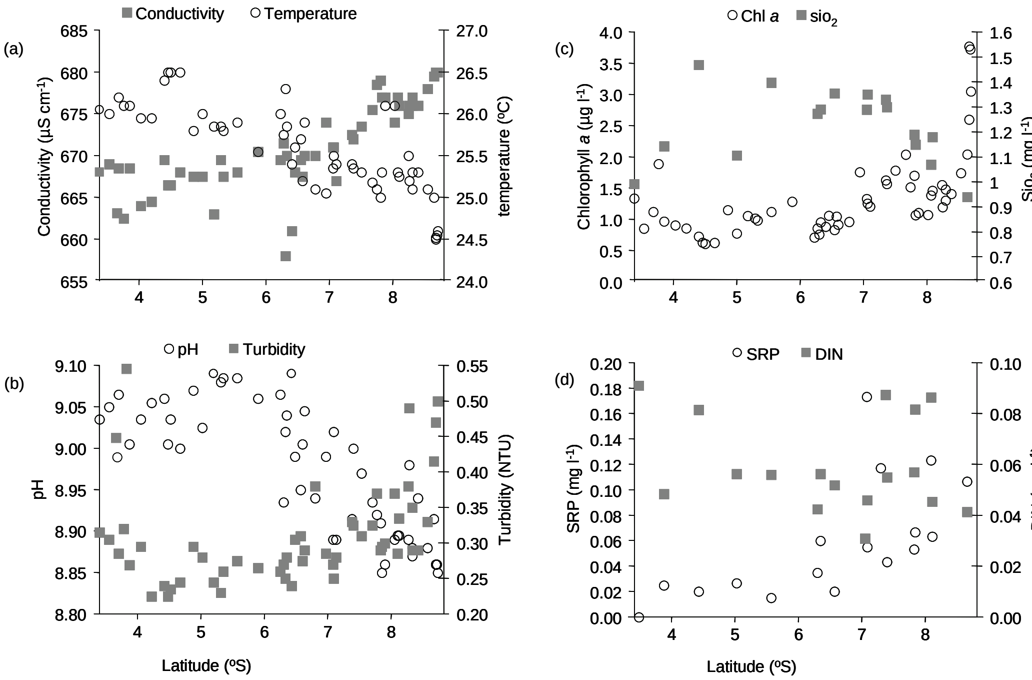


Figure 2. Limnological characteristics of the upper water layers of lake Tanganyika during 28 August-6 September. Plots (a), (b) and (c) represent mean values and concentrations for temperature, conductivity, pH, turbidity, silicate and chlorophyll-a of the upper 5 meter of water column versus latitude. Plot (d) are mean concentrations for soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (sum of NH_4-N, NO_3-N and NO_2-N) of the upper 60 meter column of water.

Table 1. Correlation coefficients r between physico-chemical properties in the surface waters of Lake Tanganyika sampled during the full-lake cruise (28 August-6 September 1995). Abbreviations: latitude (Lat), temperature (Temp), conductivity (K_{25}), turbidity (Turb.), chlorophyll-a (Chl-a), secchi disc (SD) and pH and reactive silicate (SiO_2). Significant correlation indicated by * P<0.01, ** p< 0.0001; n=54 but for SD and SiO_2 n=17.

	Lat	Temp.	K_{25}	pH	Turb.	Chl-*a*	SD
Temp.	-0.8 * *						
K_{25}	0.8 * *	-0.7 * *					
pH	-0.5 *	0.4 *	-0.5 *				
Turb.	0.6 * *	-0.6 * *	0.6 * *	-0.5 *			
Chl-*a*	0.6 * *	-0.8 * *	0.7 * *	-0.5 * *	0.7 * *		
SD	-0.5	0.7 *	-0.6 *	0.5	-0.8	-0.8 *	
SIO_2	-0.1	0.3	-0.4	0.3	-0.6	-0.4	0.8 *

Vertical sampling

Tilted isotherms, inclined to the north, were observed. The thermocline was strongest developed at around 70-90 m of depth north of 6 ^{o}S (Figure 3).

Towards the south isotherms became more widely spaced to the surface indicating more uniform thermal properties of the water column. A north to south upward extension of the isotherms was observed with the largest upward movement south of the 6 ^{o}S. An accumulation of warmer water (26-26.5 ^{o}C) characterised the north while in the south the 25 ^{o}C isotherms nearly surfaced (Figure 3).

Highest dissolved oxygen concentrations were found in the south where also oxygenated waters extended into depths greater than in the north. The water column in the north was characterised by the presence of an oxycline situated around the thermocline (70-90 m) while in the southern regions (south of 8 ^{o}S) concentrations below 6 mg l^{-1} were not observed within the upper 100 m depth. A north to south increase in oxycline depth was observed with the largest increase south of 6 ^{o}S.

Throughout the lake pH values decreased with depth. The largest pH gradients were found in the northern parts (8.7-9.2). In the southern parts of the lake the vertical distribution of pH was the most uniform (8.8-9.0).

In general, conductivity values increased with depth. In northern regions, conductivity varied between 660-688 µS cm^{-1} with a strong gradient around thermocline depth. Southern regions (south of 6^{o} 30'S) were characterised by a more uniform conductivity distribution at generally higher values (676 - 684 µS cm^{-1}) than in the north.

In general turbidity values decreased with depth. Waters were most turbid at the lake ends. North of 4 ^{o}S and south of 7^{o} 30'S turbidity reached values of 0.4-0.7 NTU while the waters in between were characterised by rather low values and a more uniform turbidity distribution at values around 0.1-0.4 NTU.

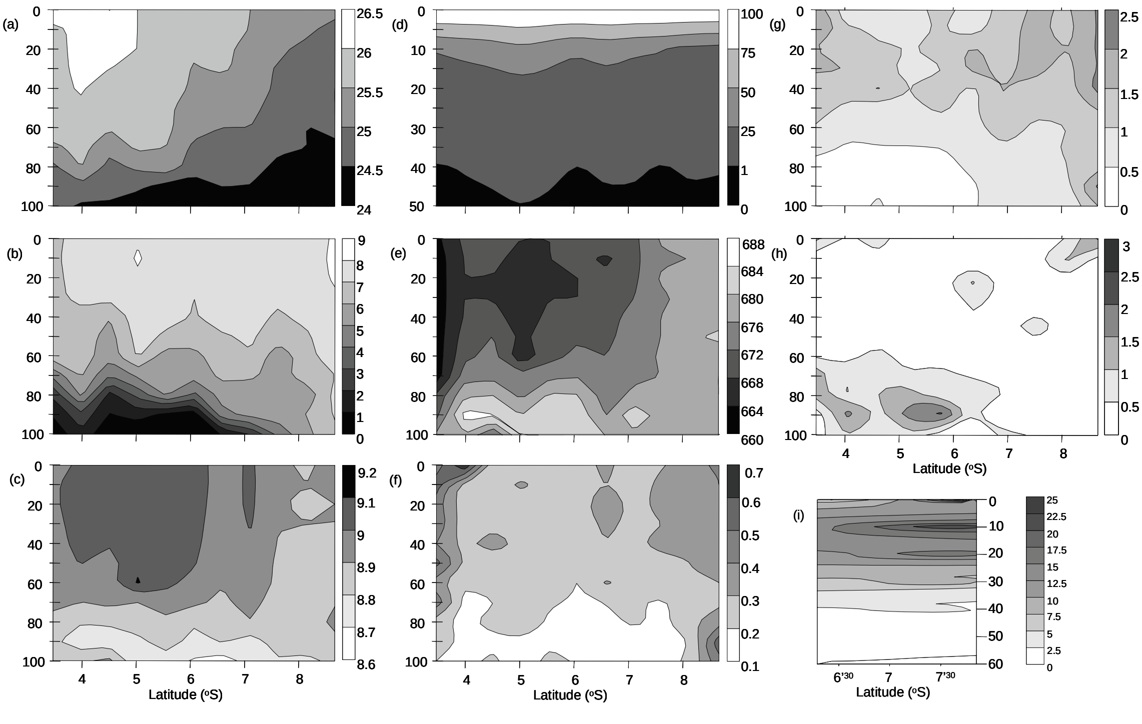


Figure 3. Depth (m) -latitude (^{o}S) plot: (a) Temperature (^{o}C), (b) dissolved oxygen (mg l^{-1}) , (c) pH, (d) PAR (in % of incident PAR), (e) conductivity (µS cm^{-1}), (f) turbidity (NTU), (g) chlorophyll-a (µg l^{-1}) and (h) squared buoyancy frequencies (N^2 values of scale bar x10^{-4} s^{-2}) and (i) carbon fixation (mg C m^{-3}) during the cruise from 28 August-6 September 1995.

In general, concentrations of chlorophyll-a decreased with depth and highest concentrations were observed in the upper 50 m. Lowest concentrations were observed north of the 6 ^{o}S in waters less than 70 m deep. Substantial chlorophyll-a concentrations were still observed deeper into the water column in the south. Highest concentrations were found in the southern

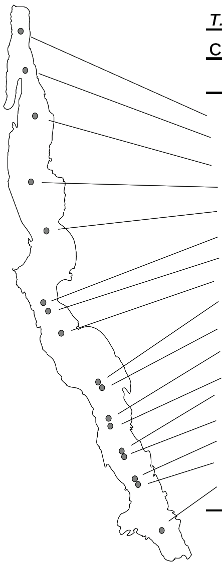
parts of the lake (ca. 3 µg l^{-1}). Phytoplankton biomass significantly increased towards the south ($p<0.01$, $n=17$) and followed the increase in SRP towards the south ($p<0.05$, $n=17$) rather than changes in DIN (see Table 2).
Relatively small spatial differences in underwater light distributions were observed throughout the lake. However, the depth range over which underwater PAR decreases from 50 to 25 % incident PAR seemed smaller at both lake ends. Overall, the photic zone depth, defined as the depth where the underwater light has decreased to 1% of incident surface light (Kirk, 1983), varied in depth between 40 and 50 m.

Primary production
During this study only the southern half of the lake was monitored (5 vertical profiles were taken between 6 and 8 ^{o}S). In all profiles, carbon fixation rates peaked at 10 m depth and were near undetectable at 50 m depth (Figure 3). South of 7 ^{o}S fixation rates at 10 m were higher (18-26 mg C m^{-3}) than north of 7 ^{o}S (11-15 mg C m^{-3}).

Table 2. Correlation coefficients r between chemical and biological properties of Lake Tanganyika sampled during the full-lake cruise (28 August-6 September 1995. Abbreviations: latitude (Lat), Soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN), Molar ratio DIN/SRP (N/P), areal chlorophyll-a upper 100 m (Chl-a_{100}), Biomass Calanoids (Cala), small Cyclopoids (Scyclo), large *Mesocyclops aequatorialis aequatorialis* (Bcyclo). Nutrients are mean values for upper 60 m of depth and organisms represent total biomass. Significant correlation indicated by * P<0.05, ** p< 0.01; n=17.

	Lat	SRP	DIN	N/P	Chl-a_{100}	Cala	Scyclo
SRP	0.7 * *						
DIN	-0.3	-0.2					
N/P	-0.8 * *	-0.8 * *	0.5				
Chl-a_{100}	0.6 * *	0.6 *	-0.2	-0.5			
Cala	0.6 *	0.5	0.1	-0.3	0.5 *		
Scyclo	-0.5	-0.4	0.0	0.4	-0.1	-0.4	
Bcyclo	-0.6 *	-0.4	0.3	0.7 * *	0.0	-0.1	0.8 * *

Table 3. Mean densities in number m^{-3} (N) and biomass in mg C m^{-2} (Bm) of the post-naupliar calanoid *Tropodiaptomus simplex* and Cyclopoida and their share of total biomass of Copepoda in percentages (%). Small Cyclopoid copepods are divided into a 'small' size class consisting of *Tropocyclops tenellus* and *Microcyclops cunningtoni* and a 'large' class of *Mesocyclops aequatorialis aequatorialis*. Indicated for Copepoda are copepodid (C) and adult stages (A). Mean densities (N m^{-3}) for jellyfish *Limnocnida tanganyicae* (Limno), pelagic Caridean shrimps (shrimp) and the ciliate *Vorticella sp*. (Vorti) are given.



Calanoid				Cyclopoid												
T. simplex				Small				*M. aequatorialis aequatorialis*				Total Copepoda				
C	A			C	A			C	A					Limno	Shrimp	Vorti
N	N	Bm	%	N	N	Bm	%	N	N	Bm	%	N	Bm	N	N	N
381	135	65	15	187	311	8	2	2825	1592	374	84	5946	447	42	10	95
120	17	14	14	70	407	9	9	118	347	74	77	1079	97	3	2	5
222	58	33	13	71	420	9	4	599	1039	210	83	2409	252	11	36	3
106	76	29	10	272	474	12	4	911	1165	256	86	3004	297	28	0	4
289	199	77	19	66	580	12	3	142	1491	306	77	2768	395	14	19	2
117	122	38	31	97	124	3	3	93	425	83	67	977	124	15	4	2
28	38	12	19	32	211	5	7	113	224	47	74	646	64	61	0	4
255	676	199	74	23	134	3	1	57	328	67	25	1473	269	15	5	1
249	165	65	23	282	576	14	5	708	945	206	72	2925	285	65	1	7
193	376	111	64	51	99	2	1	272	228	59	34	1219	173	13	3	4
176	437	129	59	15	126	3	1	110	427	86	40	1291	218	19	8	3
148	321	96	66	21	98	2	1	30	232	48	33	849	146	13	2	4
433	408	139	63	11	170	3	2	47	391	78	35	1460	221	7	1	1
123	147	44	44	27	193	4	4	43	284	52	52	818	101	6	1	1
182	454	131	75	30	79	2	1	49	205	41	23	999	174	6	10	0
563	537	189	63	22	177	4	1	135	535	110	36	1968	303	13	19	2
188	386	112	36	32	427	9	3	6	1201	190	61	2239	310	17	7	3

Zooplankton

Mean total post-naupliar copepod biomass in the upper 100 m was 228 ± 107 mg C m^{-2} (n=17) and no consistent trend in the spatial distribution along the north-south axis of the lake was observed (Table 3).

The highest biomass was observed at the most northern station (447 mg C m^{-2}). The percentage biomass of the Calanoid *T. simplex* to total copepod biomass increased from 10-19 % north of 6 ^{o}S to 19-75 % south of 6 ^{o}S ($p<0.01$, $R^2= 0.4$, n=17). The percentage biomass of *M. aequatorialis aequatorialis* decreased from 77-86 % north of 6 ^{o}S to 25-74 % south of 6 ^{o}S ($p<0.01$, $R^2= 0.4$, n=17).

In general, northern regions were, in terms of post-naupliar biomass, dominated by Cyclopoids while southern regions were dominated by Calanoids. Throughout the lake on average 5% (± 2%) of the Cyclopoid biomass consisted of small Cyclopoids.

In the north the densities of Calanoid copepods were dominated by copepodid stages while in the south adults dominated ($p<0.001$, $R^2=0.6$, n=17). The share of adult to copepodid stages of *M. aequatorialis aequatorialis* was generally higher than with *T. simplex* and tended to increase as well towards the south ($p<0.05$, $R^2=0.3$, n=17).

The Calanoid standing biomass followed phytoplankton biomass and was significantly correlated with it ($p<0.05$, n=17, Table 2). Biomass of the larger *M. aequatorialis aequatorialis* also significantly correlated with small Cyclopoids ($p<0.01$, n=17).

Besides the relatively large variation between the stations sampled no trends in the spatial distribution of *Limnocnida tanganyicae,* Caridean shrimps and *Vorticella sp*. were observed were observed. Highest densities of L. tanganyicae (> 60 ind. m^{-3}) were found around 6 and 7 ^{o}S. A very high density of *Vorticella sp*. was observed at the northernmost station (95 ind. m^{-3} compared to a mean of ca. 3 ind. m^{-3} for all other sampled stations).

Discussion and conclusion

The vertical physical and chemical conditions of Lake Tanganyika's waters showed clear spatial patterns along the north-south axis of the lake as a result of cooler windier conditions during this period. During July and August the south-east trade winds trigger an overall downward northward tilt of the isotherms northwards causing accumulation of surface waters and intensifying density structures at windward side of the lake and on the other hand upwelling combined with decreased water column stability at downward side of the lake (Kotilainen et al., 1995; Langenberg et al., 2002). Climatic forcing at the southern end of the lake has been illustrated by seasonal changes in Wedderburn numbers and thermal structures (Langenberg, 1996). During and just after the trade wind periods with low Wedderburn numbers, upwelling and related mixing events across the thermocline take place in the south of the lake (Langenberg et al., 2002).

For the duration of this cruise the values of dissolved oxygen, turbidity, conductivity, phosphorus and chlorophyll-a were in general higher whereas temperature, water column stability and pH were lower in southern than in northern regions. A general high correlation between the measured variables indicated their strong interdependence and coupling with the hydrodynamic forcing of the south-eastern trade winds during this period. The hydrodynamic forcing and related physical structures and chemistry of the upper 100 m gradually changed along the south-north axis of the lake. However, we observed that during this period the area of 6 to 7 ^{o}S appeared to be a transition zone where most vertical watercolumn structures and variables change from northern to southern conditions. The most northern areas (north of 4 ^{o}S) showed lower values for conductivity and pH while values for chlorophyll-a and turbidity were higher probably due to the outflow of river Rusizi (Langenberg et al., 2003a) On the basis of its geomorphology the lake can be divided into three sub-basins (Capart, 1949) and since the northern sub-basin is much shallower and narrower than the two other sub-basins, the outflow of the river Rusizi may be large enough to affect notably the physical structures and chemistry in the area north of 4 ^{o}S.

The meromictic condition of Lake Tanganyika is an important factor when considering the movement of water masses and solutes within the lake (Beauchamp, 1940; Kufferath, 1952; Coulter, 1988; Hecky and Bugenyi, 1992; Langenberg, 1996). The clinal boundaries in Lake Tanganyika separate the deep reservoir of nutrients from the surface waters, forming persistent barriers to vertical mixing of the water column.

Seasonal differences between stratification strength and wind regime are of major importance in determining the extent of upwelling as well as seiching activity at the boundaries which in turn affects internal loading of nutrients (Langenberg et al., 2003b). Seasonal weakening of the stratification caused a temporary increase in cross-boundary mixing of nutrients thus promoting phytoplankton growth in Lake Tanganyika (Dubois, 1958; Ferro, 1975; Hecky et al., 1991; Coulter, 1963; Crul, 1993; Langenberg et al., 2002 and 2003b). This mechanism has also been described in other lakes in the region such as Lake Victoria (Talling, 1966) and Lake Malawi (Bootsma, 1993; Patterson and Kachinjika, 1993 and 95).

Our observations show that the strength of these barriers varied along the north-south axis of the lake. A weakening of the stratification towards the south (starting south of 6 ^{o}S) coincided with increasing oxycline depths and an increase of dissolved inorganic phosphorus concentrations.

The absence of a gradual increase in dissolved nitrogen along the north to south axis may be due to the position of the oxycline. The depth of oxycline has important implications for the metabolism of nitrogen in the lake. Biological (e.g., denitrification) and chemical processes (reduction) happen at low oxygen concentrations and therefore, they are expected to take place at increasing depths towards the south. Any upwelling of nutrient-rich water may already have chemically been altered to a degree that a pronounced increase of dissolved inorganic nitrogen is not detectable. These processes may lead to nitrogen deficiency when internal loading of nitrogen is considered alone and consequently, one may well assume that the availability of nitrogen is the limiting element determining the overall level of phytoplankton productivity in Lake Tanganyika (see Hecky et al., 1991). Nevertheless, the positive correlation between chlorophyll-a and phosphorus indicate that the dissolved nitrogen concentrations varying between 0.03-0.09 mg l^{-1} seemed sufficient to sustain a higher phytoplankton biomass in the south.

Primary production increased towards the south most probably due to an increased internal nutrient input through upwelling. These relatively low production rates (< 30 mg C m^{-3}) are characteristic for most of the pelagic regions of Lake Tanganyika and are well within the range of production rates known from comparable oligotrophic environments (Sarvala et al., 1999). The most northern areas form an exception. Sarvala et al. (1999) and Langenberg et al. (2003b) showed that in the north much higher primary production rates were found probably as a consequence of increased input from the Rusizi river or from seiche triggered mixing or resuspension. Here, these nutrient pathways may be more important than elsewhere in the lake since the north is the shallowest basin of Lake Tanganyika (Langenberg et al., 2003b). Increasing chlorophyll-a concentrations in the upper water layers north of 4 ^{o}S may indicate increased nutrient input.

The densities and biomasses of the different zooplankton taxa are approximations and do not permit comprehensive comparisons with earlier zooplankton studies in Lake Tanganyika because of the different sampling methods used (Kurki et al., 1999). The efficiency of our sampling method was determined by comparing net hauls with bottle samples (Kurki et al., 1999; Sarvala et al., 1999). Although the efficiency of the net haul compared to integrated bottle samples was ca. 30% lower, the differences between the efficiencies in collecting Calanoids and Cyclopoids of both sampling methods were generally not higher than 10% (Kurki et al., 1999; Sarvala et al., 1999).

Also, in Lake Tanganyika there may as well be a size factor of ca. 2.5 between Mesocyclops and Tropocyclops (Kurki et al., 1999). Nevertheless, throughout the lake smaller Cyclopoid biomass consisted on average of 5% (± 2) of smaller species and therefore discrepancies with the actual zooplankton biomass may also be rather uniform.

We have furthermore observed that the oxygenated layer towards the south reached beyond the sampling depth. Since zooplankton is present throughout the whole oxygenated layer (Kurki et al., 1999), total standing zooplankton biomass is likely increasingly underestimated towards the south.

Considering the above, total zooplankton numbers and biomass most probably increase towards the south during this upwelling period. Nevertheless, we expect our assessment that the zooplankton community in the north was dominated by Cyclopoids while the south seemed dominated by Calanoids to hold. Earlier research also confirmed that the share of Calanoids is larger in the south than in the north (Kurki et al.,1999).

The spatial distributions of the herbivore *T. simplex* responds to increases in phytoplankton biomass which itself was a response to increased wind induced lake mixing and available supply of phosphorus. Hecky and Kling (1981, 1987) showed that Lake Tanganyika's phytoplankton was dominated by diatoms during periods of increased turbulence and deep mixing while small chlorophytes en cyanophytes were most prominent during periods of well-developed stratification. A higher supply of diatoms during upwelling in the south possibly favour the growth of large herbivores as Calanoids as well as larger carnivores (*M. aequatorialis aequatorialis*) and sustain a higher total zooplankton biomass compared to northern waters where rather opposite physical and chemical conditions occur (Langenberg et al., 2002, 2003a and 2003b). Therefore, the mechanism that drives the spatial differences is also governed by nutrient availability to the phytoplankton, subsequently utilised by the herbivorous zooplankton, and capitalised on by the predaceous zooplankton.

Consequently, as long as the hydrodynamic forcing during the upwelling period in Lake Tanganyika upholds the striking differences between physical, chemical and biological properties of the northern and southern regions two rather different food webs may come in place. Namely, a northern food web that appeared to be based on reduced internal nutrient loading due to increased stratification, smaller sized zooplankton with an important role of Cyclopoids and a food web in mixed environments in the south that seemed to be based on increased nutrient availability, larger sized zooplankton including the dominance of Calanoid grazers.

The reason for the relative increase in adults of *M. aequatorialis aequatorialis* besides the increasing dominant role of the Calanoid *T. simplex* in the zooplankton assemblages towards the south is unclear. Upwelling promoted phytoplankton production might explain part of the success of the Calanoids or *T. simplex* in the south. Also, Vuorinen et al. (1999) showed the larger sized zooplankton in the south to exhibit much clearer daily vertical migration patterns and also covering larger depth spans than the assemblages in the north, a reaction assumedly triggered by increased predation pressure in the turbulent south.

Although an increased predation pressure in the south might be a steering factor affecting zooplankton assemblages. It might well be that the larger zooplankton species prevail better in turbulent water than smaller species, irrespective of predation pressure.

Lake Tanganyika’s primary producers depend on internal (upwelling, entrainment) and external (atmosphere, rivers, terrestrial run-off) nutrient inputs (Langenberg et al., 2003a) as well as nutrient regeneration via the microzooplankton. During upwelling periods we may assume the northern and southern food chains to depend differently on the nutrient regeneration by the microzooplankton. The degree of dependency will have its effect on the efficiency of carbon transfer through the system.

A higher dependency on the heterotrophic microbial loop leads to lower efficiency due to the relatively high respiration rates involved (Sarvala et al., 1999). In this view comparisons may be made with the apparent changes in production structures present in similar oligotrophic stratified waters and turbulent upwelling areas from oceanic regions as well (Cushing, 1989). If applicable for Lake Tanganyika, we expect this type of food chain to be on overall longer, comprising more trophic levels as compared to the shorter conventional CO_2-phytoplankton-zooplankton-fish food chain that is more characteristic for upwelling areas in oligotrophic regions. A further decrease of efficiency in longer food chains is expected since it implicitly means more nutrient and energy loss transfers between trophic levels before biomass and energy is sufficiently concentrated, so that it can be capitalised upon by the larger fish at the top of the food chain.

We have found evidence that wind-driven formation of a gradual change in physical, chemical and biological properties of the pelagic zone along the north-south axis of Lake Tanganyika regionally determine nutrient flows that may consequently affect the food web structure and functioning. The construction of dynamic food web structures in Lake Tanganyika under different degrees of hydrodynamic forcing is essential for understanding short and long-term changes in the trophic status of Lake Tanganyika.

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Chapter 7

External nutrient sources for Lake Tanganyika

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Abstract

This study assessed the external nutrient sources for Lake Tanganyika from August 1994 to August 1995. The physico-chemical characteristics of the three largest inflowing rivers (Rusizi, Malagarasi, and Lufubu) and the wet atmospheric deposition in Bujumbura (Burundi), Kigoma (Tanzania), and Mpulungu (Zambia) were analyzed. The magnitude of external loading of P and N were evaluated to determine their potential for supporting biological activity. Seasonal changes in the physico-chemical composition of riverine input were detected and were linked to the altitude and morphology of the river system. A flushing effect was noted. Higher discharge rates corresponded with increased concentrations of most constituents. Rusizi provided the most and Lufubu the least of total riverine nutrient input. Rusizi's load equalled or almost doubled, depending on the nutrient, the combined loads of the other rivers. Seasonal changes in the atmospheric deposition chemistry were detected and were linked to biomass burning and atmospheric transport processes. Highest atmospheric deposition rates were encountered in more populated and industrialized Bujumbura. Long- and short-term atmospheric washouts were observed. Concentrations of rainwater components were on most occasions higher at the beginning than at the end of the rainy season. A similar trend was observed during separate rain events. Wet atmospheric deposition provided approximately 83% of dissolved inorganic nitrogen (DIN), 37% of total phosphorus (TP), 63% of total dissolved phosphorus (TDP), 65% of soluble reactive phosphorus (SRP), but only 1% of soluble reactive silicate (SRSi) of external source loading. The remaining load was derived from riverine sources. DIN, TP, TDP, SRP, and SRSi yearly net fluxes through wet deposition and riverine input were calculated as 58, 5.4, 2.5, 2, and 99 mmol per m^2 lake surface, respectively. Annual external loading of N and P potentially induced a new production of 45 to 60 g C $m^{-2}yr^{-1}$ (ca. 7 to 14 % of annual primary production).
External loading forms the main pathway for nutrients to enter the productive layers of Lake Tanganyika during stratified and oligotrophic periods (February to May).

Keywords: Nutrient fluxes, deposition chemistry, riverine input, nutrient budget, biological production, anthropogenic activities, Lake Tanganyika.

Résumé

D'Août 1994 à Août 1995, cette étude eut pour but d'évaluer les sources exogènes des nutriments du lac Tanganyika. Les caractéristiques physico-chimiques ont été étudiées pour trois des plus grands affluents de ce lac (Rusizi, Malagarasi et Lufubu) ainsi que les dépôts atmosphériques de Bujumbura (Burundi), Kigoma (Tanzanie) et Mpulungu (Zambie). Nous avons évalué le degré de l'apport extérieur en phosphore (P) et Azote (N) afin de déterminer leur potentialité à supporter l'activité biologique. Les changements saisonniers dans la composition physico-chimique des apports des rivières ont été relevés et étudiés en relation avec l'altitude et la morphologie du système de rivière. Un effet saillant a été constaté. Les taux les plus élevés de décharges correspondent à l'augmentation de la concentration de la plupart des constituants. Dans l'apport total des rivières en nutriments, la Rusizi fournit le plus grand apport et la Lufubu le moindre.
Cette contribution de la Rusizi est égale ou presque le double des effets combinés des autres rivières et, cela dépend du type de nutriment. Les changements saisonniers dans la composition chimique des chutes atmosphériques ont été déterminés et étudiés en relation avec la quantité de biomasse consumée ainsi que les mécanismes de transport atmosphérique. Les taux de dépôt atmosphérique ont été rencontrés dans la plus populeuse ville industrielle de Bujumbura. Les lavages atmosphériques à long et à court terme ont été analysés. Les concentrations des différents composants d'eaux de pluies ont été très élevées dans la plupart des cas plutôt au début qu'à la fin de la saison. Une tendance similaire a été observée lors des événements pluvieux espacés. Les chutes atmosphériques humides ont fourni approximativement 83 % d'azote inorganique dissous (NID), 37 % de phosphore total (PT) , 63 % de phosphore total dissous (PTD), 65 % de phosphore réactif soluble (PRS) et seulement 1 % de silice réactive soluble (SiRS) en provenance des sources externes; le reste de même type d'apports provenant des rivières. Les flux annuels de NID, PT, PTD, PRT et SiRS des dépôts humides et d'apports des rivières mesurés, ont été respectivement de 58, 5.4, 2.5, 2 et 99 mmol par m^2 de surface du lac. La décharge annuelle de N et P d'origine

extérieure induit potentiellement la productivité de 45-60 g de C $m^{-2}an^{-1}$ (ca. 7-14 % de la production annuelle primaire).
Les décharges extérieures constituent la principale source d'approvisionnement des nutriments entrant dans les couches productives du lac Tanganyika au cours des périodes de stratification et d'oligotrophisme (Février - Mai).

Mots clés: Flux de nutriment, atmosphère, dépôt chimique, apport des rivières, bilan des nutriments, production biologique, activités anthropogéniques.

Introduction

Primary production and mean standing crop of phytoplankton are largely determined by the extent of nutrient loading. Constructing valid nutrient loading models requires the identification of all major in- and outflowing fluxes of nutrients. Recently, the importance of the atmospheric and riverine input as a nutrient source to tropical lakes has received growing attention (Lewis, 1981; Andreae et al., 1990; Bootsma and Hecky, 1993; Clark et al., 1998). Atmospheric and riverine input can account for a significant proportion of the nutrient flux into productive surface waters (Galbally and Gillett, 1988; Pedrozo et al., 1993; Kubilay and Saydam, 1995; Seitzinger and Sanders, 1999), directly enhancing biological activity and influencing algal and fish production.
The water balance of meromictic Lake Tanganyika is mainly governed by rainfall and evaporation, while river in- and outflow make minor contributions (Coulter and Spigel, 1991). Considering the large volume of the lake (ca. 19,000 km^3), this ultimately leads to hydraulic retention times in excess of thousands of years (Spigel and Coulter, 1996). Because of the long flushing time and the abundance of nutrients in the anoxic hypolimnion, researchers have postulated that the replenishment of nutrients from deeper water layers through vertical mixing (internal nutrient loading) might be more important than external loading through inflowing waters and atmospheric deposition on an annual time scale. However, current knowledge on the nutrient content of the different hydrological inputs for Lake Tanganyika is very limited. Besides some temporal chemical and physical determinations on effluents at the northern end of the lake (Hecky et al., 1991, Vandelannoote et al., 1996 and 1999; Kimbadi et al., 1999; Brion et al., 1999), little is known about external nutrient loading. Furthermore, data on precipitation chemistry in whole Tanganyika region are virtually non-existent. This paper addresses the annual dynamics of the chemical and physical characteristics of wet atmospheric deposition and the three largest incoming river systems. The aim is (a) to evaluate the potential magnitude of nutrient input from wet deposition and riverine input, (b) to assess their relative importance to the overall nutrient budget of Lake Tanganyika, and (c) to assess the possible role of external inputs in sustaining annual primary production. The new data presented may permit future comparisons that are needed to interpret the apparent changes in the chemical composition of precipitation and riverwater in similar regions during the last few decades, probably due to intensified anthropogenic activities as well as climatic changes (Bootsma et al., 1996).

Material and methods

Rain and river water were sampled from August 1994 to August 1995. Sampling of the outlets of the rivers Rusizi, Malagarasi, and Lufubu (Fig. 1) were carried out every 3 months. Rivers were sampled across the outlet at three positions (left, middle, and right). Temperature, dissolved oxygen, conductivity, and pH were measured in the field while samples were taken to laboratory for nutrient analyses. Volume-weighted nutrient concentrations, based on mean nutrient concentrations at the time of sampling and mean river discharge rates, for 1.5 months before and after sampling, were used to calculate total masses of incoming constituents. No physicochemical analyses were carried out at Lake Tanganyika's only outflowing river Lukuga. The chemical composition of outflowing water was assumed to be similar to the regularly sampled epilimnetic waters 35 km eastward of the outflow (Langenberg, 1996). A total of 34 rain events were sampled in Bujumbura, three rain events at Kigoma and five rain events at Mpulungu. Analyses from Mpulungu 1994 and 1995 were later combined with the results from four rain events of 1997 to calculate a mean for this location.

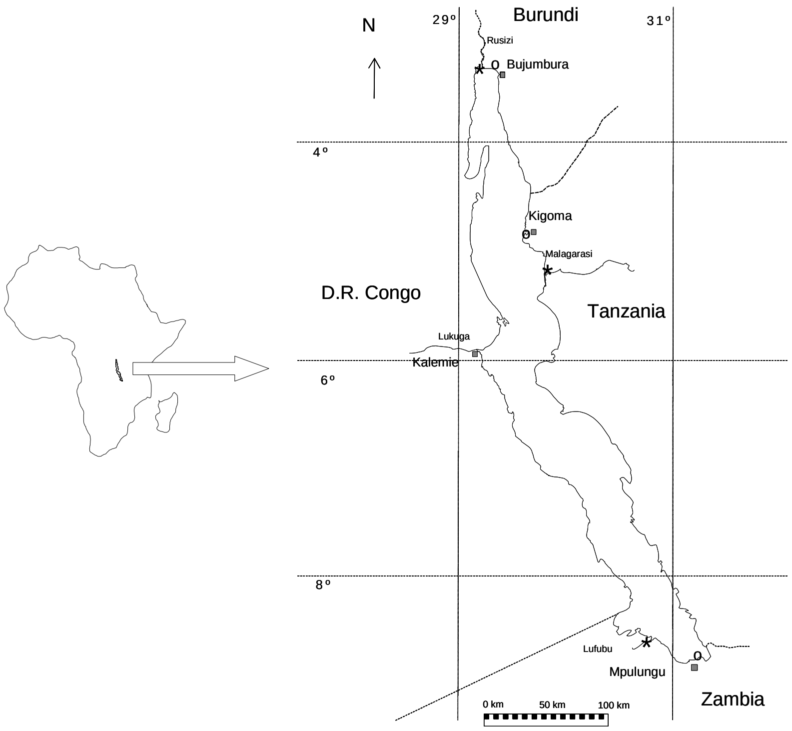


Figure 1. Lake Tanganyika, showing borders between riparian countries, sampling stations at inflowing rivers Rusizi, Malagarasi, and Lufubu (asterisks) and rainwater sampling sites (open circle). The main outlet, river Lukuga, is shown.

At Bujumbura, station rainwater samples were collected with four longitudinally intersected polyethylene pipes slightly sloped toward a central positioned collecting bucket. Prior to each precipitation event, the whole installation was cleaned, acid washed (HCl 4%) and rinsed with de-ionized water ($K_{25} < 3$ µS cm^{-1}). At the start of a rain event and before collection, rainwater was flushed through the collector for 1 to 2 minutes. Rainwater was brought back to the laboratory for immediate determinations. Time series of measurements were carried out during one rain event (pH, conductivity, turbidity, and dissolved inorganic nitrogen). At Kigoma and Mpulungu, rain was collected using 1-liter PE bottles mounted inside a stainless steel housing and funnel. During rainwater collecting, the installation was closely monitored. Leaves and insects settling on the collector were removed during collection.

Chemical Determinations

Dissolved oxygen (accuracy ± 0.01 mg/L) and temperature (accuracy 0.1 ^{o}C) were determined using YSI meters (model 5739 and 5795A, Yellow Springs Instruments, Inc. USA). Conductivity K_{25}, accuracy 1 µS cm^{-1}), pH (accuracy 0.01), and turbidity (accuracy 0.01 NTU) were measured with HACH equipment (HACH Co. USA; conductivity/ TDS meter model 44600, pH/temperature combination meter model 43800, and nephelometer model 2100A). Chloride (silver nitrate; detection limit 141 µM, accuracy 28 µM), alkalinity (H_2SO4 and bromocresol green; detection limit 0.2 meq l^{-1}, accuracy 0.1 meq l^{-1}), sulphates (HACH method sulfaver4; detection limit and accuracy 10 µM), calcium by total hardness (E.D.T.A.; detection limit 0.1 mM, accuracy 25 µM) were determined by titrimetry. A HACH DR/2000 spectrophotometer was used to determine ammonia (Nessler, detection limit 1.4 µM, Accuracy 0.7 µM), nitrate (Cd-Cu reduction, detection limit and accuracy 0.7 µM), nitrite (Azo-dye formation; detection limit and accuracy 0.14 µM), soluble reactive silicate (molybdate complex; detection limit and accuracy 0.4 µM), total phosphorus (pressure boiling, acid persulphate), total dissolved phosphorus (Whatman GF/F and acid persulphate), and soluble reactive phosphorus (molybdate method). Detection limit and accuracy for all phosphorus determinations were respectively 0.6 µM and 0.3 µM. Potassium and sodium were determined by flame emission spectroscopy (detection limit and accuracy respectively 26 and

43 µM). Only at the collection station in Bujumbura were sufficient data collected to allow an assessment of a full set of parameters, DIN (NH_4-N, NO_3-N and NO_2-N), phosphorus, conductivity, pH, and turbidity, throughout the season and separate rain events. Volume-weighted concentrations and total mass of main constituents in rainwater were based on gauge readings and chemical analyses of the collected rain. Total wet deposited nutrient masses on the lake are calculated by assuming a lake-wide mean annual precipitation amount of ca. 1200 mm yr^{-1} (derived from averaged long-term precipitation data collected at 15 meteorological stations surrounding the lake, partly summarized by Plisnier et al., 1996) and by assuming that the mean concentrations from Kigoma and Mpulungu stations are representative for 80% of the lake's surface while concentrations from Bujumbura account for the remaining 20%.

Results

The rivers Rusizi and Malagarasi had similar mean annual discharges (ca. 165 m^3s^{-1}). Malagarasi had relatively low flow during September to November, but often > 300 m^3s^{-1} during April and May. For the Rusizi the mean monthly discharge remained relatively high, ranging between ca. 100 and 250 m^3s^{-1} (Fig. 2). The Lufubu's mean monthly discharge was lower, and did not show seasonal trends similar to those seen at the other inflowing rivers. A peak was noted during April whereas for the rest of the year its discharge remained rather constant at low values. The Lukuga's mean annual discharge (ca. 75 m^3s^{-1} outflow) was less than 20% of the combined flows of the three incoming rivers. Turbidity and pH were generally higher for the Rusizi than for both of the other rivers. A similar trend was observed for conductivity (Table 1). During the rainy season, concentrations for dissolved inorganic nitrogen (DIN) and total phosphorus (TP) were higher in the Rusizi than in the Malagarasi and the Lufubu (Fig. 3).

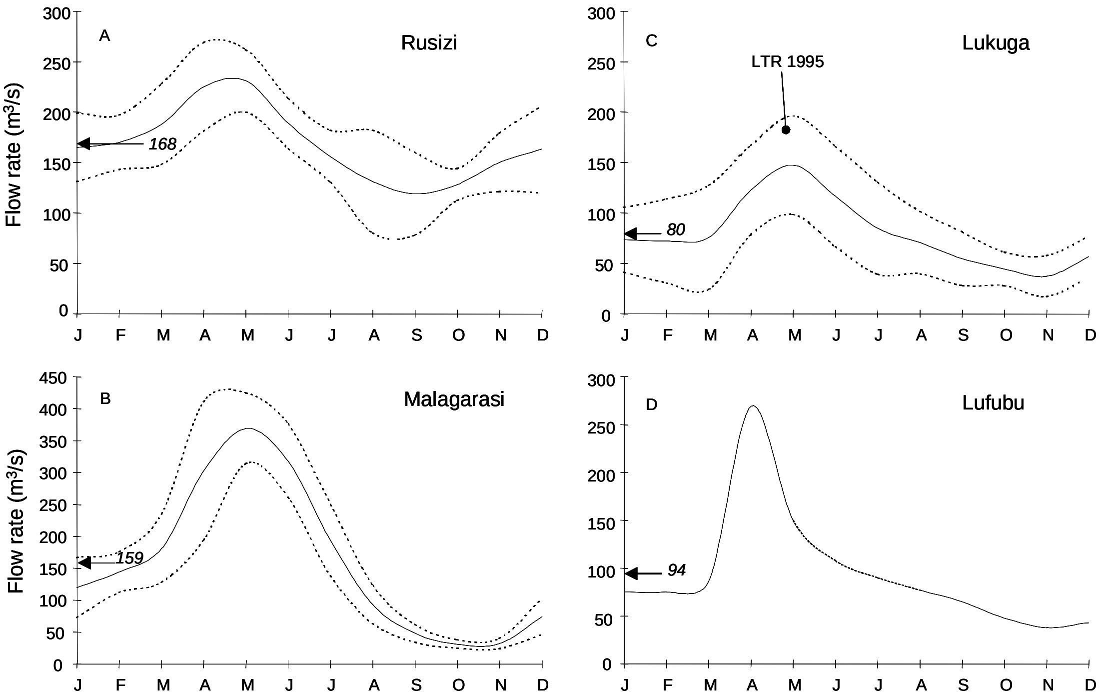


Figure 2. Mean monthly fluctuations and standard deviations (dotted lines) of inflow (m3/s) of A: River Rusizi (Burundi), B: Malagarasi (Tanzania), D: Lufubu (Zambia), and outflow of C: Lukuga (D.R. Congo). Graph A redrawn from Vandelannoote et al. (1999) (unpublished IGEBU data 1982 to 1989), Graph B redrawn from Huttula (1997) (data from NORCONSULT 1975 to 1980), Graph C drawn from Lempicka (1959) (data 1952 to 1959). Indicated is LTR-FAO outflow measurement in 1995. Graph D redrawn from Sichingabula (1999). Between May and September in graph D no data were available. Arrows are fixed at yearly averages of data presented.

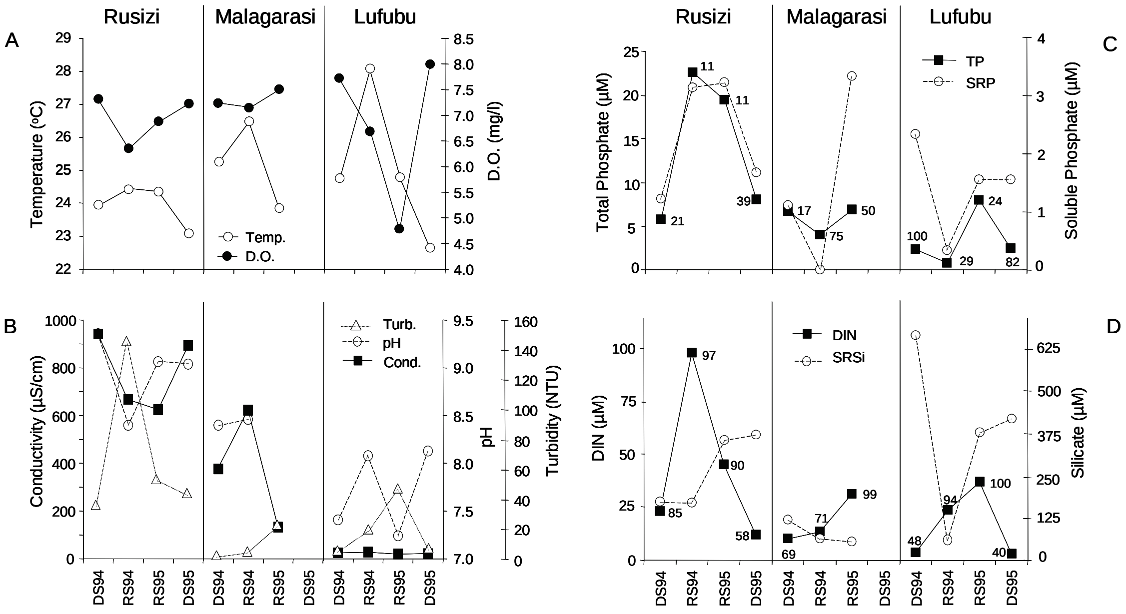


Figure 3. Seasonal variability of Rusizi, Malagarasi, and Lufubu physico-chemistry. Graph C represents concentrations of total and soluble reactive phosphate (TP and SRP) whereas the values in graph C indicate % dissolved fraction of the TP. Graph D represents concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive silicate (SRSi). Values in graph D indicate % of oxidized fraction of DIN. Seasons are indicated by dry season (DS) and RS (rainy season).

For other constituents (Mg, Cl, Na, K, SO4), a similar trend between the rivers was observed. During times of high river discharge, an increase in values for DIN, most phosphorus fractions, temperature and turbidity was found, indicating the dominance of a flushing effect over dilution. In the Rusizi, flushing was more prominent during the first half of the rainy season while at the Malagarasi and Lufubu concentrations were generally higher during the second half of the rainy season (Fig. 3) although the low frequency of sampling makes may have obscured the precise timing of maxima or minima in nutrient concentrations. The Lake Tanganyika region has a double peaked wet season. Typically, there is no rain from June to August (great dry season), largest amounts fall during the months of December (small rainy season) and April (great rainy season), with lower amounts of rainfall in between (small dry season). Total rainfall in Bujumbura during the period of study was 536 mm which is relatively low compared to normal years (Fig. 4A) where amounts of 800 to 1,100 mm are more common (Bidou et al., 1991).

During this study, rainfall peaked in November and February, which is 1 to 2 months earlier than typical. At Bujumbura, areal wet deposition rates of DIN and TP generally were largely determined by the amount of precipitation, although high concentrations of DIN in rainwater resulted in relatively high deposition rates of DIN at the beginning of the rainy season. (Fig. 4B). No apparent seasonal changes in concentrations of TP were found. In general mean monthly concentrations ranged from ca. 2 to 5 µM, although during December an elevated concentration of ca. 12 µM was found. Soluble reactive phosphorus concentrations (SRP) contributed 0 to 50% of TP whereas TDP contributed ca. 50 to 96% of TP (Table 1). Higher values for pH and conductivity were more common in the beginning of the rainy season and tended to decrease up to May, the end of the rainy season in 1994 and 1995 (Fig. 4C). Rainwater turbidity decreased over the course of the study (Fig. 4D).

Precipitation chemistry at stations Kigoma and Mpulungu differed from that of Bujumbura. In general concentrations or values for DIN, TDP, TP, SRSi, alkalinity, turbidity, and conductivity were lower and pH was higher than at Bujumbura (Table 1).

Table 1. Chemical composition of rivers Rusizi (Burundi), Malagarasi (Tanzania), Lufubu (Zambia), and rain collected at Bujumbura, Kigoma, and Mpulungu. Data from all rain events sampled are presented as percentile values (if n > 16), volume weighted means and ranges with sample size in parenthesis; 1. Data from Vandelannoote et al. (1999); 2. Beauchamp (1939). Used abbreviations: Secchi disk (SD), temperature (T), dissolved oxygen (D.O.), conductivity (K_{25}). turbidity (Turb.), total phosphorus (TP), total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN as ammonium, nitrate and nitrite), alkalinity (Alkal.), chloride (Cl), soluble reactive silicate (SRSi).

	Rivers								Wet deposition								
	Rusizi				Malagarasi		Lufubu		Bujumbura					Kigoma [a]		Mpulungu [b]	
Variables	mean	range	1	2	mean	range	mean	range	25%	50%	75%	mean	range	mean	range	mean	range
SD (m)	0.2	0.1-0.4	-	-	1.1	0.4-2.1	1.0	0.6-1.6				-	-	-	-	-	-
T (ºC)	23.9	23.0-24.4	25	23	25.2	23.8-26.7	25.1	22.6-28.1	19.3	20.5	21.1	20.5 (26)	18.5-23.1	20.7	20.1-21.6	21.6	19.5-23.4
D.O. (mg/l)	6.9	6.3-7.4	7	-	7.3	7.1-7.6	6.5	4.8-8.0				-	-	-	-	-	-
K_{25} (µS/cm)	782	622-945	789	1010	377	125-626	23	19-27	14	18	33	25 (28)	6-83	19	8-28	10	5-46
pH	9.0	8.3-9.5	9.2	9.3	8.4	8.4-8.5	7.8	6.6-8.4	6.3	6.9	7.2	6.8 (26)	4.9-8.6	7.7	6.8-8.6	7.1	5.8-9.2
Turb. (NTU)	71	35-150	-	-	10	2-24	20	6-48	1.4	2.8	5.3	3.7 (68)	0.2-15.5	2.3	0.9-3.7	3.3	0.8-10.3
TP (µM)	12.9	3.2-38.1	-	-	6.4	3.2-9.3	3.1	0.0-12.8	2.0	2.6	3.1	3.5 (17)	0.0-11.9	1.3	0.0-2.0	1.6	0.0-6.6
TDP (µM)	2.6	0.6-7.4	-	-	2.3	0.0-5.1	1.5	0.0-3.4	0.4	2.9	4.7	3.5 (17)	0.0-11.2	0.6	0.0-1.6	1.4	0.0-6.4
SRP (µM)	2.4	0.0-5.2	1.2	-	1.6	0.0-4.5	1.4	0.0-2.6	0.3	1.2	2.4	1.2 (18)	0.0-2.5	2.1	1.3-2.6	0.3	0.0-0.9
DIN (µM)	47	0-121	36	20*	17	7-47	16	0-38	50	57	102	78 (47)	17-177	27	17-44	43	0-115
Ca (mM)	0.4	0.3-0.5	0.2	0.2	1.3	0.8-1.7	trace	-				-	-	-	-	-	-
Mg (mM)	7.5	6.2-9.6	2.1	2.8	2.4	1.2-3.6	0.6	0.5-0.6				-	-	-	-	-	-
Alkal. (meq/l)	7.3	4.4-9.6	8.4	10.5	2.0	1.0-2.9	0.3	0.2-0.4				-	-	-	-	-	-
Cl (µM)	1098	704-1492	611	670	732	282-1211	479	338-648				-	-	-	-	-	-
SO_4 (µM)	124	83-156	93	187	10	0-42	10	0-31				trace	-	-	-	-	-
SRSi (µM)	264	153-403	168	156	78	46-170	405	57-702				2	1-5	1	1-2	1	0-1
Na (mM)	3.1	2.6-4.0	-	-	2.4	1.2-3.3	0.2	n.s.				-	-	-	-	-	-
K (mM)	1.3	1.0-1.8	-	-	0.1	0.1-0.2	0.1	n.s.				-	-	-	-	-	-

n.s. = no sufficient data
* = only oxidized forms
[a] data from 3 rain events October, December and June 1994-95
[b] combined data from 5 rain events 1994-95 and 4 from 1997

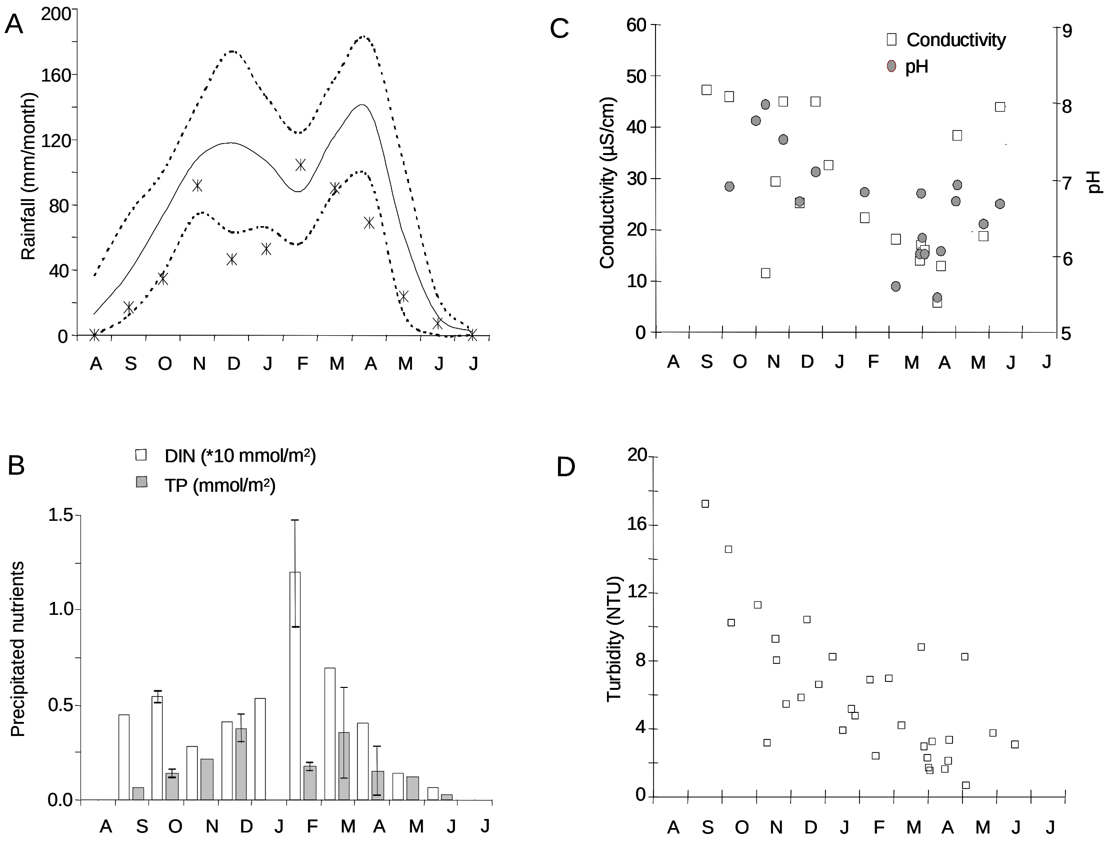
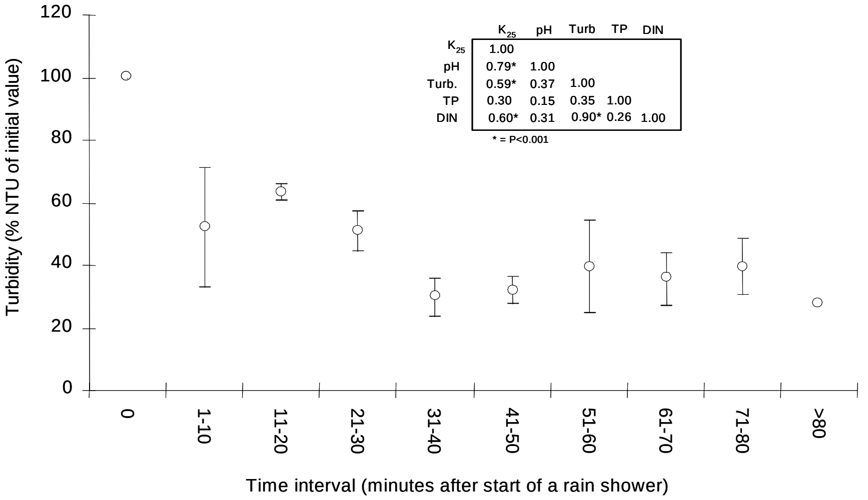


Figure 4. Annual fluctuations of physico-chemical characteristics of rain water during the sampling period of August 1994 to July 1995 at Bujumbura, Burundi. Graph A; pluviometry (monthly means and standard deviation) redrawn from Vandelannoote et al. (1999) (averaged unpublished IGEBU data 1982 to 1989, Bujumbura, Burundi). Asterisks indicate mean monthly rainfall during this study. Graph B; dissolved inorganic nitrogen (DIN) and total phosphate (TP), volume weighted monthly means and standard deviation are given where possible. No phosphorus determinations were carried out in January. Graph C; conductivity and pH. Graph D; turbidity. Note: Results based on first samples collected during each rain event.



	K_{25}	pH	Turb	TP	DIN
K_{25}	1.00				
pH	0.79*	1.00			
Turb.	0.59*	0.37	1.00		
TP	0.30	0.15	0.35	1.00	
DIN	0.60*	0.31	0.90*	0.26	1.00

* = P<0.001

Figure 5. Turbidity values for precipitated rainwater of four events expressed as mean percentage of their initial value at the beginning of a rain shower (T = 0) versus time intervals of 10 minutes. Notes: shower duration > 80 minutes was monitored once. Addition shows correlation matrix of some rain variables. Results based on all measurements made at Bujumbura, Burundi.

Time series of rainwater turbidity showed that after 30 minutes values tended to level out at ca. 60 to 70 % of their initial value (Fig. 5 inset). From all measurements made on wet deposition in

Bujumbura (separately sampled rain events plus time series) a correlation matrix was constructed (Fig. 5). Because SRP and TDP were strongly correlated to TP only TP was included in the matrix. The matrix indicates that the parameters conductivity, pH and DIN showed trends similar to turbidity (Figs. 4 and 5).

Discussion and conclusion

The three major rivers differed widely in their chemistry. Research on some adjacent rivers of Lake Tanganyika showed that altitude and morphology of the whole river system largely determine the annual dynamics of river chemistry and discharge (Hecky et al. 1991; Vandelannoote et al. 1999; Kimbadi et al. 1999). Basin geomorphology also explains the river chemistry and discharge characteristics of the rivers in the present study. The Malagarasi (50% of total lake catchment area) drains a large semi-arid area of relatively low elevations and it flows through several vast wetlands before entering the lake (Coulter and Spigel 1991). The Lufubu meanders for ca. 200 km through a small catchment area at low elevations, and the Rusizi drains a smaller area at higher elevations while also receiving water from Lake Kivu. The high discharge of brownish, sediment-loaded water of Rusizi throughout the year indicates substantial erosion, due to slope and altitude of its watershed (Vandelannoote et al. 1999). A low retention of eroded materials within its catchment and high discharge rates of solids and suspended particles probably explain why, compared to the other two rivers, Rusizi was the main contributor of nutrients to Lake Tanganyika during this study (more than 50% for all P fractions, DIN, and SRSi). During separate rain events in Malawi, Bootsma et al. (1999) found significant relationships between areal deposition rates of various nutrients (DOC, TDN, and SRSi) and amount of rainfall. They suggested that strong correlations between deposited nutrients and rainfall are unlikely to reflect changes in rain chemistry which in turn indicates that a constituent is not directly washed from the atmosphere, depending on its abundance or low solubility and ruling scavenging processes. Other constituents (NO_3, SRP, and TDP) showed low correlations with rainfall (a relatively quick atmospheric washout), indicating opposite conditions. Total rainfall amount per event was not determined. However, if it is assumed that rain event duration is an equivalent to rainfall amount per event then more rain would mean higher deposition rates of the constituents that determined conductivity, pH, turbidity, and DIN. This would confirm the results of Bootsma et al. (1999). However, our results showed that deposition rate of the constituents and related rain chemistry may fluctuate during the rainy season and even during one rain event. For example, seasonal variability in deposition rate of DIN in the beginning of the rainy season seemed to be due to variability in concentrations rather than to rainfall amount, whereas for the rest of the season rainfall amount explained most of the variability. Furthermore, substantial amounts of the constituents determining turbidity, DIN, pH and conductivity (Fig. 5) were deposited at the beginning of a rain event. This indicates that on longer and shorter time scales these compounds might be stripped sometimes more easily than other times but never completely from the atmosphere. Possible sources of atmospheric fixed nitrogen are emissions from soil bacterial processes, lightning, combustion of fossil fuels or biomass, and ammonia volatilization (from animal and human excreta, soil, and senescing vegetation). Near Lake Malawi, Bootsma et al. (1996) invoked biomass burning as mainly responsible for the elevated N concentrations in precipitation. Likewise, the relatively high DIN concentrations found in rainwater during this study are most likely caused by biomass burning. Biomass burning is widespread in the riparian countries of Tanzania, D. R. Congo, Burundi, and Zambia. Vast areas adjacent to the lake are burned during the second half of the dry season when fires become uncontrollable. Burning greatly decreases visibility near the lake and can affect areas outside Tanganyika region as well (Andreae 1993; pers. obs.). Dust and other airborne particulate matter from burning are expected to be washed out at the very initial onset of the wet season (Andreae 1993). High turbidity in rainwater at the beginning of the rainy season and decreasing turbidity in the course of the rainy season during this study (when there is atmospheric washout and reduced burning) suggest a washout mechanism similar to that described by Andreae (1993). This indicates that airborne particles and rainwater turbidity as well as correlated DIN, conductivity, and pH are associated.

Biomass burning is associated with acidic deposition since nitric and sulphuric acids are produced (Lewis, 1981; Crutzen and Andreae, 1990; Carvalho et al., 1995). The relatively high pH values in rainwater found during the study (up to 9.2 in Mpulungu) indicate the presence of alkali. This agrees with the findings from studies in Malawi (Bootsma et al., 1996). The decreasing pH with the onset of the wet season during this study might well be explained by washout of alkaline dusts from the atmosphere. Because stable gaseous phosphorus forms do not exist, phosphorus is normally associated with particulate material, predominantly aerosols and minerals (Galbally and Gillett, 1988). Contrary to DIN, pH, conductivity, and turbidity, phosphorus did not correlate with any other rainwater constituent or show any clear trend in seasonal washout. This indicates that phosphorus fractions depend on quick washout; its deposition reflects differences in atmospheric transport processes.

The nitrogen balance of the meromictic Lake Tanganyika is assumed to depend on external loading (rivers, groundwater, atmospheric wet and dry deposition), internal loading (upwelling, diffusion, and mixing), and in situ N fixation. Phosphorus has fewer pathways to (re) enter the productive layers (Horne and Goldman, 1994; Hecky, 2000) and overall phosphorus budget in Lake Tanganyika is supposedly dominated by internal loading, but with atmosphere and rivers supplying part of the input. Recent estimates show that primary production in Lake Tanganyika ranges between 426 and 662 g C $m^{-2}yr^{-1}$ (Sarvala et al., 1999). Phytoplankton C:N:P ratios of 168:19:1 (Järvinen et al., 1999) can be used to estimate that net DIN loading by rivers and wet atmospheric deposition (58 mmol N $m^{-2}yr^{-1}$, Table 2) can induce a new production of 6 g C $m^{-2}yr^{-1}$ or ca. 1% of the annual primary production. Similar, if only total dissolved phosphorus (2.4 mmol P $m^{-2}yr^{-1}$) is considered to become bioavailable it could induce 5 g C $m^{-2}yr^{-1}$.

The actual contribution of external nutrient sources to new production will differ from the above nutrient assessments, since other sources of nitrogen (particulate and organic), precipitated nutrients through atmospheric dryfall and loading by terrestrial runoff or ground water were not taken into account. However, we might make some assumptions based on earlier work.

Table 2. External source loading to Lake Tanganyika. TP (total phosphorus; in parenthesis average dissolved fraction in percentage), SRP (soluble reactive phosphorus), DIN (dissolved inorganic nitrogen), and SRSi (soluble reactive silicate) are considered. Annual nutrient fluxes expressed as mmol per m2 lake surface. Outlet of the Lukuga is shown.

	mmol/m²/yr			
	TP	SRP	DIN	SRSi
Lukuga[b]	0.2 (97)	0.1	1	2
Rusizi	2.1 (21)	0.3	7	45
Malagarasi[a]	1.0 (28)	0.2	2	15
Lufubu	0.3 (54)	0.1	1	38
Rain[c]	2.0 (73)	1.3	48	1
Total inputs	5.4 (44)	2.0	58	99

[a] measurements of dry season 1994 were used to replace hiatus in sampling dry season 1995.

[b] outlet calculations based on mean epilimnetic concentrations 35 km eastwards (See Langenberg, 1996).

[c] calculations based on lake-wide annual mean of 1200 mm precipitation in 1994-1995 and mean volume weighted concentrations (see text) from measurements made at Bujumbura (Burundi), Kigoma (Tanzania) and Mpulungu (Zambia).

Dissolved organic nitrogen (DON) in rainwater can be an important source of N to aquatic ecosystems (Bootsma et al. 1999). At Lake Malawi, they estimated DON to contribute as much as 30 to 50% to total dissolved nitrogen, which in turn could make up 70 to 95% of total nitrogen input

Their results agree closely to those found by Seitzinger and Sanders (1999) for oceanic regions. Bootsma et al. (1999) found that daily deposition rates of nutrients by dryfall to be nearly equal to the amount precipitated by wetfall. Because there are more dry days than wet days they concluded that on an annual basis dry deposition is greater than wet deposition. During the present study, approximately three times more dry than rainy days were recorded at Bujumbura, Burundi. Also, lake-wide research (Lindqvist et al., 1999; Plisnier 1996) showed that in general the biological and physico-chemical characteristics of coastal waters did not differ from those of pelagic waters. Because these coastal zones are most immediately affected by terrestrial run-off or ground water, and considering the great dilution effect by the lake's volume, it can be concluded that coastal inputs have little direct bearing on nutrient input into the pelagic waters. The combined discharges of the rivers measured in this study represent ca 65 to 75% of the total inflow estimated during earlier studies (Spigel and Coulter, 1996). Considering the above it is possible to roughly estimate that the external dissolved nitrogen load could support 7 to 14% and the dissolved phosphorus load ca. 3 to 5% of the annual primary production in Lake Tanganyika.

Although the annual contribution of external nutrient fluxes to Lake Tanganyika appears significant, the relative importance of the described fluxes to the overall epilimnetic production will differ locally and seasonally. These results showed that the wet deposition differed among the stations. Although not a full year was sampled at Kigoma and Mpulungu it appeared that the deposition rates at Bujumbura were higher. The deposition rates are notably higher (by a factor of 10 to 20) than results from similar studies carried out at Lake Malawi (Bootsma and Hecky, 1993; Bootsma et al., 1999) and are more comparable for example to the results of Herut et al. (1999) for southeast Mediterranean areas. As the capital of Burundi, the whole Bujumbura area is characterized by intense industrial, agricultural, and other anthropogenic activities more than Kigoma or Mpulungu, and this could explain the relative high deposition rates at Bujumbura. An increased atmospheric loading combined with substantial loading from the Rusizi may be key factors determining the elevated epilimnetic primary production rates in Burundian waters (Sarvala et al., 1999; Langenberg et al., 2003). Langenberg et al. (2002) showed that from July to December 1995 wind generated upwelling, internal wave action and deep mixing that cause nutrient loading from the hypolimnion promoting phytoplankton growth indicating the dominance of internal loading over other fluxes during this period. However, during February to May the water column is characterized by a well-developed stratification, low seiching activity of internal waves and a deep thermocline (Langenberg et al., 2002), i.e., the surface waters are then expected to be most isolated from underlying nutrient rich hypolimnion water. During this period wet deposition and riverine input of N and P, which then peak, may constitute a more important pathway of nutrients to the upper waters of the lake securing primary production. Rain and riverwater chemistry are closely linked to soil exposure, deforestation, agricultural activities, and animal and human excreta. Increasing human development of catchment areas will ultimately effect the dynamics and chemistry of river loading and atmospheric deposition (Galloway et al., 1994). This process of development and population increase is currently affecting nutrient loading to Lake Tanganyika and it will for the foreseeable future. Further research should focus on how much of the external nutrients can be directly utilized in the productive zone of Lake Tanganyika. The bioavailability of nitrogen and phosphorus fractions determines the significance of external nutrient fluxes to total lake production. Knowledge on internal loading and recycling, nitrogen fixation, and output fluxes (sedimentation and harvested biomass) will clarify the relative importance of all other fluxes making up the nutrient cycles in the lake. Clarifying nutrient cycles is an a priori requirement to understanding the production and ecosystem functioning in Lake Tanganyika.

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Chapter 8

Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web

Sarvala, J., Salonen, K., Järvinen, M., Aro, E., Huttula, T., Kotilainen, P., Kurki, H., Langenberg, V.T., Mannini, P., Peltonen, A., Plisnier, P-d, Vuorinen, I., Mölsä, H. and Lindqvist, O. V.

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Abstract

The sources of carbon for the pelagic fish production in Lake Tanganyika, East Africa, were evaluated in a comprehensive multi-year study. Phytoplankton production was assessed from seasonal in situ 14C and simulated in situ results, using on-board incubator measurements and knowledge of the vertical distributions of chlorophyll and irradiance. Bacterioplankton production was measured on two cruises with the leucine incorporation method. Zooplankton production was calculated from seasonal population samples, the carbon contents of different developmental stages, and growth rates derived from published sources. Fish production estimates were based on hydroacoustic assessment of pelagic fish biomass and data on growth rates obtained from length frequency analyses and checked against daily increment rings of fish otoliths. Estimates for primary production (426-662 g C m^{-2} a^{-1}) were 47-128 % higher than previously published values. Bacterioplankton production amounted to about 20 % of the primary production. Zooplankton biomass (1 g C m^{-2}) and production (23 g C m^{-2} a^{-1}) were 50 % lower than earlier reported, suggesting that the carbon transfer efficiency from phytoplankton to zooplankton was low, in contrast to earlier speculations. Planktivorous fish biomass (0.4 g C m^{-2}) and production (1.4-1.7 g C m^{-2} a^{-1}) likewise indicated a low carbon transfer efficiency from zooplankton into planktivorous fish production. Relatively low transfer efficiencies are not unexpected in a deep tropical lake, because of the generally high metabolic losses due to the high temperatures and presumably high costs of predator avoidance. The total fisheries yield in Lake Tanganyika in the mid-1990s was 0.08-0.14 % of pelagic primary production, i.e. within the range of typical values in lakes. Thus, no special mechanisms need be invoked to explain the productivity of fisheries in Lake Tanganyika.

Keywords: Lake Tanganyika, plankton production, carbon flow, trophic structure, food web, fishery yield.

Résumé

Les sources de carbone soutenant la production des poisons pélagiques du lac Tanganyika, Afrique Orientale, furent évaluées lors d’une étude approfondie de plusieurs années. La production de phytoplancton fut évaluée à partir des valeurs saisonnières de 14C in situ ou mesurées à bord du navire de recherche, ainsi que la connaissance de la distribution verticale de chlorophylle et de la radiation solaire. La production du bactérioplancton fut mesurée lors de deux croisières, en utilisant la méthode d’incorporation de leucine. La production de zooplancton fut calculée à partir d’échantillons saisonniers de la population, le contenu carbonique de différents stades de développement et les taux de croissance furent dérivés de sources publiées. L’estimation de la production en poisson fut basée sur des évaluations hydroacoustiques de la biomasse des poissons pélagiques ainsi que sur les taux de croissance calculés à partir de l’analyse des fréquences de longueur, vérifiés par l’étude de la formation journalière d’annaux sur les otolithes. Les valeurs obtenues pour la production primaire (426-662 g C m^{-2} a^{-1}) furent de 47-128% supérieures aux valeurs publiées antérieurement. La production du bactérioplancton formait environ 20% de cette production primaire. La biomasse (1 g C m^{-2}) et la production (23 g C m^{-2} a^{-1}) du zooplancton furent de 50% inférieures aux valeurs précédemment trouvées, suggérant un transfert de carbone peu efficace de phytoplancton au zooplancton, contrairement aux spéculations antérieures. La biomasse des poissons planctivores (0,4 g C m^{-2}) et leur production (1,4-1,7 g C m^{-2} a^{-1}) témoignent de la même façon d’un manque d’efficacité lors du transfert de carbone entre le zooplancton et les poissons planctivores. Un tel manque d’efficacité dans un lac tropical profond n’est pas inattendu et doit être attribué aux pertes métaboliques considérables causées par les températures élevées ainsi qu’aux coûts présumés élevés d’évitement du prédateur. La production piscicole du lac Tanganyika au milieu des années 1990 fut 0,08-0,14 de la production primaire pélagique, représentant une valeur typique dans un lac. Ainsi, pour expliquer la production halieutique du lac Tanganyika, il n’est pas nécessaire de faire appel à des mécanismes spéciaux.

Mots clés: Lac Tanganyika; Productivité du plancton; Flux de carbone; structure trophique; Chaîne alimentaire; Production de la pêche.

Introduction

Lake Tanganyika in East Africa is known for its productive pelagic fishery, which is reported to yield higher catches per unit area than in most great lakes of the world (Coulter, 1981, 1991; Hecky et al., 1981; Lindqvist and Mikkola, 1989; Hecky, 1991; Roest, 1992). Ultimately, the fish yield is a function of primary production, which in turn depends on solar radiation and external nutrient inputs. The fisheries yield in lakes usually ranges between 0.02 and 0.2 % of primary production (e.g. Morgan et al., 1980), while marine coastal seas often show values an order of magnitude higher (Nixon, 1988). For Lake Tanganyika, a preliminary estimate of 0.45 %, resembling those in the marine systems, has been given (Hecky et al., 1981; Hecky, 1984, 1991).

Several hypotheses have been presented to explain the high productivity of the pelagic fishery in Tanganyika (Hecky et al., 1981). Hecky (1991) noted that the food web of Tanganyika has a marine character. As in many productive marine systems, the primary grazer is a diaptomid copepod, and the dominant primary planktivores as well as the piscivores belong to predominantly marine fish families. The phytoplankton and bacterial biomasses are low but the growth rates are high. Organic carbon is not accumulated in the plankton but is channelled into fish biomass and harvested as fish yield. The long geological history of the lake, combined with the special ecological conditions of a deep, continuously warm tropical lake, may have resulted in the evolution of a trophic structure consisting of highly efficient species (Hecky, 1984). As another explanation Hecky et al. (1981) proposed that the flux of dissolved organic matter (DOM) from the anoxic hypolimnion might complement phytoplankton primary production; however, later analyses of available data have not supported this hypothesis (Hecky, 1991).

Earlier assessments of system structure and fish production efficiency were based on fairly limited data. New data have been collected by the FAO/Finnida project "Research for the Management of the Fisheries on Lake Tanganyika" (LTR) (Mölsä and Lindqvist, 1999). Rational fisheries management requires good knowledge of the fish production potential. The basic question in the LTR project is whether the present fish catches from Tanganyika are on a sustainable basis and whether or not there are further possibilities to increase the yield by developing the fishery. Total lake-wide catches seem to be increasing (Hanek, 1994; Coenen, 1995; Coenen et al., 1998), but recently, decreasing catches per unit effort both in the Burundi sector in the north and in the Mpulungu (Zambia) waters in the south have aroused concerns about possible overfishing (Roest, 1992; Coenen et al., 1998). On the other hand, there is still considerable local pressure to increase fishing effort to acquire more fish protein. One of the LTR objectives was, therefore, to determine the biological basis of fish production as a basis for management.

In Lake Tanganyika, as in other large and deep clearwater lakes, primary production of phytoplankton is expected to be the major source of energy to higher pelagic trophic levels, including fish. Knowledge of the trophic structure of the lake and the transfer efficiencies in the food chain is of interest for assessing the fishery potential, and also for comparison with other lakes. The LTR scientific sampling program covered the major components of the pelagic ecosystem over three years in different parts of the lake. Primary data have been made available in numerous technical documents published by the LTR project; in addition, we present some new data here. Because the analysis of these data still continues, our treatment here is necessarily preliminary. It, nevertheless, provides useful insights about the flow and availability of organic carbon that maintains the pelagic fisheries. This enables a reassessment of the trophic structure of Lake Tanganyika.

Methods and material

Sampling scheme

Physical, chemical and biological components of the pelagic ecosystem of Lake Tanganyika were sampled weekly or fortnightly at three localities (Figure1) in a comprehensive scientific sampling program from July 1993 to June 1996 (Plisnier et al., 1999); data for the first two years were available for the present account. In addition, representative data were available from 20 lake-wide scientific cruises with the R/V Tanganyika Explorer in 1995-1998.

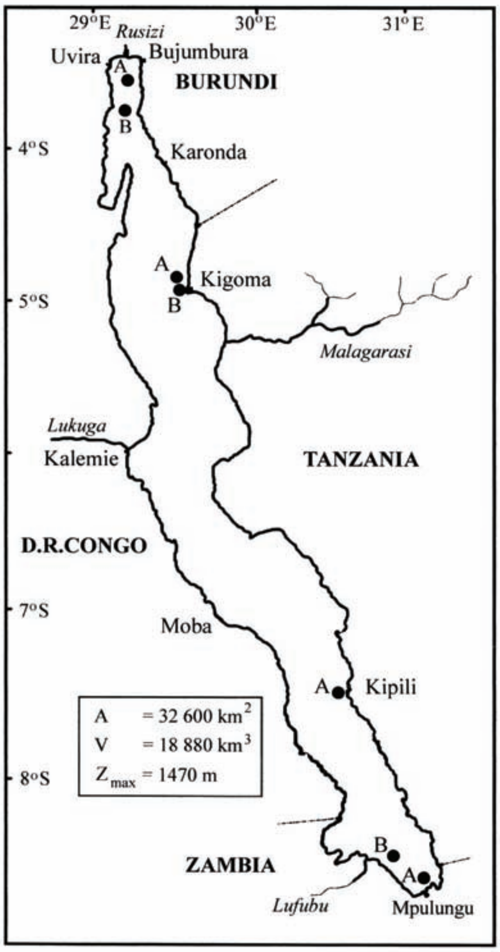


Figure 1. Lake Tanganyika and the locations of the seasonal sampling sites (A = weekly sampling sites, B = vertical migration study sites). Lake area (A), volume (V) and maximum depth (Z_{max}) are also indicated.

Solar irradiance

Total irradiance was recorded along with other weather variables at automatic weather stations (land-based in Bujumbura and on a buoy off Mpulungu and Kigoma) (Kotilainen et al., 1995). Irradiance data recorded at Kigoma airport were also available. A LI-COR instrument with a spherical scalar underwater quantum sensor (LI-193SA) and data logger (LI-COR Inc, Lincoln, USA) was used to record the depth attenuation of photosynthetically active radiation (PAR: 400-700 nm). Vertical profiles of in situ irradiance were measured during the cruises and during the weekly monitoring at the three field stations.

Phytoplankton

In vivo fluorescence of chlorophyll *a* at different depths (down to 100 m) and horizontal positions was measured using a Turner AU-10-005 field fluorometer (with the traditional 10-037 chlorophyll optical kit using F4T5D daylight white lamp, CS-5-60 excitation filter (340-500 nm), CS-2-64 emission filter (>665 nm) and red-sensitive photomultiplier; Salonen and Sarvala, 1994; Sarvala and Salonen, 1995; Salonen et al., 1999). Water samples were taken with a darkened 1-m long Limnos sampler (Limnos Ltd, Finland). Vertical fluorescence profiles at several sites plus numerous additional surface water measurements were made off Bujumbura in April 1994, off Kigoma in April and December 1994 (Salonen and Sarvala, 1994; Sarvala and Salonen, 1995), and throughout the lake in April-May 1995 (Järvinen et al., 1996), October-November 1995, November 1996 (Salonen et al. 1999) and in March-April 1998. Fluorescence readings were calibrated against determinations of extracted chlorophyll *a*. One- or two-litre samples of the same water were filtered on preignited Whatman GF/F glassfibre filters, dried, stored in darkness, and extracted in ethanol. Chlorophyll *a* was then determined spectrophotometrically (Salonen and Sarvala 1995; a modified ISO procedure) or using a fluorescence spectrophotometer (Järvinen et al., 1996; Salonen et al., 1999). Vertical series of extracted chlorophyll *a* determinations were also made on two-weekly samples from the permanent field stations off Bujumbura, Kigoma and Mpulungu, starting from August 1995. A biomass estimate for phytoplankton was obtained from the average chlorophyll (0-40 m depth) by assuming a carbon:chlorophyll ratio of 35 (Sarvala et al. 1982).

Phytoplankton primary production was assessed with the whole-water modification of the radiocarbon method (Schindler et al., 1972). Radiolabelled samples and formaldehyde treated controls were incubated *in situ* at different depths in 20-mL glass liquid scintillation vials attached horizontally to a suspending rack (Salonen and Sarvala, 1994). No filtration was applied; the unassimilated radiocarbon was removed through acidification and exchange with air (Niemi et al., 1983). Radioactivities of acid preserved samples were counted with a Wallac Ultrobeta 1200 liquid scintillation counter. Dissolved inorganic carbon (DIC) in water was determined in Finland with a carbon analyser according to Salonen (1981). Because of very high alkalinity (6.7-6.9) and pH (ca. 9; Edmond et al., 1993), the storage of samples did not significantly affect equilibrium concentrations of DIC. Short 3-hour incubations around noon plus diel series of 2-3-hour successive incubations were done off Kigoma in April and December 1994 (down to 20 m in April and down to 60 m in December) and additional vertical series in September 1994. Further series of seasonal *in situ* measurements with 4-hour incubations were made off Bujumbura, Kigoma and Mpulungu between July 1995 and June 1996. These vertically integrated 4-hour results were converted to daily values using the ratio between the cumulative daily PAR and the PAR cumulated during the incubation period. Off Bujumbura, 38 % of the cumulative daily PAR was received during the incubation period, and the same value was applied to Kigoma data (at both stations the incubations were started at 7:30 h). Off Mpulungu, the incubations started at 11:00 h and the corresponding percentage was 50 %.

During two lake-wide cruises (April-May 1995 and October-November 1995), primary production was also measured in an on-board incubator at different light intensities (25-508 µmol photon m^{-2} s^{-1} PAR) to obtain representative photosynthesis-irradiance (P-I) curves (Järvinen et al., 1996: 8 series; K. Salonen, unpublished: 4 series). During the April-May cruise, phytoplankton samples from 0, 5, 10, and 20 m were combined for the incubations; during the October-November cruise samples from 1, 10, 20, 30 and 40 m depths were incubated separately. Chlorophyll *a* for the incubated samples was estimated from fluorescence readings. Chlorophyll-specific productivity was related to irradiance by fitting the hyperbolic tangent model: $P = P_{max} \tanh(\alpha I/P_{max})$ without a term for photoinhibition (Jassby and Platt, 1976; for an evaluation of production-irradiance models, see Frenette et al., 1993). Fitting was done with the NLIN procedure of SAS computer package. Using this photosynthesis-irradiance relationship, estimates of simulated in situ primary production (e.g. Lohrenz et al., 1992) were calculated from irradiance and chlorophyll data. Hourly PAR for each depth was calculated from the annual average of total surface irradiance for that hour, using measured light attenuation coefficients, assuming 5 % albedo and taking PAR to be 47 % of the total irradiance, and using a conversion factor of 1 Wm^{-2} = 4.59 µmol photon m^{-2} s^{-1} between the electromagnetic radiation flux and the photon flux density (Reynolds, 1990). From these irradiance values, chlorophyll-specific productivity was calculated for each depth and hour, and daily production values for the whole euphotic water column were obtained by temporal and vertical integration.

Simulated *in situ* primary production was calculated separately for the dry and wet seasons. Dry season calculations were based on the light extinction and chlorophyll measurements and production-irradiance curves obtained during the April-May 1995 cruise, while wet season calculations were based on a higher light extinction coefficient deduced from transparency data, chlorophyll profiles from the cruises in October-November in 1995 and 1996, and production-irradiance curves obtained during the October-November cruise in 1995. For both seasons, calculations were performed with irradiance data from the Bujumbura and Mpulungu weather stations, and the results averaged.

Bacterioplankton, community respiration and DOC

Bacterioplankton production was assessed with the leucine incorporation method (Kirchman, 1995) during two cruises (April-May 1995; Järvinen et al., 1996, and October-November 1995). Total respiration of plankton was measured as oxygen consumption off Kigoma in April 1994 (Salonen and Sarvala, 1994), using glass bottles and the Winkler titration method.

Dissolved organic carbon (DOC) was determined from two vertical series from 0 to 80 m depth on 30 April and 5 May 1995 at the southern and northern ends of the lake (Järvinen et al., 1996). Carbon was determined by igniting the acidified and dried water samples in sealed glass ampoules and leading the CO_2 produced to the infrared detector of the carbon analyser of Salonen (1979), as described in Järvinen et al. (1996).

Zooplankton

Zooplankton abundance was monitored weekly (fortnightly during the first year) at the three field stations beginning from July 1993 (Kurki et al., 1999a). Three (one in the first year) replicate hauls from 100 m to surface were taken with a 100-μm plankton net of mouth diameter 25 cm. For the only calanoid species (*Tropodiaptomus simplex* (Sars)) and the cyclopoids as a group (consisting of Mesocyclops *aequatorialis aequatorialis* (Kiefer), *Tropocyclops tenellus* (Sars) and *Microcyclops cunningtoni* (Sars)), nauplii, copepodids, adult males and adult females with or without eggs were distinguished. *Limnocnida tanganyicae* Günther medusae, decapod shrimps and fish eggs or larvae were also counted (Kurki et al., 1999b). Nets with mesh sizes of 50 and 100 μm were compared on five occasions in October-November 1993 off Kigoma (Vuorinen and Kurki, 1994) and in 1994 off Bujumbura. Important additional information was obtained from the vertical migration studies (Vuorinen et al., 1999), in which samples were taken at six-week intervals with a transparent 7.4-l tube sampler (Limnos Ltd., Finland) at 20 m depth intervals down to 140 m off Bujumbura and Kigoma and to 220 m off Mpulungu; mesh size was 50 μm.

Individual carbon contents of the main crustacean zooplankton species were determined in Finland with the analyser of Salonen (1979) from two samples preserved in 4 % glutaraldehyde (Kigoma, 6 December 1994; southern Burundi waters, April 1995). Preservation in glutaraldehyde should yield carbon values similar to fresh determinations (Salonen and Sarvala, 1985; Kimmerer and McKinnon, 1986). Carbon-length regressions ($\log_e$[carbon] *vs*. $\log_e$[total length including the furcal rami]) were established. Mean carbon values for nauplii and copepodids were derived from these determinations assuming a constant mortality of 21 % during each stage. This mortality rate was obtained from the difference between the mean copepodid and naupliar abundances in the vertical migration data. Because cyclopoid species were not distinguished in routine counting, the mean carbon values for cyclopoids were adjusted for the relative abundance of the small species (Kurki et al. 1999a: 45 % off Bujumbura, 94 % off Kigoma and 14 % off Mpulungu). Dry mass-diameter regression for the medusa *Limnocnida* was established from individuals dried in the field on preweighed aluminium foil sheets and weighed later in Finland. The average individual biomass of medusae was obtained with this regression from two sample series covering the 0-100 m water column in April 1998 off Kigoma. Carbon was taken to be 50 % of dry mass (Salonen et al., 1976). For the shrimp *Limnocaridina parvula* Calman, an organic dry mass-carapace length regression was constructed from a 0-100 m net sample off Kigoma in April 1998. Mean shrimp biomass was calculated using the carapace measurements in 105 oblique 0-100 m Gulf net samples taken during five lake-wide cruises (Bosma et al., 1998). The same regression was used for all species, because L. parvula accounted for >99 % of the total shrimp numbers. Zooplankton production was calculated with the instantaneous growth rate method (Downing and Rigler, 1984; Kimmerer, 1987):

$$P = g * B,$$

where

$$g = \log_e (M_{fin}/M_{ini}) / D_i$$

$$B = (\text{numbers}) * (\text{individual carbon content})$$

(M_{ini}, M_{fin} = initial and final carbon contents of the stage i; D_i = duration of stage i)

There is no practical way to work out the average initial and final carbon contents of a developmental stage; the range of observed values would be an overestimate, because it is inflated by variation in individual size. Therefore, approximate *ad hoc* solutions were necessary. The carbon mass of the first naupliar stage was taken as the initial naupliar mass. The mean of the sixth naupliar and the first copepodid stage was used as the final naupliar mass and the initial copepodid mass, and the mean of the fifth copepodid and the adult stage was used as the final copepodid mass. For aggregated developmental stages this routine is more appropriate than the procedure of Irvine and Waya (1999), who used the mean biomasses of successive stages for deriving instantaneous growth rates. Adult female production consisted of egg production which was assessed separately using the numbers of ovigerous females: for instantaneous growth rates the carbon contents of egg-bearing females were related to the initial female mass and the egg development time.

Development times were derived from the literature. For *T. simplex*, we averaged values published for the slightly larger *Tropodiaptomus spectabilis* from South Africa (Hart, 1994) and the similarly-sized *Tropodiaptomus cunningtoni* from Lake Malawi (Irvine and Waya, 1995). For *M. aequatorialis*, we used the recently published values from Lake Malawi (Irvine and Waya, 1995). For the smaller cyclopoid species, we calculated tentative development times from the temperature regressions of *Thermocyclops oblongatus* from Lake Naivasha (Mavuti, 1994). Comparisons with recent LTR rearings of *T. simplex* and *M. aequatorialis* in Kigoma (Hyvönen, 1997) showed reasonable agreement with the adopted values. All development times were adjusted to a temperature of 26°C, close to the average experienced by Lake Tanganyika copepods during their vertical migrations that expose them daily to almost the maximum seasonal temperature range from 24 to 28°C (annual average temperatures for the upper 100 m were 25.5, 25.6 and 25.1°C off Bujumbura, Kigoma and Mpulungu, respectively; Kurki et al., 1999a). Because of the narrow range of possible values, errors owing to the temperature variation remained small.

Fish

Population analyses of pelagic fish (the clupeids *Stolothrissa tanganyicae* Regan, *Limnothrissa miodon* (Boulenger) and the predatory *Lates stappersi* (Boulenger)) were based on weekly catch samples from commercial catches at three main stations and five substations around the lake (Aro and Mannini, 1995). Sampling covered all methods used in the traditional, artisanal and industrial fisheries (lift nets, beach seine and purse seine). Most fishing is done at night as virtually all of these methods rely on light attraction. In the first year of sampling, 429-443 catch samples were taken for each species. Length, weight, sex and reproductive status were recorded for each fish. Length-frequency analyses (LFA) were applied to derive growth and mortality rates from these data (Mannini et al., 1996). To check the growth information thus obtained, age determinations of the clupeids were also made by counting daily increment rings in the otoliths (Pakkasmaa and Sarvala, 1995; H. Ahonen, unpubl.). Length-specific growth rates were derived from the von Bertalanffy growth curves and converted to weight-specific rates using biomass-length-regressions and, finally, these were combined to average size distributions at each sampling locality to yield daily and annual production rates and production to biomass ratios.

Fish biomass was estimated from five lake-wide hydroacoustic surveys combined with experimental trawling (Szczucka, 1998). Because of high noise levels observed during two cruises, acoustic data from only three cruises (June 1995, November-December 1997, February 1998) could be used for absolute biomass estimation. Additional mortality estimates for each fish species were derived from the combined size distributions in the trawl catches. Biomass proportions of different species were averaged from the results of all five cruises (Mannini, 1998). Total fish production in Tanganyika was obtained using the calculated production to biomass ratios and estimates of fish biomass. Collection of fish catch statistics was done in collaboration with the local fisheries administration of each country (Coenen, 1995; Coenen et al., 1998).

Results

Irradiance

The mean diurnal pattern of total solar irradiance was very similar at the northern and southern ends of the lake, although slightly lower values were recorded before noon in Bujumbura (Figure 2). This may be due to the shading effect of the mountainous terrain or to more frequent clouds in the northern end of the lake. In Bujumbura, the average total irradiance in January-October 1995 was 230 Wm^{-2} (218 Wm^{-2} during the wet season, 232 Wm^{-2} during the dry season); off Mpulungu the average for May-November 1995 was 256 Wm^{-2}. The 1993 annual average of total irradiance at Kigoma airport, some kilometres east of the lake shore, was 206 Wm^{-2}; higher values would be expected on the lake, because clouds tend to be more common over the land in this area.

During the whole-lake cruise in April-May 1995, the measured daytime (7:00-17:00) total irradiance varied between 236-988 (average 554) Wm^{-2} (n = 41). The corresponding long-term averages for the Bujumbura and Mpulungu weather stations in 1995 were 543 and 595

Wm^{-2}, respectively. Average maximum hourly irradiance (PAR) below surface calculated (see below) from the weather station total radiation (Figure 2) was 1700-1800 µmol photon m^{-2} s^{-1}, and the corresponding average for the daytime (7:00-17:00) was about 1160 µmol photon m^{-2} s^{-1}. This compared well with the average daytime irradiance (1192 µmol photon m^{-2} s^{-1}) measured during the April-May 1995 cruise immediately below water surface in six light profiles from three sites covering the whole lake length.

Light extinction coefficients obtained from three vertical profiles off Bujumbura in February-March 1995 ranged from 0.130 to 0.188 m^{-1} and seemed to be inversely related to Secchi depth transparency (11.2-8.5 m). The clearly lower (mean 0.112 m^{-1}, range 0.102-0.117 m^{-1}, n = 6) extinction coefficients obtained from measured irradiance profiles during the April-May 1995 cruise were associated with higher transparency of water (14-16 m), typical for the April-August season. In 1993-1995, the average transparency off Bujumbura and Kigoma was 12.3 m (n = 88). Therefore, the extinction coefficient of 0.15 m^{-1}, roughly corresponding to a Secchi reading of 9.5-10 m, was chosen to represent the wet season, while the value measured during the April-May 1995 cruise (0.112 m^{-1}) was used for the dry season.

Phytoplankton primary production

Fluorescence and chlorophyll profiles showed values approaching 1 mg chl *a* m^{-3} down to 50-60 m depth, in sunny weather a surface depression around noon, and often a maximum in fairly deep water at 30-40 m (Figure 3; Sarvala and Salonen, 1995; Järvinen et al., 1996; Salonen et al., 1999). In connection with local bluegreen blooms, much higher values (tens of mg m^{-3}) were observed immediately below the water surface. Likewise, maximum primary production was usually at the depth of 10-20 m, with measurable production down to 40-50 m (Figure 4). The depth of the euphotic layer, defined as the depth to which 1 % of the surface irradiance could penetrate, was also normally between 40 and 50 m throughout the lake in different seasons (Langenberg, 1996). The photic zone was usually deepest off Kigoma, which was the only permanent sampling station that represented the conditions in the open central parts of Tanganyika.

During the first cruise in April-May 1995 the average fluorescence in surface water (excluding the midday depression) indicated a mean chlorophyll *a* concentration of 1.4 mg m^{-3} for the whole lake (Salonen et al., 1999).

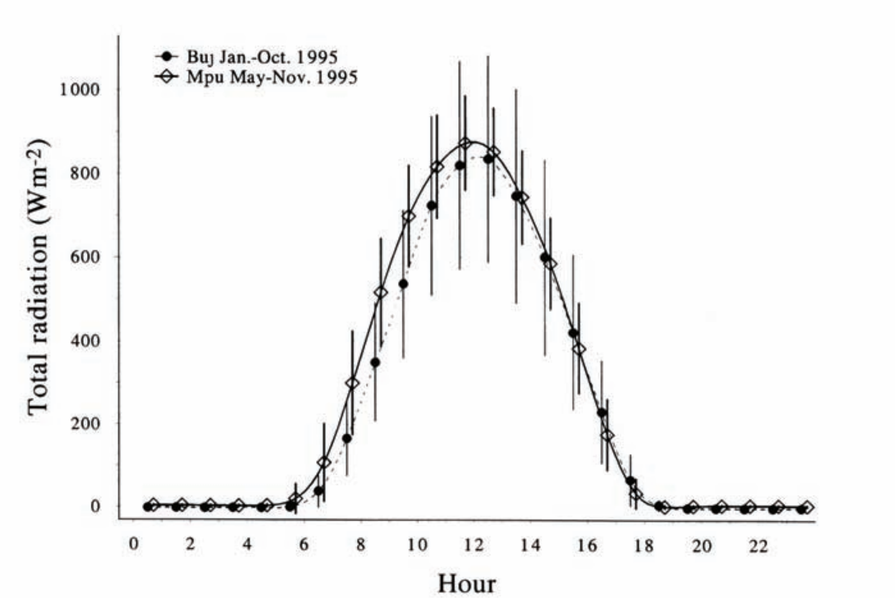


Figure 2. Average daily pattern of total radiation flux (hourly averages; Wm^{-2}) at the automatic weather stations in Bujumbura harbour (Burundi; 13 January - 3 November 1995) and off Mpulungu (Zambia; buoy meteo: 1 May - 28 November 1995). Vertical bars show standard deviations of the hourly averages (time axes slightly displaced for clarity).

For the uppermost 40 m the fluorescence-derived overall mean value was 0.96 mg m^{-3} (n = 53) and the corresponding mean for extracted chlorophyll *a* was 1.0 mg m^{-3} (n = 27). The vertical profiles measured off Kigoma in April and December 1994 indicated much lower values, with especially pronounced surface depression in April (Figure3). Vertical profiles from the cruises in October-November 1995 and November 1996 showed higher fluorescence levels and maxima at or close to the surface (Figure 3); the latter series included some surface blooms of bluegreen algae resulting in very high fluorescence values (Salonen et al., 1999). The average chlorophyll in the uppermost 40 m (calculated from fluorescence) was 2.2 mg m^{-3} in October-November 1995 (n = 76) and 2.8 mg m^{-3} in November 1996 (n = 27). Seasonal average values obtained from the first five months of weekly chlorophyll samples from off Bujumbura, Kigoma and Mpulungu were 0.6-1.6 mg extracted chlorophyll *a* m^{-3} (Langenberg, 1996).

Incubator measurements of primary production at different irradiance levels resulted in relatively flat photosynthesis-irradiance curves (Figure 5), showing that the Tanganyika phytoplankton was capable of efficient photosynthesis even at the low irradiance levels occurring at 30-40 m depth. No signs of photoinhibition were observed up to the highest experimental irradiance level of 512 µmol photon m^{-2} s^{-1}. Variability between experiments was high especially for maximum level of production. One of the October-November 1995 experiments (30 m) was omitted because of practically zero production at all irradiances, indicating a technical failure. DIC determinations were consistently 72 mg C l^{-1}. Average primary production assimilation numbers varied from 2.1 mg C (mg chl *a*)$^{-1}$ h^{-1} during the April-May 1995 whole-lake cruise to 3.2 mg C (mg chl *a*)$^{-1}$ h^{-1} during the October-November cruise in 1995. The assimilation number obtained from *in situ* incubations in December 1994 off Kigoma (3.0 mg C (mg chl *a*)$^{-1}$ h^{-1}) was similar to the latter value.

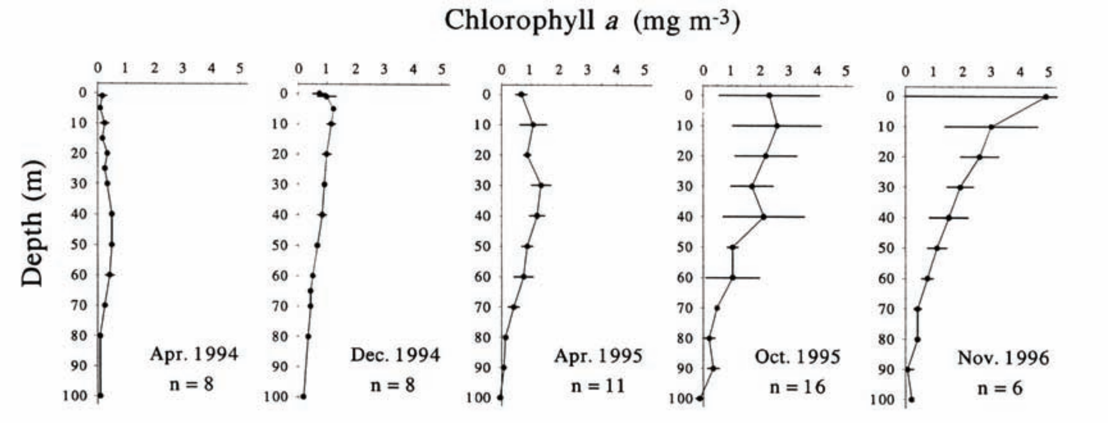


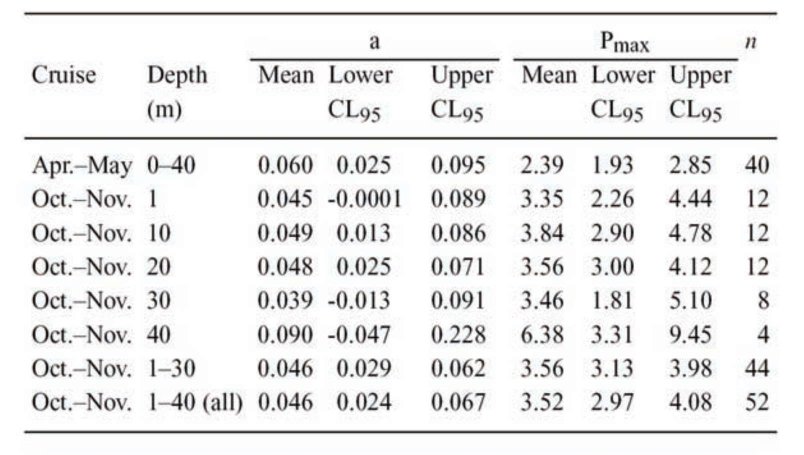
Figure 3. Average vertical profiles of phytoplankton chlorophyll (calculated from fluorescence) off Kigoma in April and December 1994 and during three whole-lake cruises in April-May 1995 (Järvinen et al., 1996), October-November 1995 and November 1996 (horizontal bars show standard deviations; n = number of averaged profiles). All profiles taken at different times of day are included.

In the incubator experiments in October-November 1995 the chlorophyll-specific productivity *vs*. irradiance curves were practically identical from 1 to 30 m depth, allowing the use of common photosynthetic parameters for these depths (Table 1). Phytoplankton from 40 m showed a steeper photosynthesis-light slope and higher maximum productivity (Figure 5), although the difference was not statistically significant. The examination of residuals did not reveal any systematic deviations from the model.

The similar light responses suggest that phytoplankton in the uppermost 30 m had an identical history of light exposure, probably because of only partial mixing within the epilimnion. Indeed, vertical temperature profiles often showed secondary discontinuities at various depths above the major thermocline at 50-70 m (Salonen and Sarvala, 1994; Huttula et al., 1994). At least down to a depth of 5 m, occasionally even down to 9-10 m, the irradiance levels were so high (>500 µmol photons m^{-2} s^{-1}; e.g. Kirk, 1983) that photoinhibition was likely for several hours per day; detectable as declining fluorescence values towards the surface in many profiles.

Because epilimnetic mixing ameliorates deleterious effects of excessive radiation, surface inhibition was ignored in calculating photosynthetic rates, with any inhibition effect incorporated in the measured chlorophyll values.

Table 1. Photosynthetic parameters (photosynthetic efficiency (a) and photosynthetic capacity (P_{max})) for Lake Tanganyika phytoplankton, calculated with the hyperbolic tangent model of the chlorophyll-specific production vs. irradiance relationship without a term for photoinhibition (Jassby and Platt, 1976). Data derived from incubation experiments during the cruises in April–May 1995 (samples from different depths combined) and October–November 1995 (depths incubated separately). For the latter cruise, parameters are also given for the combined data of 1–30 m and 1–40 m.



		a			P_{max}			*n*
Cruise	Depth (m)	Mean	Lower CL_{95}	Upper CL_{95}	Mean	Lower CL_{95}	Upper CL_{95}	
Apr.–May	0–40	0.060	0.025	0.095	2.39	1.93	2.85	40
Oct.–Nov.	1	0.045	-0.0001	0.089	3.35	2.26	4.44	12
Oct.–Nov.	10	0.049	0.013	0.086	3.84	2.90	4.78	12
Oct.–Nov.	20	0.048	0.025	0.071	3.56	3.00	4.12	12
Oct.–Nov.	30	0.039	-0.013	0.091	3.46	1.81	5.10	8
Oct.–Nov.	40	0.090	-0.047	0.228	6.38	3.31	9.45	4
Oct.–Nov.	1–30	0.046	0.029	0.062	3.56	3.13	3.98	44
Oct.–Nov.	1–40 (all)	0.046	0.024	0.067	3.52	2.97	4.08	52

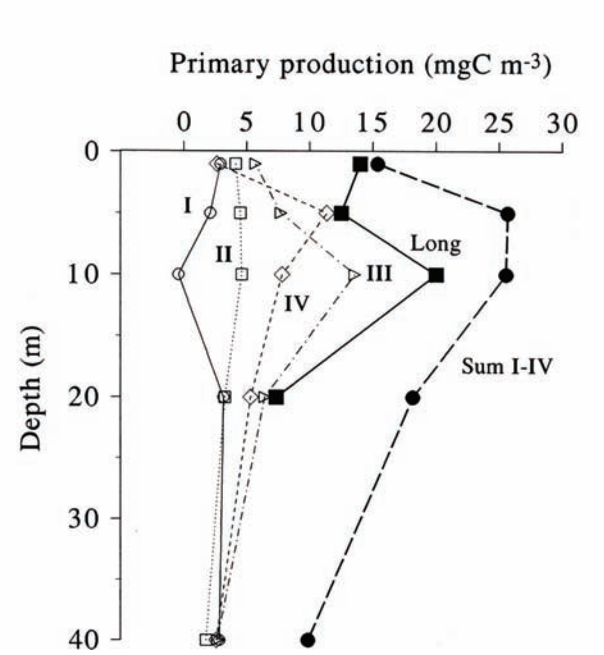


Figure 4. Vertical profiles of phytoplankton primary production measured with the radiocarbon method off Kigoma 2 December 1994 (Sarvala and Salonen, 1995). Results are shown for four successive two-hour incubations (I-IV, between 7:50 and 17:30), their sum (Sum I-IV: black dots), and a whole-day incubation (7:55-17:35; filled squares).

Thus, ignoring photoinhibition, the simulated in situ production calculations indicated a photosynthetically saturating light climate for 12 hours per day immediately below the surface and for 5-6 hours at 15-20 m depth.

In April-May 1995, multiplication of the average assimilation number by the average surface chlorophyll value resulted in an estimate for the overall lake-wide primary production rate of 2.0-2.1 mg C m^{-3} h^{-1}, or, approximately 20-21 mg C m^{-3} d^{-1}. Depth-integrated daily primary production for the uppermost 40 m was 0.80-0.86 g C m^{-2} d^{-1}.

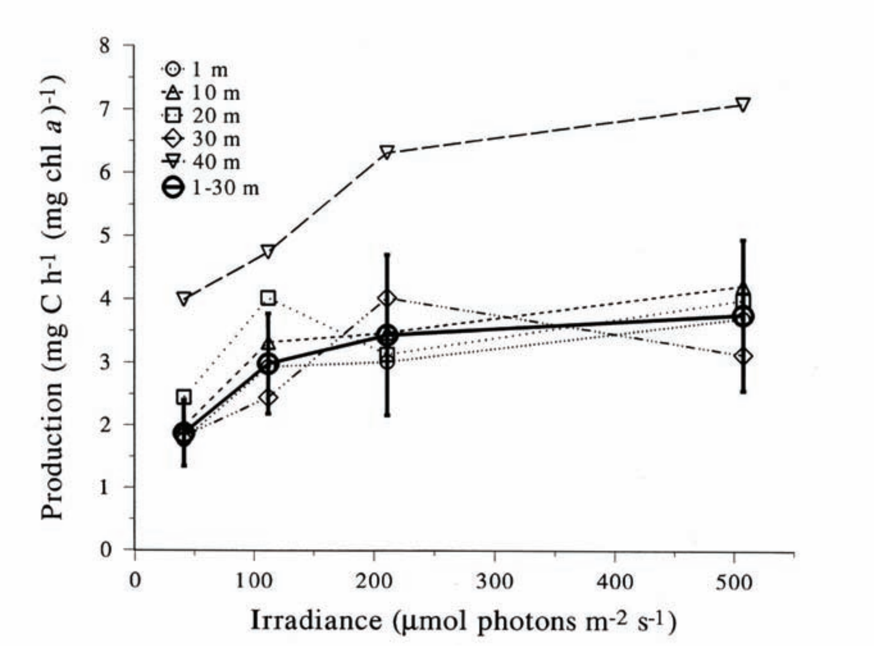


Figure 5. Photosynthesis-irradiance curves for Lake Tanganyika phytoplankton from different depths, obtained from incubator experiments in October 1995. Combined curve for the depths 0-30 m given with standard deviations (vertical bars).

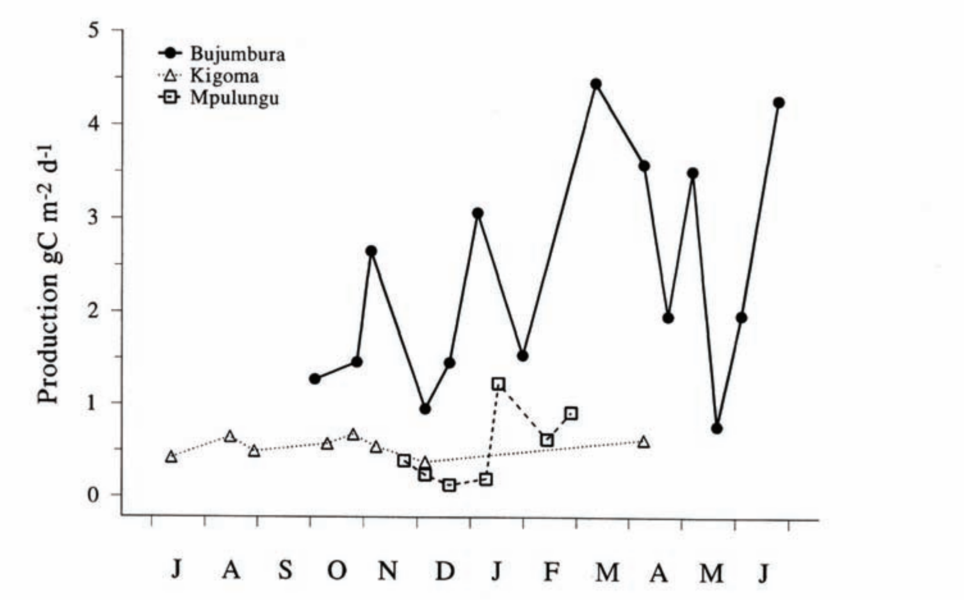


Figure 6. *In situ* primary production in Lake Tanganyika at the three permanent field sampling stations in 1995-1996. Original results of 4-hour incubations at different depths were converted into daily values using the hourly distribution of irradiance and integrated for the whole euphotic water column.

In October-November 1995, the corresponding production rate was estimated as 7.0 mg C m^{-3} h^{-1}, resulting in a daily productivity of 2.8 g C m^{-2} d^{-1}. Averaging these estimates yields an annual production of 662 g C m^{-2} a^{-1}.

The average simulated *in situ* production was 1.06 g C m^{-2} d^{-1} for the dry season and 2.49 g C m^{-2} d^{-1} for the wet season. Assuming 6-month duration for both seasons, these values resulted in an annual production estimate of 647 g C m^{-2} a^{-1} for the whole lake.

Third, completely independent estimate for primary production was obtained from the weekly in situ radiocarbon measurements carried out since August 1995 at the three permanent sampling localities in different parts of the lake (Figure 6). The highest values were found off Bujumbura and the lowest off Mpulungu (the mean values (95 % CL) for the whole measurement period were 2.44 ± 0.71 g C m^{-2} d^{-1} (number of measuring dates = 14), 0.52 ± 0.09 (n = 8) and 0.54 ± 0.38 (n = 7) for Bujumbura, Kigoma and Mpulungu, respectively). An overall average for the whole lake was estimated as 1.2 g C m^{-2} d^{-1} or 426 g C m^{-2} a^{-1}; variability of the *in situ* measurements suggests that the 95 % confidence belt of this estimate might be 35 %.

Bacterioplankton production
In the experiments during the first research cruise in April-May 1995 (Järvinen et al., 1996) the rate of leucine uptake varied between 0.0027-0.1292 nM Leu l^{-1} h^{-1}. In terms of bacterial biomass production this rate was equivalent to 0.1-4.9 (average 2.8) mg C m^{-3} d^{-1} (assuming equal rate day and night). This rate was slightly more than 20 % of the average phytoplankton primary production (13.6 mg C m^{-3} d^{-1}) measured in two-day experiments during the same cruise. During the second cruise in October 1995, at two sites the bacterial production rates were similar to those measured in April-May of the same year, but at three sites much higher values were obtained (Figure 7).

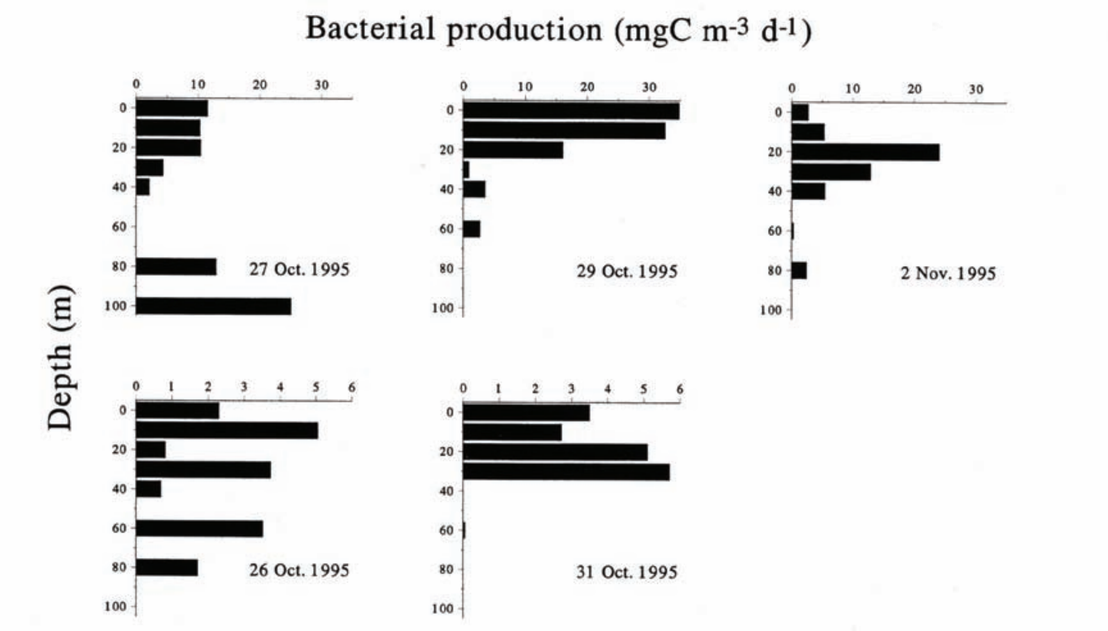


Figure 7. Vertical profiles of bacterial production (mg C m^{-3} d^{-1}; calculated from leucine incorporation) (note different scales) in different parts of Lake Tanganyika in October-November 1995.

Highest values usually occurred in the upper water layers, although at one site the maximum values were recorded below the thermocline; the small number of measurements from the hypolimnion does not allow any firm conclusions as to the potential importance of hypolimnetic bacteria. Bacterial production correlated positively with the chlorophyll *a* concentrations of the same samples ($r^2 = 0.76$, n = 23; Figure 8).
Consistent with the results from the first cruise, bacterioplankton production was on an average 21 % of phytoplankton production estimated from chlorophyll a and the average assimilation number.

Zooplankton production
Significant carbon to length regressions were obtained for the three main species of pelagic copepods in Tanganyika from a sample in southern Burundi waters in early May 1995 (Figure 9; equations in Table 2; average carbon values for each developmental stage in Table 3).

The instantaneous growth rates obtained for reproducing females and naupliar stages did not vary much between copepod species (Table 4). Because estimates for the small cyclopoids were the most uncertain, the growth rates of *Mesocyclops* were used for all cyclopoids.
The zooplankton biomass and production estimates calculated from the vertical migration data and from the weekly sampling series (Table 5) were expected to be somewhat different, because of the different sampling sites, mesh sizes and water column depths sampled. The distance between the sites was largest at the southern end of the lake, where the weekly sampling site was only some 10 km from Mpulungu, while the vertical migration study site was more than 30 km further north, over deeper water and close to the deep open area of the southernmost basin. Differences between the two Mpulungu data sets thus mainly reflect variation between sites. In contrast, especially off Kigoma both series were expected to represent roughly the same water mass.

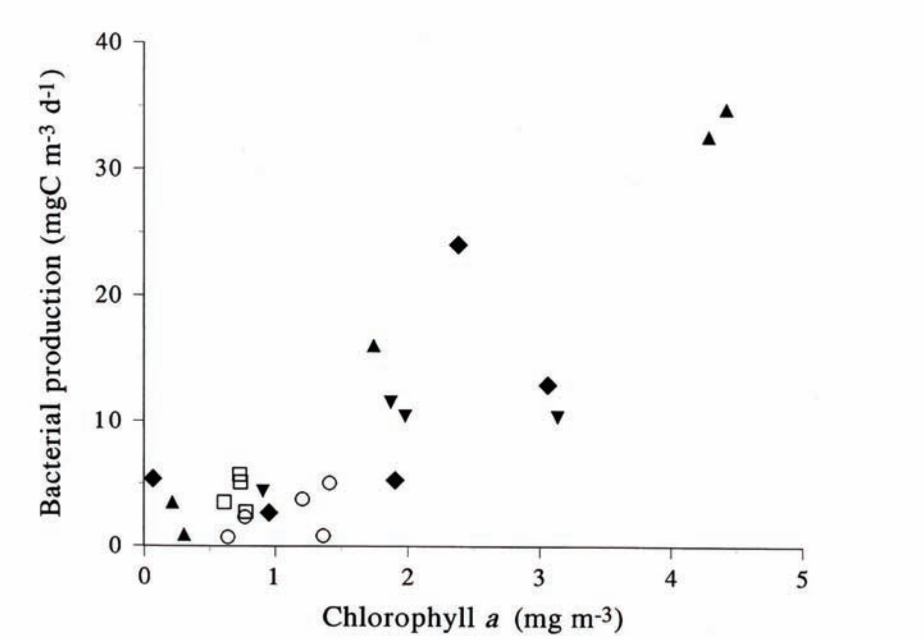
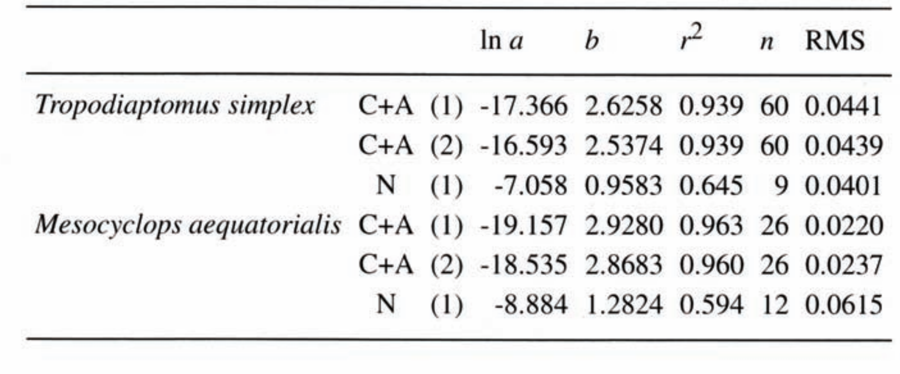


Figure 8. Bacterial production in relation to phytoplankton chlorophyll (calculated from fluorescence) during the cruise in October-November 1995. Different sample series shown with different symbols.

Table 2. Total body carbon to length regressions [ln*W* (µg carbon) = ln*a* + b ln*L*(µm)] for the pelagic copepods of Lake Tanganyika (sample from southern Burundi waters in early May 1995). In regression (1) total length including furcal rami; in regression (2) length without furcal rami. r^2= adjusted coefficient of determination, n= number of carbon determinations, RMS= residual mean square; N= nauplii, C= copepodids, A= adults.



			ln *a*	*b*	r^2	*n*	RMS
Tropodiaptomus simplex	C+A	(1)	-17.366	2.6258	0.939	60	0.0441
	C+A	(2)	-16.593	2.5374	0.939	60	0.0439
	N	(1)	-7.058	0.9583	0.645	9	0.0401
Mesocyclops aequatorialis	C+A	(1)	-19.157	2.9280	0.963	26	0.0220
	C+A	(2)	-18.535	2.8683	0.960	26	0.0237
	N	(1)	-8.884	1.2824	0.594	12	0.0615

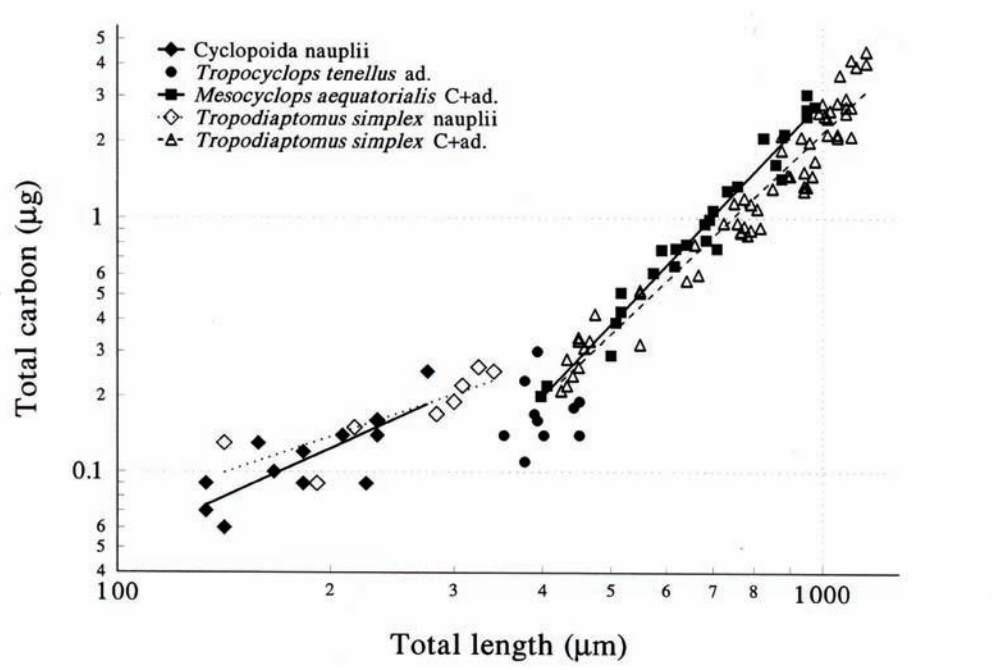


Figure 9. Regressions of individual carbon biomass on total length in the pelagic copepods of Tanganyika based on a sample from southern Burundi waters in early May 1995.

Table 3. Total length and individual carbon biomass (mean ± SD) of the developmental stages of the pelagic copepods in Lake Tanganyika (sample from southern Burundi waters in early May 1995) and total lengths for a sample from Kigoma 6 December 1994. N6 = nauplius 6, C1 = copepodid 1 etc.

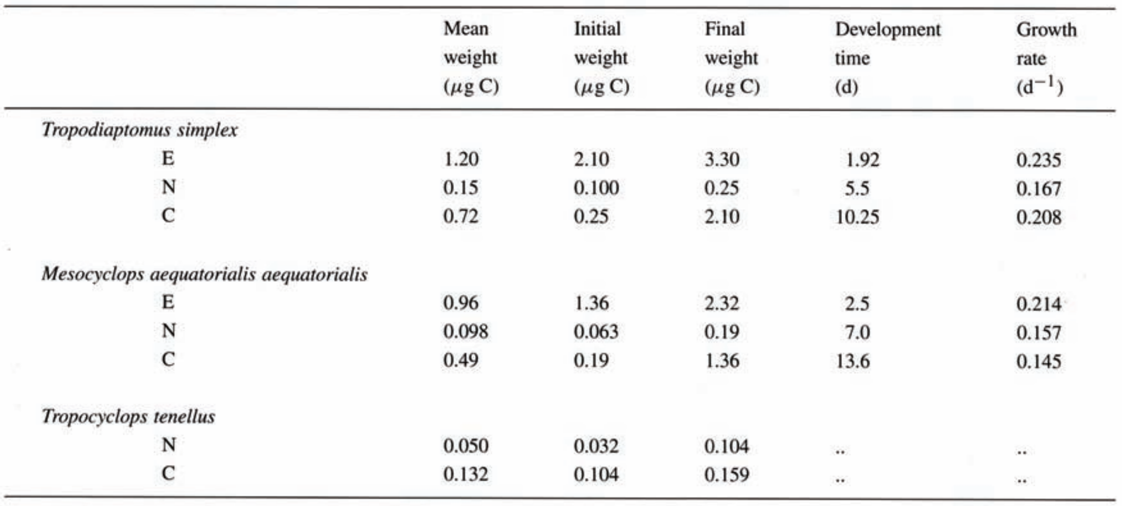
	Stage	Burundi Total length (µm) B	Total carbon (µg) B	*n* B	Kigoma Total length (µm) K	*n* K
Tropodiaptomus simplex	egg	150	0.30±0.07	5	109±5	7
	nauplii	260±68	0.18±0.06	9	297±13 (N6)	4
	C1	448±14	0.29±0.06	10	411±16	5
	C2	550±0	0.45±0.11	3	524±8	3
	C3	660±14	0.65±0.12	3	..	-
	C4	776±24	0.99±0.12	12	765	1
	C5 female	946±11	1.50±0.30	6	..	-
	C5 male	905±64	1.49±0.19	3	879±133	2
	ad. female	1061±56	2.95±0.76	20	1085±50	12
	ad. male	943±84	2.01±0.38	5	931±12	3
Mesocyclops aequatorialis	nauplii	190±46	0.12±0.05	12	248±3 (N6)	4
	C1	402±6	0.21±0.01	2	396±7	3
	C2	500±0	0.29±0	1	489±35	6
	C3	514±5	0.44±0.06	3	573±18	5
	C4	600±21	0.69±0.07	4	626±59	2
	C5	695±42	1.01±0.26	4	737±54	6
	ad. female	908±57	2.28±0.50	8	939±48	7
	ad. male	704±20	1.00±0.21	4	704±32	3
Tropocyclops tenellus	ad. female	418±29	0.18±0.06	7	386±10	7
	ad. male	369±14	0.16±0.06	3	336±6	6
	nauplii	..	..	-	156±5(N6)	2

Comparative tests with 50-μm and 100-μm net hauls off Bujumbura showed that the 100 μm mesh retained all copepodids and adults and most of the nauplii of *T. simplex*, but that most of the small cyclopoid nauplii passed through. In contrast, the 100-μm net seemed more effective than a 50-μm net in capturing the adult copepods. The Limnos sampler was more effective in catching zooplankton than the vertical 100-μm net hauls: off Kigoma, the average abundances of copepodids and adults obtained from the weekly net hauls were 64 % for calanoids, 54 % for cyclopoids, of those obtained from the Limnos samples for the 0-100 m water column. For calanoid and cyclopoid nauplii the corresponding percentages were 54 % and 3 %, respectively.

Off Bujumbura and Kigoma, the volume-specific biomass estimates for *T. simplex* obtained from the vertical migration studies were higher than those from the weekly time series (Table 5).

The biomass values for herbivorous copepods were 1.18, 0.88 and 0.36 g C m^{-2} off Bujumbura, Kigoma and Mpulungu respectively and 0.38, 0.02 and 0.19 g C m^{-2} for predatory copepods. Off Mpulungu, both calanoid and cyclopoid biomass in the weekly series was higher than in the vertical migration series, probably reflecting higher zooplankton abundances in the shallower part of the southern end. For cyclopoids, the large biomass difference between the data sets off Kigoma was caused mainly by the different retention of the cyclopoid nauplii by the 50- and 100- μm meshes.

Table 4. Instantaneous biomass growth rates of the main categories of Lake Tanganyika crustacean zooplankton used in calculating zooplankton production. E = eggs (mean weight and development time refer to an average egg batch, initial and final weights and growth rate to females with developing ovaries); n = nauplii; C = copepodids. For the derivation of different values, see text.



	Mean weight (μg C)	Initial weight (μg C)	Final weight (μg C)	Development time (d)	Growth rate (d^{-1})
Tropodiaptomus simplex					
E	1.20	2.10	3.30	1.92	0.235
N	0.15	0.100	0.25	5.5	0.167
C	0.72	0.25	2.10	10.25	0.208
Mesocyclops aequatorialis aequatorialis					
E	0.96	1.36	2.32	2.5	0.214
N	0.098	0.063	0.19	7.0	0.157
C	0.49	0.19	1.36	13.6	0.145
Tropocyclops tenellus					
N	0.050	0.032	0.104	..	..
C	0.132	0.104	0.159	..	..

For areal biomass estimates the differences between the data sets became even more pronounced, because notable numbers of zooplankton were found deeper than 100 m.

Production and production-to-biomass estimates obtained from the weekly sampling series were likewise biased, because the numbers of nauplii were underestimated. In weekly sampling data for Bujumbura, Kigoma and Mpulungu, the contribution of nauplii to the total calanoid production was 19, 31 and 12 %, and to the cyclopoid production 19, 21 and 17 %, respectively, while the corresponding figures for the vertical migration data were 65, 27 and 14 % (calanoids), and 55, 75 and 43 % (cyclopoids).

For both calanoids and cyclopoids, total areal biomass and production estimates were always highest off Bujumbura, while the order of Kigoma and Mpulungu varied between the data sets (Table 5). This variation precludes further areal comparisons.

T. simplex, cyclopoid nauplii, and copepodids of small cyclopoids were regarded as herbivores, while the copepodids and adults of large cyclopoids were considered carnivores. Thus defined, the production of herbivorous copepods off Bujumbura, Kigoma and Mpulungu was 35.3, 27.3 and 6.5, and the production of predatory cyclopoids was 4.1, 0.3 and 2.1 g C m^{-2} a^{-1}, respectively. The resulting averages for the whole lake 23.0 and 2.2 g C m^{-2} a^{-1} for the herbivorous and predatory copepods, respectively (Table 8). From these figures, annual P/B ratios for the herbivorous and predatory copepods were estimated to be 28.5 and 11.1 a^{-1}, respectively.

A collection of *Limnocnida* specimens of 2-18 mm in diameter yielded an organic dry mass-diameter regression:

$$\log_e(\text{mass [mg AFDM]}) = -5.64 + 2.31*\log_e(\text{diameter [mm]})$$

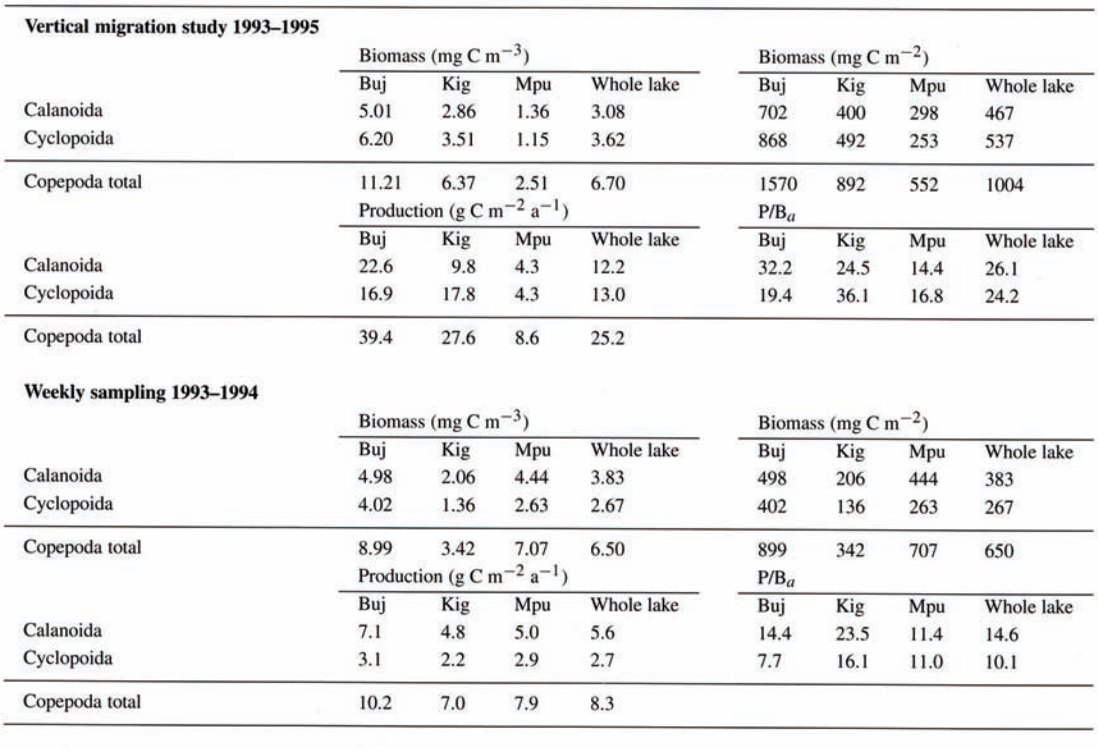
(r^2 = 0.95, n = 29). From this regression the average individual mass of *Limnocnida* off Kigoma in April 1998 was 0.061 mg AFDM (n = 629), or 0.03 mg C. Routine zooplankton counting did not include any size classification of the medusae, and therefore this average value was used to give a rough indication of the potential role of *Limnocnida* in the pelagic system. Biomass-carapace length regression for the shrimp *Limnocaridina parvula* was:

$$\log_e(\text{mass [mg AFDM]}) = -28.205 + 3.828*\log_e(\text{carapace length [µm]})$$

(r^2 = 0.87, n = 49). The average mass of an individual shrimp derived from the length measurement data of five cruises (105 samples) was 0.059 mg AFDM, or 0.03 mg C.

According to the weekly samples the abundance of shrimps increased from north to south (Kurki et al., 1999b; mean abundances in 1993-1995 off Bujumbura, Kigoma and Mpulungu were 2.8, 6.0 and 11.9 individuals m^{-3} in the 0-100 m water column, respectively), while the abundance of medusae was higher in the north (Kurki et al., 1999b; mean abundances in 1993-1995 off Bujumbura, Kigoma and Mpulungu 79, 25 and 25 individuals m^{-3}, respectively). From these figures approximate average standing biomass estimates off Bujumbura, Kigoma and Mpulungu were 237, 75 and 75 mg C m^{-2}, respectively, for *Limnocnida* and 8, 18 and 36 mg C m^{-2} , respectively, for the shrimps. These values suggest a whole-lake mean biomass of 129 mg C m^{-2} for *Limnocnida* and 21 mg C m^{-2} for the shrimps. Especially the latter value may be an underestimate, because of possible net avoidance and because a considerable part of the shrimp population may also have been deeper than 100 m at the time of routine sampling. Indeed, data from five lake-wide cruises (Bosma et al., 1998), collected with oblique hauls of a Gulf V sampler better suited for catching shrimps, resulted in a biomass estimate of 88 mg C m^{-2}. In the cruise material no consistent regional trends in the abundance of medusae or shrimps were observed along the north-south axis of the lake.

Table 5. Average biomass and annual production of crustacean zooplankton in Lake Tanganyika at the permanent sampling localities in the sampling years 1993–1994 and 1994–1995. Buj = Bujumbura, Kig = Kigoma, Mpu = Mpulungu. Vertical migration study: Limnos tube samples, 50 µm mesh, 0–140 m (Bujumbura and Kigoma) or 0–220 m (Mpulungu); Weekly sampling: vertical net hauls, 100 µm mesh, 0–100 m. P/B$_a$ = annual production to biomass ratio.

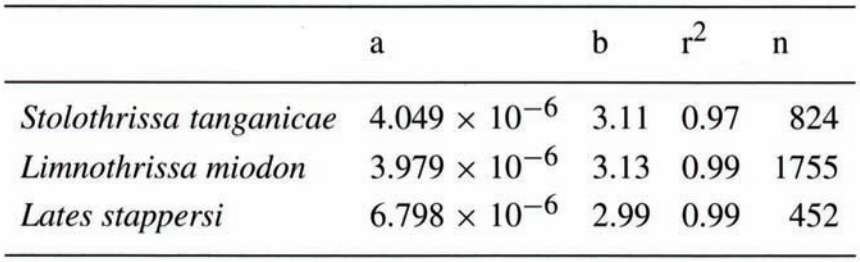


Vertical migration study 1993–1995								
	Biomass (mg C m^{-3})				Biomass (mg C m^{-2})			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	5.01	2.86	1.36	3.08	702	400	298	467
Cyclopoida	6.20	3.51	1.15	3.62	868	492	253	537
Copepoda total	11.21	6.37	2.51	6.70	1570	892	552	1004
	Production (g C m^{-2} a^{-1})				P/B$_a$			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	22.6	9.8	4.3	12.2	32.2	24.5	14.4	26.1
Cyclopoida	16.9	17.8	4.3	13.0	19.4	36.1	16.8	24.2
Copepoda total	39.4	27.6	8.6	25.2				
Weekly sampling 1993–1994								
	Biomass (mg C m^{-3})				Biomass (mg C m^{-2})			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	4.98	2.06	4.44	3.83	498	206	444	383
Cyclopoida	4.02	1.36	2.63	2.67	402	136	263	267
Copepoda total	8.99	3.42	7.07	6.50	899	342	707	650
	Production (g C m^{-2} a^{-1})				P/B$_a$			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	7.1	4.8	5.0	5.6	14.4	23.5	11.4	14.6
Cyclopoida	3.1	2.2	2.9	2.7	7.7	16.1	11.0	10.1
Copepoda total	10.2	7.0	7.9	8.3				

Fish

Growth rates derived from the length frequency analyses (LFA) did not vary much between localities, and both clupeid species had similar growth rates (Figures 10-12). Extrapolation of the LFA growth curves to small fish (length < 40-50 mm) normally not present in the catches is arguable, and to reduce the potential bias, the von Bertalanffy growth curves were here forced to go through zero length at zero age. At least for *Limnothrissa* off Bujumbura the LFA results were reasonably consistent with those from the counting of daily otolith increments (Figure10), but here the lift net catches included high numbers of small fish down to the length of 25 mm. Also off Mpulungu, where even smaller *Limnothrissa* (down to 15 mm length), caught with the beach seines, were included in the LFA estimates, the latter were probably reliable even for the small size groups. For *Stolothrissa*, the length classes < 30 mm were poorly represented in catch samples, making the LFA growth estimates more uncertain. The mass-length regressions of all three species had exponents close to 3.0 (Table 6; Mannini et al., 1996).

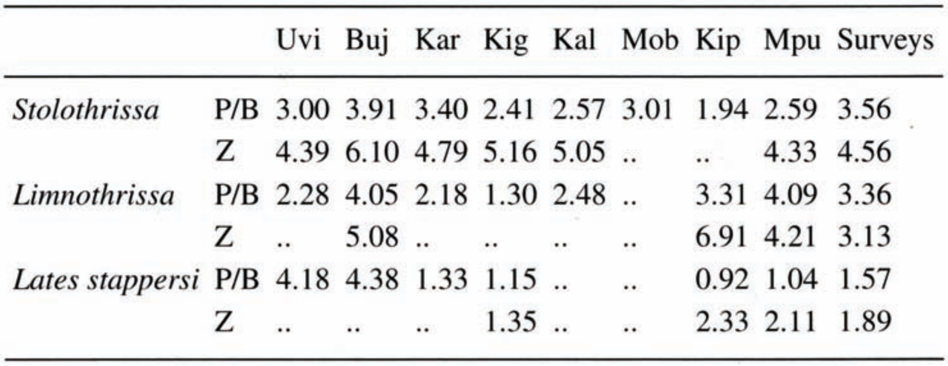
Table 6. Regression of fresh mass on length (mass (g) = a * (total length (mm))^b) for the main pelagic fish species in Lake Tanganyika (from Aro and Mannini, 1995).



	a	b	r^2	n
Stolothrissa tanganicae	4.049×10^{-6}	3.11	0.97	824
Limnothrissa miodon	3.979×10^{-6}	3.13	0.99	1755
Lates stappersi	6.798×10^{-6}	2.99	0.99	452

Because the growth rates declined steeply with increasing fish size, the production to biomass ratios were dependent on the size-frequency distributions of fish, affected by variable fishing and natural mortalities in each area and by ontogenetic migrations of fish. Very high P/B ratios were obtained for *Lates* off Uvira and Bujumbura, because practically only juveniles were caught in these areas. Anomalously low P/B ratios were always linked to a lack of small fish from catch samples (e.g. *Limnothrissa* off Kigoma; Table 7). In *Limnothrissa*, large adult fish occur almost exclusively offshore in the central areas of the lake, and are thus underrepresented in the catch samples, while in *Stolothrissa*, the juveniles (length < 30-40 mm) remain offshore and adults tend to move inshore (Mannini et al., 1996; Mannini, 1998). Therefore, the P/B ratios obtained from the size distributions of catch samples were biased, being too low for *Stolothrissa* and too high for

Table 7. Annual production to biomass ratios (P/B) (data from Mannini et al., 1996) and mortalities (Z; from Mannini et al., 1996) of the main pelagic fish species in different parts of Lake Tanganyika (July 1993 – Dec. 1995; Uvi= Uvira, Buj= Bujumbura, Kar= Karonda, Kig= Kigoma, Kal= Kalemie, Mob= Moba, Kip= Kipili, Mpu= Mpulungu, Surveys= lake-wide trawling cruises 1–5 between June 1995 and February 1998). For details of calculation, see text.



		Uvi	Buj	Kar	Kig	Kal	Mob	Kip	Mpu	Surveys
Stolothrissa	P/B	3.00	3.91	3.40	2.41	2.57	3.01	1.94	2.59	3.56
	Z	4.39	6.10	4.79	5.16	5.05	..	..	4.33	4.56
Limnothrissa	P/B	2.28	4.05	2.18	1.30	2.48	..	3.31	4.09	3.36
	Z	..	5.08	..	..	..	..	6.91	4.21	3.13
Lates stappersi	P/B	4.18	4.38	1.33	1.15	..	..	0.92	1.04	1.57
	Z	..	..	..	1.35	..	..	2.33	2.11	1.89

Limnothrissa (provided that small fish were well represented as off Bujumbura and Mpulungu). Trawl catches during the lake-wide cruises yielded more representative size distributions, but even they did not include the smallest fish (Mannini et al., 1996). Moreover, owing to the limited number of cruises, these size distributions may still have been influenced by the seasonal cohort succession. In spite of these reservations, P/B ratios based on the combined data from all experimental trawl hauls (Table 7) were considered the most reliable, and were chosen for production calculations (Table 8).

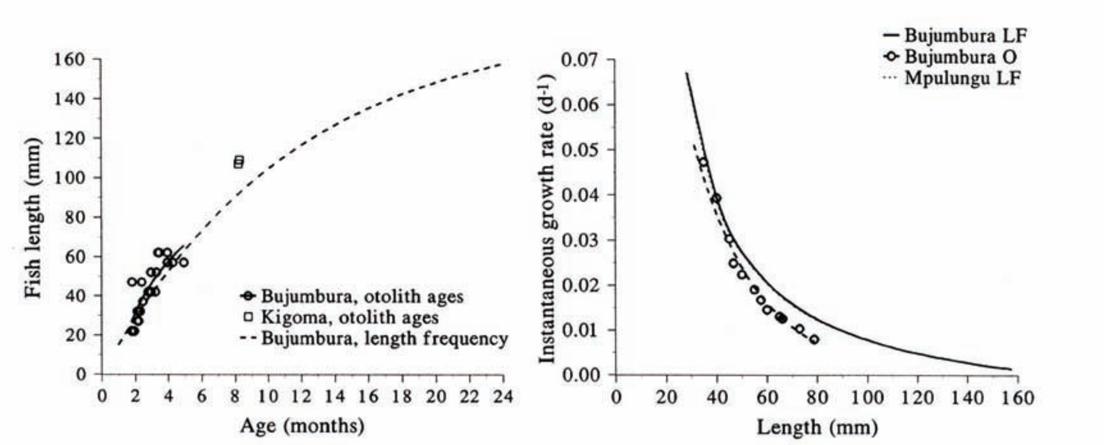


Figure 10. (a) Length growth of *Limnothrissa miodon* off Bujumbura as estimated from the length frequency analyses (Mannini et al., 1996) and from daily otolith increments (Pakkasmaa and Sarvala, 1995). Two otolith-based length-at-age values for larger fish from Kigoma are shown for comparison. (b) Instantaneous length growth rates of *Limnothrissa miodon* off Bujumbura and Mpulungu as estimated from the length frequency analyses (LF; Mannini et al., 1996) and on the basis of daily otolith increments (O; Pakkasmaa and Sarvala, 1995).

In fish populations exhibiting exponential biomass growth, the instantaneous mortality rate equals P/B ratio (Allen, 1971). For all species, the mortality coefficients calculated from the LFA analysis of the commercial catch samples were always higher than the corresponding annual P/B rates (Table 7), but the difference was smaller in the trawl data, especially for *Limnothrissa*. Mortality rates derived from the experimental trawl data (Table 7) were used as P/B ratios to calculate a second estimate of fish production (Table 8).

Table 8. Annual biomass and production at different trophic levels in Lake Tanganyika. For derivation of values, see text

	Biomass $\mathrm{g\,C\,m^{-2}}$	Production $\mathrm{g\,C\,m^{-2}\,a^{-1}}$	%
Phytoplankton	2.4	426–662	100
Bacterioplankton	..	..	20
Herbivorous copepods	0.81	23.0	3.5–5.4
Predatory copepods	0.20	2.2	0.3–0.5
Shrimps	0.09	1.3	0.2–0.3
Limnocnida	0.13	?	?
Fish (clupeids)	0.40	1.4–1.7	0.21–0.40
Fish (*Lates* etc.)	0.18	0.3	0.04–0.08
Fish yield (total)	..	0.5–0.6	0.08–0.14

Hydroacoustic fish biomass estimates for the whole lake were 91193, 175681 and 304463 tonnes in June 1995, November-December 1997 and February 1998, respectively (Szczucka 1998). The observed wide range may reflect seasonal differences, because the catches per haul in experimental trawling were consistent between cruises performed in the same season, i.e. between June 1995 and April 1996, and between November-December 1995 and November-December 1997, respectively (data from Mannini, 1998). The ratio between the acoustic biomass estimate and the mean catch-per-unit-effort in experimental trawling was very similar on all cruises. The overall mean for the hydroacoustic estimates was 190446 tonnes lake^{-1} (58 kg ha^{-1}) or 0.58 g C m^{-2}. According to the five lake-wide trawling surveys (142 hauls, 4592 kg), the contributions of *Stolothrissa tanganicae*, *Limnothrissa miodon*, *Lates stappersi*, other *Lates* spp. and all other species were 56.7, 12.0, 10.7, 12.7 and 7.9 % of total fish biomass, respectively (Mannini, 1998). Using these proportions and the derived P/B ratios, the production of the pelagic clupeids (*Stolothrissa* and *Limnothrissa*) was 1.4-1.7 g C m^{-2} a^{-1} and that of the *Lates* and other mostly piscivorous species 0.3 (0.29-0.34) g C m^{-2} a^{-1}.

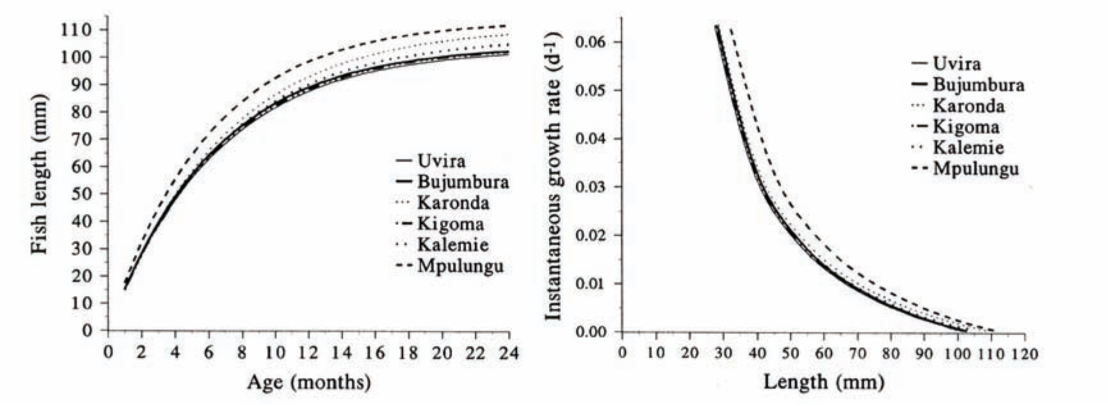


Figure 11. Length growth (left) and instantaneous growth rate relative to length (right) of *Stolothrissa tanganicae* at the main sampling stations. Based on the length frequency analyses by Mannini et al. (1996).

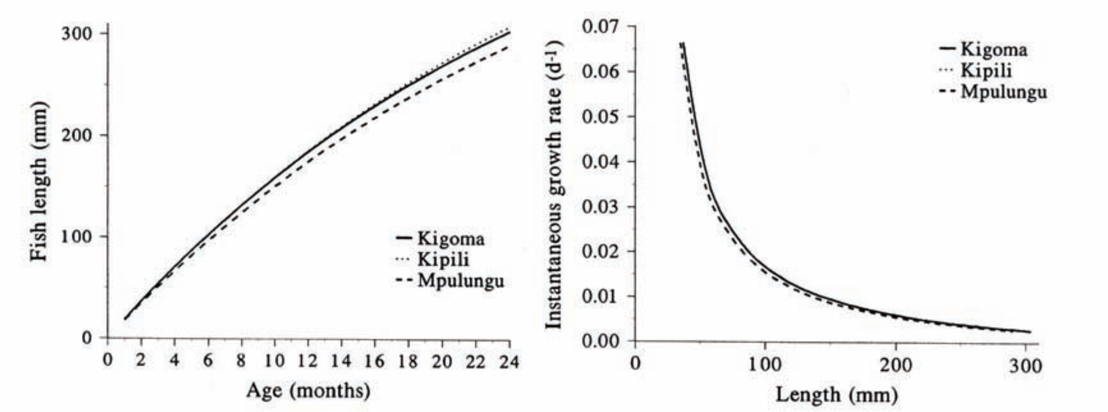


Figure 12. Length growth (left) and instantaneous growth rate relative to length (right) of *Lates stappersi* at three sampling stations. Based on the length frequency analyses by Mannini et al. (1996).

DOC determinations and total community respiration

The mean concentration of DOC varied between 2.2 and 2.9 mg C l^{-1}, and was highest close to the surface (Järvinen et al., 1996). The ampoule technique of DOC determination reduced the background 'noise' to low levels (0.2 mg C l^{-1}). Oxygen consumption by the whole plankton community at 0 and 30 m depth off Kigoma in April 1994 was estimated as 4.3-6.7

mg O_2 m^{-3} h^{-1}. Assuming an RQ of 0.85 (Wetzel, 1983), this corresponds to 1.4-2.1 mg C m^{-3} h^{-1}, or 33-51 mg C m^{-3} d^{-1}. In a 0-50 m water column, representing the fully oxygenated epilimnion, the community respiration would thus be 1.6-2.5 g C m^{-2} d^{-1}. This daily carbon consumption rate is less than 2 % of the DOC storage, but it is almost in balance with the phytoplankton primary production estimated for the season, suggesting efficient carbon cycling and steady state conditions within the epilimnion.

Trophic structure and carbon flows in the food web

Our results enable a reassessment of the trophic structure of Lake Tanganyika (Table 8). Trophic level biomass declined steadily from the phytoplankton primary producers through invertebrate consumers to planktivorous fish and piscivorous fish. The medusae seem to be an important component of the system, although their trophic role is enigmatic, and they can, at least occasionally, harbour photosynthesizing picoalgae (unpubl. observations). The shrimps seem to be mainly herbivorous (the dominant species *Limnocaridina parvula* feeds on phytoplankton, the larger *Macrobrachium moorei* (Calman) on zooplankton; M. Viherluoto, unpubl.). The production figures indicated fairly low carbon transfer efficiencies between trophic groupings (Table 8), especially from phytoplankton to herbivorous copepods (3.5-5.4 %). The ratio of planktivorous fish production to herbivorous copepod production was 6.1-7.4 %, and the corresponding ratio between the piscivorous and planktivorous fish was 20.0-20.3 %. Assuming a production to assimilation ratio of 0.25 for invertebrates and 0.10 for fish (Humphreys, 1979), the food requirements of predatory copepods were 8.8 g C m^{-2} a^{-1} and those of planktivorous and piscivorous fish 14-17 and 2.9-3.4 g C m^{-2} a^{-1}, respectively. Thus, deducting the food consumption by predatory copepods from the herbivorous copepod production and adding the production of predatory copepods and shrimps, the food production available for planktivorous fish was 17.7 g C m^{-2} a^{-1}, well matching the calculated food demand of fish. In contrast, the food consumption estimate for *Lates* and other potentially piscivorous fish was higher than prey fish production. However, these fish are not entirely piscivorous: e.g. in *Lates stappersi*, shrimps and copepods comprise >50 % of the diet (Mannini, 1998). The total fisheries yield in Lake Tanganyika was in the mid-1990s 0.08-0.14 % of pelagic primary production, i.e., within the range of typical values in lakes. In the whole lake, clupeids accounted for about 65 % and the *Lates* species for ca. 30 % of total catch (Hanek, 1994), clupeids (mainly *Stolothrissa*) being more dominant in the north and *Lates stappersi* in the south (Coenen et al., 1998).

Discussion and conclusion

Sources of organic matter: primary production and DOC

Our primary production estimates were 47-128 % higher than the values given for Lake Tanganyika by Hecky and Fee (1981). Although the present values still contain uncertainties, they are based on the largest data base so far available from Tanganyika, including satisfactory seasonal coverage at three stations plus three lake-wide surveys. That the *in situ* measurements gave somewhat lower values than the simulated *in situ* procedure may have a methodological origin. The *in situ* incubations at constant depths are likely to result in an exaggerated surface inhibition of photosynthesis by UV radiation. Incubator measurements used in the simulated in situ method exclude direct UV effects, but the observed vertical chlorophyll distributions incorporate the natural inhibition effect on freely circulating algal cells. The true level of primary production in Lake Tanganyika may thus be closer to the simulated *in situ* results, i.e. the upper bound of our range of estimates.

Dissolved inorganic carbon determinations were not the reason for different production estimates: the DIC concentration calculated by Hecky and Fee (1981) was 6.4 mM (77 mg C l^{-1}), or very close to our determinations (Hecky and Bugenyi 1992 reported 5.88 mM or 70.6 mg C l^{-1}). However, the primary production estimates of Hecky and Fee (1981) were based on a shallower water column and included only the particulate production, while our results comprised both particulate and dissolved production. Irrespective of whether the so-called dissolved production derives from true algal exudates or is partly a methodological artefact (discussed by e.g. Baines and Pace, 1991), ignoring it may lead to a major underestimation of the total primary production.

Our results for the concentration of DOC were within the ranges given for Tanganyika by Hecky (1991, based on Hecky et al. 1978; around 2-5 mg l-1 or 150-400 µM l^{-1}) and Degens et al. (1971). Our new measurements thus confirmed the relatively low DOC levels in Tanganyika. The much higher and unusually variable DOC values (13.5-43.5 mg C l^{-1} in the epilimnion) reported by Degens and Ittekkot (1983) seem unreliable. Considering the general water quality in the lake, low DOC levels sound realistic, and do not suggest a major role for DOM in the planktonic food web. This conclusion is supported by our preliminary oxygen consumption values that were lower than those given by Hecky et al. (1981: 9.4-13 mg O_2 m^{-3} h^{-1}) and did not require any large additional inputs of organic matter besides phytoplankton production.

Zooplankton biomass and production

The present estimates for zooplankton biomass and production were only half of those earlier given for Lake Tanganyika by Burgis (1984: biomass 2 g C m^{-2}, production 50 g C m^{-2} a^{-1}), but very similar to those reported from Lake Malawi (Irvine and Waya, 1999) and Lake Awasa (Mengestou and Fernando, 1991). Also, our average figures for the whole Lake Tanganyika were not far from the estimates presented by Kurki et al. (1999a: biomass 2.3 g dry mass m^{-2}, production 28 g C m^{-2} a^{-1}), based on the same original abundance data, but derived from literature-based individual biomass and production-to-biomass ratios. Our biomass calculations, in contrast, were based on own carbon determinations, and production was calculated by developmental stage using literature-derived but locally checked development times. The resulting P/B ratios (24-26 a^{-1}) did not differ much from those obtained for copepods in Malawi by Irvine and Waya (1999) (31 a^{-1}), or from those used by Burgis (1984) and Kurki et al. (1999a: 23-29 a^{-1}).

The present abundance data had a good temporal coverage with short-interval samples of crustacean zooplankton for two successive years, but regional coverage was low with only three sampling areas. However, data from four lake-wide cruises in June 1995 - April 1996, comprising 7-27 stations, showed no consistent regional differences in zooplankton abundance (Kurki, 1998); the average values were still lower than our figures. Starting from the second sampling year, within-site variation was reduced by taking three replicate vertical hauls on each sampling occasion. The variability between the successive samples from each locality was also reasonably small (Kurki et al., 1999a). However, abundance estimates from the weekly sampling suffer from at least two sources of bias. First, as shown by the vertical migration study (Vuorinen et al., 1999), some of the crustaceans were found below the routine 0-100 m net hauls in the morning when these samples were taken. Second, considerable numbers of cyclopoid nauplii and small copepodids could escape through the 100-µm mesh of the vertical hauls. Both biases could be largely circumvented in the production calculations by utilizing data from the vertical migration study, which used tube sampler and a 50-µm mesh net and in which sampling was extended as deep as copepods were found. Although nauplii may contribute relatively little to the copepod biomass, as found e.g. in Lake Malawi (Irvine and Waya, 1995; Irvine, 1995), their growth is a major part of the total production.

Our values of individual carbon contents for the pelagic copepods were in reasonable correspondence with dry mass values published previously for copepods in African lakes. There was one earlier determination from Lake Tanganyika: Burgis (in Chene 1975) obtained for *adult T. simplex* from Burundi waters a dry mass of 5.7 ± 0.5 µg, and for *M. aequatorialis* a value of 3.3 ± 0.4 µg per individual, corresponding roughly to 2.8 and 1.6 µg carbon, respectively. Regressions for *Thermocyclops* sp. adults from Masundire (1994) gave estimates of 0.15 and 0.11 µg carbon for female and male *T. tenellus*, respectively, which are very close to our values. On the other hand, Masundire's regression for *Tropodiaptomus* sp. adults underestimated the biomass of Lake Tanganyika *T. simplex* (predicted individual carbon values were 1.64 and 1.19 µg for females and males, respectively). Likewise, the equation for Lake Malawi *T. cunningtoni* (Irvine and Waya, 1995, 1999) underestimated the size of the Tanganyikan *Tropodiaptomus* (predicted carbon for females 1.82 µg C). In *M. aequatorialis*, biomass estimates derived from the regressions for this species in Lake Malawi (Irvine and Waya, 1995, 1999) were clearly lower than our observations; this may have been because the exponent in this equation seems unrealistically low. Individual biomass values derived from the general copepod mass-length-regressions (Bottrell et al., 1976) were not far from our observed values. These comparisons show, however, that even estimates derived from the mass-length regressions of closely related or the same species from a different lake may be tens of percents in error compared to the real values. Thus, it is always advisable to obtain at least a few own dry mass or carbon determinations to check the correct levels.

Possible regional or temporal differences in the individual biomasses within the lake could cause additional error in our estimates. However, at least the linear dimensions of different developmental stages of copepods obtained from a sample off Kigoma in December 1994 tallied well with those from the Burundi sample (Table 3). The carbon values obtained for the Burundi sample were therefore used for the whole Tanganyika as the most representative values available.

The individual biomass values used in our calculations differed somewhat from those adopted by Kurki et al. (1999a). For calanoids the difference was minor, but for cyclopoids the values of Kurki et al. (1999a) probably lead to slight overestimates of the biomass, or, if the proportion of the small species among the cyclopoids is large, to great overestimates. Our carbon content values are the most accurate biomass measures available for Lake Tanganyika zooplankton. However, our final biomass estimates remain rough, because the routine counting procedure did not distinguish between different copepodid or naupliar stages, and the large and small cyclopoid species were not differentiated during the first sampling year.

All uncertainties notwithstanding, the close correspondence between the biomass and production figures obtained here and by Kurki et al. (1999a) is encouraging, because it shows that calculations using literature-complemented parameters may result in realistic zooplankton production figures. This was not unexpected, because the major errors in zooplankton production studies derive from the precision of field abundance data. Possible errors owing to stage-specific or length-specific individual biomass differences or to variation in temperature-specific stage durations are generally small compared to the sampling variation of abundance. Therefore, in zooplankton production studies, it is advisable to invest most of the labour in obtaining reliable field estimates of abundance, because accurate abundance estimates will reduce most of the total error variance. Counting should also be done to the finest possible taxonomic and ontogenetic resolution, or size distributions directly measured to enable reliable biomass conversions.

Fish production and yield

The average production-to-biomass ratios of fish derived from our length-frequency analyses (Table 7) were roughly similar to the annual values calculated by Coulter (1981) for *Stolothrissa* in the northernmost part of the lake (3.9 from the graphical Allen curve method, and 3.7 from mortality rate, assuming von Bertalanffy type growth). Thus, the intensified fishery seems not to have caused any changes in fish growth. However, growth and mortality estimations using LFA are always somewhat suspect, although our results were in good correspondence with earlier analyses and for *Limnothrissa* were supported by otolith readings (Kimura, 1995; Pakkasmaa and Sarvala, 1995; H. Ahonen, unpubl.). However, for *Stolothrissa*, the otolith studies by Kimura (1995) in southern Tanganyika and by H. Ahonen in central Tanganyika (unpubl.) both indicated faster growth than our LFA analysis. Further work utilizing daily otolith increments is clearly needed to confirm the observed growth patterns of fish.

As anticipated from the growth and longevity characteristics, *Stolothrissa* had the highest and *Lates stappersi* the lowest P/B ratio. However, the difference between *Stolothrissa* and *Limnothrissa* was smaller than expected: while both clupeids had roughly similar growth rates, *Stolothrissa* has a lower maximum size and shorter longevity, and should thus have a clearly higher P/B ratio. Indeed, the total mortality deduced from the cruise data was higher, and this value may be closer to the true P/B ratio for *Stolothrissa*. In *Limnothrissa* and *Lates stappersi* the P/B ratios and mortality values were satisfactorily consistent, suggesting that they were reliable.

Our fish biomass estimates were lower than previously published values for Lake Tanganyika which show wide variation. Biomass estimates obtained from FAO hydroacoustic surveys in 1973-1976 (Chapman et al., 1978; Coulter, 1991) varied from 211 to 1237 kg ha^{-1}, of which the largest value seems unrealistically high. Roest (1977), using catch samples and acoustic estimates in Burundi waters, ended up at an estimate of 160 kg ha^{-1} for *Stolothrissa* alone. Extrapolating from catch statistics in heavily exploited areas in the north and south, Coulter (1977) estimated the virgin pelagic fish biomass in the north end of Tanganyika at 32-45 kg ha^{-1}, which is only one fourth of the value of Roest (1977). Fish biomass values calculated with the ECOPATH model from a trophic analysis of the pelagic system in the Burundi sector (Moreau et al., 1993) were 63-181 kg ha^{-1} for the planktivorous fish and 37-102 kg ha^{-1} for the piscivorous fish in the early 1980s and the mid-1970s, respectively. Converted to carbon units, the corresponding production estimates were 3.2-7.9 and 0.3-0.7 g C m^{-2} a^{-1}, or higher than our estimates. The P/B ratios applied by Moreau et al. (1993), based on Moreau et al. (1991), and the fish yield figures used as the starting point for the ECOPATH model were also somewhat higher than ours. Interestingly, according to recent acoustic estimates (Menz et al., 1995), the average pelagic fish biomass in Lake Malawi was 70 kg ha^{-1}, i.e. close to the value adopted here for Tanganyika.

Our fish production estimates can be compared to the realized catch. It is admittedly difficult to obtain reliable catch statistics from a large lake like Tanganyika, where artisanal fisheries take the majority of the catch. However, the recorded total catches from Tanganyika show a clearly increasing trend. Coulter (1977) reported an annual fish yield of 73000 tonnes in the late 1960s and Roest (1992) estimated 85000 tonnes for 1987. According to the most recent and probably the most accurate lake-wide statistics produced during the LTR project, the total catch was 167000 metric tonnes (or 51 kg ha^{-1}) in 1992 (Hanek, 1994; Coenen, 1995), and 196570 tonnes (60 kg ha^{-1}) in 1995 (Coenen et al., 1998). In 1992, the catch amounted in Burundi waters to 94.5 kg ha^{-1} yr^{-1}, in Zambia to 69, in Tanzania to 60 and in Zaire to 34 kg ha^{-1} yr^{-1} (Hanek, 1994); for 1995 the corresponding figures were 111.5, 53, 40 and 62 kg ha^{-1} yr^{-1}, respectively (Coenen et al., 1998; the Zambian figure came from the year 1994).

Although the present catch figures are the highest so far reported from Lake Tanganyika, they still remain clearly lower than the potential yield levels of 380000-460000 tonnes (116-140 kg ha^{-1}) per year postulated in previous papers (e.g. Coulter, 1977). However, the final potential yield estimate of Coulter (1977), 100 kg ha^{-1} yr^{-1}, is close to the present realized yield in Burundi, where the fishing pressure is highest. There, the catches per unit area have in fact decreased since 1967-1971 (Coulter, 1977). During the 1990s, Coenen et al. (1998) recorded declining trends in the catch per unit effort in the industrial fishery in all areas studied and in the lift net fishery in Tanzania. On the other hand, increasing unit catches were noted for apollo units in Burundi where this type of fishery was gradually replacing the industrial fishery. These trends suggest that sustainable catch levels are lower than previously thought. This is also supported by calculations based on the observed zooplankton production, which is lower than previous estimates. Moreover, because the primary production in Tanganyika is mainly dependent on internal nutrient cycling and mixing regimes, productivity in the large central open area may be lower than along the coasts (Ostrovsky et al., 1996). In 1995, the realized catch of the planktivorous fish was in the whole lake 23-28 %, and in the most heavily fished Burundi waters 43-52 % of the estimated production; for piscivorous fish in the whole lake the catch was 61-73 % of the calculated production. These figures suggest that the present fishing pressure in Lake Tanganyika is very high; normally only 20-25 % of fish production can be taken as fisheries yield (Houde and Rutherford, 1993).

Carbon flows and the trophic structure

A new view of the trophic structure of Lake Tanganyika is emerging from our data. Our phytoplankton production and carbon biomass figures are higher than the earlier estimates (primary production: Hecky and Fee, 1981; the annual mean phytoplankton biomass reported by Hecky and Kling (1987), extrapolated to a 0-40 m water column, would give ca. 50 % lower value than reported here). In contrast, our new zooplankton data indicate lower biomass and production than previously estimated. Thus, contrary to earlier claims (Burgis, 1984; Hecky, 1984, 1991), our data show that, compared to lakes in general (e.g. Pauly and Christensen, 1995), the trophic efficiency between zooplankton and phytoplankton in Lake Tanganyika is low. Likewise, the fish yield seems to be relatively low in comparison with the primary production, as in many other large lakes (Oglesby, 1977; Morgan et al., 1980). According to our estimates, also the fish production in Lake Tanganyika relative to primary production falls within the normal range reported from other lakes (Morgan et al., 1980; Downing et al., 1990). The suggested role of bacterioplankton compares well with the literature (Cole et al., 1988; White et al., 1991).

High carbon transfer efficiency from phytoplankton to zooplankton (17 %), suggested by Burgis (1984) for Tanganyika, was strongly dependent on a large correction factor for the filtration efficiency of the coarse plankton nets used, and her zooplankton production estimate may well be inflated. On the other hand, Hecky et al. (1981) obtained an unusually high transfer efficiency from phytoplankton production to fish yield (0.45 %). However, the fish yield figure they used (125 kg ha^{-1} a^{-1} or 1.3 g C m^{-2} a^{-1}; Coulter, 1977) represented only the small intensively fished areas in the northern and southern ends of the lake. Both transfer efficiencies were also dependent on the primary production estimate of Hecky and Fee (1981:

290 g C m^{-2} a^{-1}), which may have been an underestimate, as discussed above. For the 1970s, the ECOPATH analysis of the pelagic system in the Burundi waters (Moreau et al., 1993) likewise suggested very high transfer efficiencies from phytoplankton to zooplankton (25 %), to planktivorous fish (2.4 %) and to fish yield (0.36 %). For the 1980s, the calculated efficiencies were clearly lower (13, 1.1 and 0.2 %, respectively), but still higher than our results, especially for the herbivorous zooplankton and fish yield.

It is tempting to speculate that the differences observed between the published values and our new biomass and production estimates for the different trophic groupings might represent real changes in the pelagic ecosystem over the years, owing to e.g. intensified fishing or climatic changes. However, none of the earlier estimates are accurate enough to allow definite conclusions about long-term changes, although at least the phytoplankton chlorophyll concentrations seem to have remained largely similar from the 1970s to the 1990s. We hope that the present monitoring program can be continued for several years to produce a long-term temporal series which are so rare in the tropics.

In fact, low production efficiency of the crustacean zooplankton is not unexpected in a deep, clearwater tropical lake with high epilimnion temperatures. Low efficiency would result from high respiration costs owing to the high temperatures, and/or from the costs of the long vertical migration enforced by the high predation pressure by fish in the clear pelagic waters. Low efficiency of zooplankton production was likewise found in Lake Malawi (Irvine and Waya, 1999), which resembles Tanganyika in many respects. However, similarly low transfer efficiencies have been reported from Lake Michigan (Sprules et al., 1991), which suggests that low efficiency may be a general feature of all deep, oligotrophic lakes. Low phytoplankton densities increase feeding costs and decrease growth rates, tending to diminish the role of cladocerans that are the most productive zooplankton crustaceans. The microbial loop may also have a prominent role in the pelagic food web of oligotrophic systems (Weisse and Stockner, 1993; but see Riemann and Christoffersen, 1993 for opposite view). This leads to inflated respiration costs to the extent that such systems act as net sources of carbon dioxide to the atmosphere (del Giorgio et al., 1996). High dependence of primary production on nutrient regeneration, as in Lake Tanganyika (Hecky, 1991), implicitly suggests low efficiency of carbon transfer through the food web, because nutrients are mainly regenerated by the microzooplankton, which have high respiration rates. Thus, in Lake Tanganyika, the temporally and regionally variable nutrient inputs from the huge hypolimnetic store, through long-range transport via atmosphere, and from the land runoff are not only crucial to the absolute levels of production, but, by modulating the role of the microbial loop, they may also affect the efficiency of carbon transfer through the system.

The estimated carbon transfer efficiency from crustacean zooplankton to planktivorous fish was lower than the values reported from Lake Malawi between herbivorous zooplankton and their predators (invertebrates and fish larvae; Allison et al., 1995). The efficiency at this step in Tanganyika may be affected by the fact that part of the fish production is based on deep-water shrimps which may not have been caught quantitatively with the present sampling scheme. The extremely simple food web structure in the open waters of Tanganyika might enhance fish production: the food chain leading to planktivorous fish production is short. The fishery itself has simplified the food web by decimating piscivorous fish stocks at an early stage of the commercial fishery (Coulter, 1970). On the other hand, a low production efficiency can be expected in a high-temperature environment (Edwards, 1984). In Tanganyika, the upper, almost anoxic layers of hypolimnion may provide zooplankton with a partial refuge from fish predation. This combined with the energetic costs of extensive vertical migrations, necessary in order to avoid piscivorous fish, may lead to a relatively low efficiency of planktivorous fish production. It should be noted that, in spite of the high temperatures, the growth rate of the pelagic clupeids in Tanganyika is in fact low compared with the growth of the specialist planktivorous fish in some cool-temperate northern lakes (e.g. vendace (*Coregonus albula*) in Lake Pyhäjärvi, SW Finland; Sarvala et al., 1994).

We thus conclude that the trophic efficiencies in the pelagic food web of Lake Tanganyika are not unusually high. The crustacean zooplankton production is small, but the recorded fish yields quite normal relative to the measured primary production of pelagic phytoplankton. Thus, as in Lake Pyhäjärvi in southwest Finland (Sarvala et al., 1998), the flourishing fisheries in Lake Tanganyika are not so much based on any exceptional productivity of the system, but on the fact that most of the pelagic production is channelled into a few fish species that have short life cycles and rapid reproduction. Those fish are furthermore easy to catch and thus suitable for an economic fishery.

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Chapter 9

Climate change versus productivity in Lake Tanganyika: cases fish and primary production

Based on:

Sarvala, J., Langenberg, V. T., Salonen, K., Chitamwebwa, D., Coulter, G. W., Huttula, T., Kanyaru, R., Kotilainen, P., Makasa, L., Mulimbwa, N. and Mölsä, H., 2006. Fish Catches from Lake Tanganyika mainly reflect changes in fishery practices, not climate. *Verh. Internat. Verein. Limnol.* 29 (2006): 1182-1188.

and;

Sarvala, J., Langenberg, V. T., Salonen, K., Chitamwebwa, D., Coulter, G. W., Huttula, T., Kotilainen, P., Mulimbwa, N. and Mölsä, H., 2006. Changes in dissolved silica and transparency are not sufficient evidence for decreased primary productivity due to climate warming in Lake Tanganyika. *Verh. Internat. Verein. Limnol.* 29 (2006): 2339-2342.

Abstract

Recently it was claimed that increase in regional temperature, related to global climate change, has resulted in substantial decline in the pelagic fish catches from Lake Tanganyika, East Africa. Surface temperatures of Tanganyika indeed show warming trends, but evidence for decreased productivity is ambiguous, and no overall decline in fish catches has been documented. In contrast, total lake-wide fish catches increased up to 1995; regional declines reported for industrial fishery have been compensated by lake-wide increases in artisanal catch. We conclude that the present evidence is not sufficient to demonstrate the effects of climate change on fish stocks. Evidence indicates rather that fishery intensification has been the major factor.

Keywords: Lake Tanganyika, climate change, pelagic food web, fish catches, fishery yield.

Résumé

Il a été suggéré récemment que l'augmentation de la température régionale, en relation avec le changement global du climat, ait provoqué une diminution substantielle des captures de poissons pélagiques du lac Tanganyika, Afrique Orientale. Bien que les températures superficielles du Tanganyika démontrent des tendances à la hausse, une chute dans la productivité n'a pas été prouvée et les captures totales du lac n'ont pas diminué. Bien au contraire, les captures globales ont augmenté jusqu'en 1995; les diminutions localisées des pêcheries industrielles ont été compensées par des augmentations globales des captures de la pêche artisanale. Nous considérons donc que les données disponibles ne permettent pas la conclusion de l'effet d'un changement de climat sur les stocks de poissons. Il semble plutôt que l'intensification de la pêche en soit le facteur principal.

Mots clés : Lac Tanganyika, Changement de climat, Intensité de la pêche, Production.

Introduction

Current global warming models predict increases in mean annual air temperature of 1.4–5.8ºC over the next 50–100 years (IPCC 2001), with similar increases in the temperature of aquatic systems. Temperature is a key environmental factor directly controlling growth, metabolism and reproduction in all organisms. Temperature may also have indirect effects, e.g. by altering patterns of stratification in lakes it may impose changes in their ecology.

Clear cases of ecosystem effects arising from temperature increases have been documented in several marine areas (e.g. Beaugrand and Reid, 2003; Beaugrand et al., 2003; Edwards and Richardson, 2004). Examples of climate-driven changes in temperate lakes also exist (Straille, 2002), but information on tropical lakes is scanty. Two recent papers on the tropical Lake Tanganyika (Verburg et al., 2003; O'Reilly et al., 2003) based on the same historical data, reported a 0.5–0.7ºC increase in regional air temperature over the last 100 years in the Tanganyika area, with corresponding increases in water temperature. This was postulated to relate to global climate change.

Both Verburg et al. (2003) and O'Reilly et al. (2003) suggested that higher temperatures and lower wind stress have resulted in increased stability of the water column and sharpening of the vertical temperature gradient. The increased stability was thought to diminish mixing of hypolimnetic nutrients into the euphotic zone and consequently to decrease primary productivity. O'Reilly et al. (2003) found support for this suggestion from the changing stable carbon isotope ratios of organic matter of algal origin in sediment cores, while Verburg et al. compared phytoplankton biomass values from different decades. O'Reilly et al. (2003) went further, claiming that decreased productivity, caused by the temperature increase, has already resulted in a substantial decline (30–50%) in pelagic fish catches from Lake Tanganyika. This appears to them a concrete example of climate warming diminishing ecosystem productivity, a conclusion that has gained considerable publicity (e.g. Livingstone, 2003; Verschuren, 2003; ENS news, 2003; Khimiya i Zhizn, 2003).

We do not question here the recent warming of Lake Tanganyika and its consequences to stratification (as indicated by Huttula, 1997), although the evidence of rising air temperatures and falling winds in the Tanganyika area has been challenged (Eschenbach, 2004). Critical

analyses of historical meteorological data from East Africa (Hay et al., 2002: two sites north of Tanganyika likewise do not show any significant increases of temperature during the 1900s.
We show here that the analyses of O'Reilly et al. and Verburg et al. are not sufficient to prove a strong causality between lake warming and decreased productivity. In particular, we show that the fishery information presented by O'Reilly et al. is misleading, and that the available fisheries statistics from Lake Tanganyika do not support their conclusions about decreased fish catches due to climate change. Evidence indicates rather that fishery intensification is the major factor affecting the catches. It is important to distinguish the two effects because large populations around Tanganyika depend crucially on its fish, and the four riparian countries are placing hope in rational fisheries and catchment management.

Case: Fish catches

Study area and the fisheries

Lake Tanganyika is the second largest of African lakes (area 32900 km^2, maximum depth 1470 m) and a unique resource for the four riparian countries (Burundi, Democratic Republic of Congo, United Republic of Tanzania, and Zambia). Lake Tanganyika is permanently stratified. However, stratification intensity varies according to seasonal climatic change (being sharper in the wet season when winds are weak) and along the longitudinal lake axis (e.g. Huttula, 1997). Phytoplankton production is to a large extent based on nutrients supplied from the anoxic hypolimnion through various mixing processes (Coulter, 1991). The littoral communities are highly diverse, but the structure of the pelagic food web, mainly responsible for fish production, is very simple (Coulter, 1991; Sarvala et al., 2002 and 2003a).

Lake Tanganyika is renowned for its productive pelagic fishery, which is an important source of protein for millions of people in the surrounding area. About 45000 fishermen are directly engaged in fishing. There are three main types of fisheries in Lake Tanganyika: industrial purse-seines, artisanal lift-nets, and various traditional methods (Coulter, 1991). Most fishing is done at night using light attraction. A typical industrial fishing unit consists of a purse-seiner, an auxiliary vessel for the seine and 3–4 lamp boats. At present, the industrial purse seine fishery targets mainly *Lates stappersi*, the smallest of the four endemic Nile perch species in Tanganyika. It can grow to 50 cm length (Mannini et al., 1996, Mannini 1998) but is typically 30-35 cm in the purse seine catch. With increasing size, *L. stappersi* food shifts from zooplankton to shrimps and finally fish prey. The other large Nile perch species, *Lates mariae*, *Lates microlepis* and *Lates angustifrons*, became sparse soon after the beginning of purse seining in the 1960s, although the deep-living *Lates mariae* is still caught to some extent. *Lates mariae* and *L. angustifrons* feed largely on benthic fish and partly on shrimps and on the small clupeids *Stolothrissa tanganicae* and *Limnothrissa miodon*. *Lates microlepis* is a specialised predator on *Stolothrissa*.

Most of the catch derives from the artisanal fishery in which *Stolothrissa* and *Limnothrissa* compose about 65 %. *Stolothrissa* (12cm max. measured total length in the 1990s; Mannini et al., 1996, Mannini 1998) spends most of its life in the pelagic, feeding mainly on copepod zooplankton and also on shrimps. *Limnothrissa* contributing 10–15 % of the pelagic catch can grow to 17 cm total length (Mannini et al., 1996, Mannini, 1998) and feeds on copepods, shrimps and especially on young *Stolothrissa*.

The biological basis of the fishery was investigated in 1992-2001 in a comprehensive ecosystem study "Research for the Management of the Fisheries on Lake Tanganyika" (LTR; Mölsä et al., 1999 and 2002; Sarvala et al., 1999a). The LTR results are here used to evaluate whether climate change has influenced the fisheries of Tanganyika.

Results and discussion

Wind speed data may not be representative.

Wind data used by O'Reilly et al. (2003) came from Bujumbura harbour, Burundi, and Mbala, Zambia. The wind climate at Mbala (situated 40 km away from and 800 m above the lake) may not be typical of winds at lake level in the south. The reliability of the meteorological data series from Bujumbura harbour has not been verified. Thus both data sets must be viewed with caution.

Evidence for decreased productivity is ambiguous

O'Reilly et al. (2003) assume an inverse correlation between weather-induced stratification strength and nutrient loading from the hypolimnion. We have indeed documented such a correlation for confined and momentary upwellings in the very south of the lake (Langenberg et al., 2003), but even at that location more nutrients did not lead to noticeably increased primary production. Highest primary production is found in the northern end of the lake (Sarvala et al., 1999a), while wind-induced mixing is strongest in the south.

Time series for phytoplankton are short and inconclusive. The few existing phytoplankton data from Lake Tanganyika suggest lower biomass in 1998–2001 than in 1975 (Verburg et al., 2003, Vuorio et al., 2003; Sarvala et al., 2003a), thus favouring O'Reilly's et al. reasoning; note, however, that only two points in time can so far be compared. Moreover, the degree of accuracy of phytoplankton biomass counts is rather low, and thus only large differences can be regarded as significant. In contrast, chlorophyll a (Sarvala et al., 1999a; Vuorio et al., 2003) and water transparency (Verburg et al., 2003) – both less prone to variation – remained constant between these periods.

Available data on the abundance of copepod zooplankton, the key prey of the planktivorous fish, do not indicate consistent trends. Few representative data exist, and methodological differences have been large (Sarvala et al., 1999a). Between-region comparisons failed to show a direct connection between low fish catches and food availability. Copepods were most abundant and possibly increase towards the north where clupeid catch-per-effort (CPUE) is low, while copepod biomass is stable and low off Kigoma in mid-lake where clupeid CPUE is similar or higher than in the north (unpublished data).

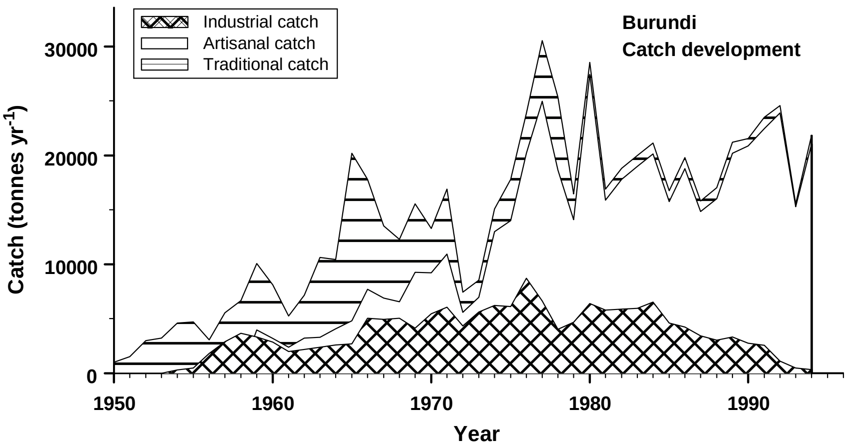

Fig. 1. Development of total fish catch by gear type in Burundi (data source: Lake Tanganyika Research Scientific Sampling Programme Data Archives).

Fishery information is misleading.

O'Reilly et al. (2003) stated that pelagic clupeid catches have declined 30% to 50% since the late 1970s and the contribution of predatory Lates species from 20–60% in the 1950s to 2% after 1977, citing these changes as evidence of a lake-wide shift in ecosystem function. These numbers were evidently derived from the data of Zwieten et al. (2002), covering the period 1956-1992 which relate only to industrial purse-seine catches of clupeids and *Lates* in Burundian waters. They thus represent only a minor percentage of the total lake-wide catch. Industrial catches in Burundi indeed show a decline both in CPUE (Table 1) and total catch since the 1970s (Fig. 1); consequently the industrial fishery in Burundi practically ceased.

These long-term changes were most likely due to the intensifying fishery (Coulter, 1991; Chitamwebwa and Kimirei, 2005; Mulimbwa, 2005), as evidenced by the typical shift in catch composition from large to small fish as shown by Zwieten et al. (2002). In contrast, CPUE (Table 1) and total catches (Fig. 1) in the artisanal fishery increased up to the early 1990s, compensating for the declining industrial and traditional fisheries.

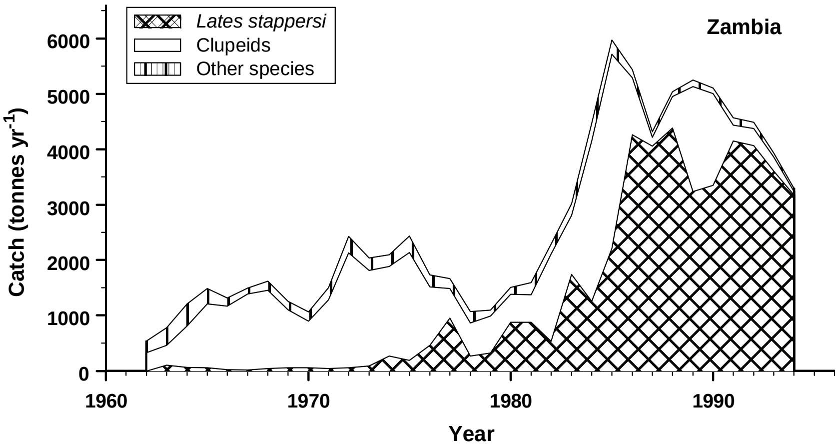

Fig. 2. Development of industrial fish catch by species in Zambia (from Mölsä et al. 2002; data source: Lake Tanganyika Research Scientific Sampling Programme Data Archives).

Although CPUE data from the industrial fishery of Burundi have been successfully used to indicate changes in fish abundance and to study predator-prey cycles (Roest 1992), CPUE rates in a pelagic fishery using light attraction may be only weakly related to true fish abundance, particularly if accompanied by major changes in fishing technologies. For example the increases in CPUE in Burundi mainly reflect the introduction of advanced fishing techniques. Effects of fishery on the fish populations can be more reliably be traced from changes in population structures. Thus in reality the statistics from Burundi show (1) a disappearing traditional fishery, (2) increasing artisanal catches, (3) boom and bust of the industrial fishery, and (4) overall catches increasing up to late 1970s and fluctuating thereafter with no consistent trend (Fig. 1).

At the Zambia end of the lake, industrial catches peaked in late 1980s, followed by declining trends after that both in CPUE and total catches (Fig. 2; Mölsä et al., 2002). Both in Burundi and Zambia, the heavily fished stocks have estimated catch/production ratios of 0.35 for *Stolothrissa* and 0.85-0.87 for *Lates stappersi* (Sarvala et al., 2002). The decreases in CPUE thus likely result from intensive fishing (Table 2), also indicated by the high mortality rates and dominance of small size classes (Mannini, 1998). In Burundi waters in the 1990s, clearly separate *Stolothrissa* cohorts were observed in the catches for only three, or maximally four, months. At a total length of 8-9 cm, each cohort disappeared from the catch, after which fish longer than 7-8 cm were not caught for a month or two until the next cohort reaches this size (Mölsä et al., 2002).

Table 1. Decadal averages of the number of fishing vessels and catch per night and vessel in the industrial (Ind), artisanal (Art) and traditional (Trad) fisheries in Burundi from the 1950s to 1995. Calculated from the national fisheries statitstics of Burundi as stored in Lake Tanganyika Research Scientific Sampling Programme Data archives.

Decade	Fishing vessels			Catch per night and vessel (kg)		
	Ind	Art	Trad	Ind	Art	Trad
1950s	7	22	1461	1116	70	29
1960s	9	168	1508	1392	52	42
1970s	17	413	904	1301	104	40
1980s	19	606	314	959	109	30
early 1990s	13	626	379	326	152	17

Table 2. Decadal averages of fishing efforts indices in Zambia and Tanzania from the 1960s to 1995. Ind = number of Industrial fishing vessels; Art + Trad = number of artisanal and traditional fishing vessels; Out. eng = number of outboard engines; Art. Gear = total number of artisanal fishing gear; Trad. Gear = number of traditional fishing gear. Calculated from the national fisheries statitstics of Burundi as stored in Lake Tanganyika Research Scientific Sampling Programme Data archives

	Zambia		Tanzania			
Decade	Ind	Art +Trad	Art +Trad	Our. eng	Art. gear	Trad. gear
1960s	2	755	3492	…	185	28931
1970s	4	957	6465	102	502	30428
1980s	10	946	5910	222	965	28877
early 1990s	19	1068	3914	274	1495	24644

According to counts of daily otoliths rings (H. Ahonen, unpubl. MS thesis, Univ. Turku, Finland) Stolothrissa were about 3 months old when entering the fishery at 4 cm length and 7 months old just before disappearance from the catches at 8-9 cm total length.

Similar data were reported recently by Mulimbwa (2005) in the Uvira region adjacent to Burundi where fishing intensity is the highest in the lake (Coenen et al., 1998).

Further, the fished waters of Burundi and Zambia together comprise only 15% of lake area, and therefore catch data from these two countries alone are inadequate for the assessment of climate effects on the lake.

The best available fisheries statistics from Lake Tanganyika from the years 1950–1995 (Mölsä et al., 2002) indicated that, contrary to the view of O'Reilly et al. (2003), total lake-wide catches increased up to 1995, or fluctuated around a level of the mid-1980s (Fig. 3). Total catch data for the lake are not available for more recent years, but fisheries statistics from Burundi and Kigoma regions showed no declines of average lift-net CPUE from 1993–1996 to 1999–2001 (unpublished records of the LTR project and the Lake Tanganyika Fisheries Monitoring Program).

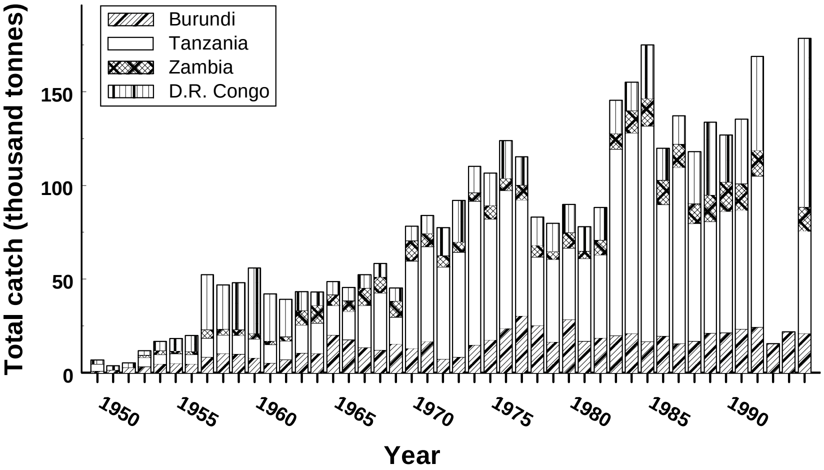

Fig. 3. Development of total fish catches from Lake Tanganyika by country (from Mölsä et al. 2002; data source: Lake Tanganyika Research Scientific Sampling Programme Data Archives; for 1993-1994 total catch data available only from Burundi).

We conclude that the major trends in catches were largely dependent on fishing intensity which, incorporating more effective fishing techniques (larger nets, improved lights, increased motorisation; Table 2), has dramatically increased during the last decades (Tables 1 and 2; Coulter, 1991; Coenen et al., 1998).

We believe that in principle fish production is ultimately dependent upon primary production (e.g. Sarvala et al., 2003b), and thus subject to climate-induced changes. However, the path from the physical and chemical modifiers of productivity to fish yields is complex, and human interventions are great. The present evidence from Lake Tanganyika is not yet sufficient to demonstrate effects of climate change on the fish stocks.

Case: Primary production

Discussion and conclusion

Verburg et al. (2006) comment on our recent paper (Sarvala et al., 2006) in which we concluded that there is insufficient evidence for a climate-driven decrease in productivity in Lake Tanganyika, particularly that observed changes in fish catches mainly reflect changes in fishery practices and total effort, not climate. Their comment focuses on (1) phytoplankton biomass differences, (2) increase of dissolved silica, (3) transparency changes, (4) inadequacy of wind data, (5) paleolimnological 13C data, and (6) changes in fish catches.

We agree with Verburg et al. (2006) on some major deficiencies in the data and interpretation of O'Reilly et al. (2003). First, Verburg et al. (2006) confirm our doubts and those of Eschenbach (2004) on the validity of the wind speed data used by O'Reilly et al. (2003). Second, Verburg (2006) has shown that, when analysed properly, the carbon isotope (δ13C) data presented by O'Reilly et al. (2003) do not indicate a decline in productivity. Third, Verburg et al. (2006) confirm our main message (Sarvala et al., 2006) that the fish catch records from Lake Tanganyika mainly reflect changes in fishery practices, not climate.

Instead, we cannot agree with the arguments of Verburg et al. (2006) that changes in phytoplankton biomass (biovolume), in dissolved silica and in transparency support the idea of declining productivity. We are cautious of their view that the lower phytoplankton biomass observed in 1998-2001 compared to 1975 is evidence of decreased productivity. Recent research has indicated that a large part of the total pelagic primary production in Lake Tanganyika may be due to picocyanobacteria (Salonen et al., 1999, Sarvala et al., 2003, Vuorio et al., 2003, Descy et al., 2005). Because there is no historical information about their proportion in total phytoplankton, it is not feasible to derive productivity trends based alone on phytoplankton densities or biomasses of larger cells. Moreover, picocyanobacteria in Lake Tanganyika contain very little, if any, chlorophyll a, so that routine chlorophyll data cannot either give any historic indication of the development of picophytoplankton biomass. Finally, microscopically derived phytoplankton biomasses are affected by high variations due to sampling, counting and biomass conversion, even if the whole procedure is done by the same person. Consequently phytoplankton biomasses available from Tanganyika supply no evidence of changes in productivity.

Verburg et al. maintain that the increase in silicate concentration would be a valid indicator of decreased productivity. Silicate level seems indeed have increased in Lake Tanganyika during the recent years. Moreover, Alleman et al. (2005) have presented silicon isotope data supporting the view that changes in silicate concentrations in Tanganyika are biologically mediated, i.e. related to diatom abundance. However, changes in silicate concentrations do not yet prove that there have been any productivity changes. They only suggest that diatom abundances have changed, but changes in diatoms can be compensated by reverse changes in other groups, including picocyanobacteria. According to Cocquyt & Vyverman (2005) phytoplankton community composition in the northern part of Lake Tanganyika indeed has changed, but the share of diatoms increased from 1975 to 2002-2003.

Finally, Verburg et al. (2006) claim that transparency in Tanganyika increased significantly between 1913 and 1947, was stable between 1947 and 1975, and increased significantly between 1975 and 1996. In fact Verburg et al. (2003) did not show transparency data for 1996, but based their conclusion for the increase from 1975 to 1996 on light attenuation measurements in 1975 and 1995-1996. However, the underwater irradiance measurements in 1975 and 1995-1996 are not directly comparable. In 1975, a flat cosine PAR sensor was used which measures only downward irradiance, while in 1995-1996 measurements were made with a spherical quantum sensor which receives also scattered light from all directions and therefore gives considerably higher readings under similar light conditions. The actual Secchi depth measurements do not show any increase in transparency after 1946. Based on historical information, Secchi disk visibility was 6 ± 2 m in 1913, 16 ± 4 m in 1946-1947, and 14 ± 2 m in 1975 (Verburg et al., 2003, supporting online information). For comparison, the average transparency measured by the FAO/FINNIDA Lake Tanganyika project (LTR) off

Bujumbura and Kigoma in 1993-1995 was 12 m (n=88) (Sarvala et al., 1999a), and at ten deep-water stations between Kigoma and Mpulungu between 21 and 28 March 1998 it was 13 m (SD 2.2 m, range 11-16 m, n=17; own unpublished data). Thus, there was no increase in transparency neither between 1947 and 1975 nor between 1975 and 1993-1998. This conclusion expressed in our previous paper (Sarvala et al., 2006) was thus based on a comparison of our own measurements with data given by Verburg et al. (2003) (although reference to our own data was unintentionally lacking). Our interpretation of the transparency data is consistent with the chlorophyll measurements which did not either show any significant change between 1975 (Hecky & Kling 1981) and 1995-1998 (Sarvala et al., 1999a; more detailed discussion in Descy et al., 2005). In fact, estimates for primary production obtained with the radiocarbon method were higher in 1995-1996 than in 1975 (Sarvala et al., 1999a), but because of different methods we do not want to emphasise this observation.

It is also necessary to take into account the crude nature of transparency measurements. A large number of Secchi depth readings during the LTR project in the 1990s (Langenberg et al., unpublished information), showed, in line with Salonen et al. (1999), that the results were very dynamic even within hours (maximum variability within 3 hours from 8 to 17 m). In Tanganyika most of the phytoplankton, especially the picocyanobacteria, are in the daytime at a considerable depth (below 10 m, often at 20-40 m; Salonen et al., 1999, Vuorio et al., 2003, Descy et al., 2005), and thus phytoplankton abundance can affect the Secchi depth readings very variably. Strong seasonal variability was also indicated by Verburg et al. (2003, supporting online information, Fig. S3).

In Tanganyika the effects of changes in stratification on plankton productivity are not at all straightforward. Light limitation due to deep mixing may be more important for phytoplankton production than enhanced nutrient availability (Sarvala et al., 1999b). Indeed, higher phytoplankton production was observed when thermocline depth was shallow and the high hypolimnetic nutrient concentrations were close to the euphotic zone (Langenberg et al., 2003). This means that increasing temperatures that lead to shallower mixed layer need not necessarily result in lower productivity.

The effect of climate change on Lake Tanganyika is of world interest, and to the riparian countries its productivity is crucial. For the moment, we feel that the large number and dynamic nature of various bottom-up and top-down factors controlling phytoplankton in Lake Tanganyika tends to impede progress in understanding the possible role of climate change in its productivity changes. We agree with Verburg et al. (2006) that further long-term research using best available methodology is needed to solve this important question, but we maintain the evidence available is insufficient to conclude that climate warming has decreased productivity. Most importantly, however, there seems to be a consensus that climate warming is not yet a major factor limiting fish catches in Lake Tanganyika, which at the practical level means that wise management by the countries surrounding Tanganyika is still of primary importance to the sustainability of the fishery.

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Chapter 10

The problems confronting survival of biodiversity in ancient lakes

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Abstract

The highest lacustrine biodiversity is found in a few, very old lakes. We refer to three outstanding examples. Survival of the unique faunas has to be managed along with vital resource uses. Acceleration of exploitation and catchment development poses urgent problems. We conclude as follows: In these lakes the current paradigm of "sustainability" is not adequate to ensure species survival, so maintenance of genetic resources requires other approaches. The species (and the lakes) vary widely in vulnerability to anthropogenic pressures. Refuges comprising suitable areas of lake and adjacent catchment appear to function effectively if financed and managed. Success in this will depend largely on the extent to which cost-benefit perspectives are international.

Keywords: Ancient Lakes, Biodiversity, Conservation, Development, Reserves, Coastal Management Zones.

Résumé

La plus grande biodiversité lacustre dans le monde a été observée dans quelques lacs très anciens. Nous considérons trois exemples typiques. La survie de faunes uniques doit être gérée simultanément à l'utilisation rationnelle des principales ressources. L'accélération de l'exploitation et le développement des bassins versants causent des problèmes urgents. Nous concluons : pour ces lacs, le paradigme de pérennité n'est pas adéquat pour assurer la survie des espèces. Par conséquent, le maintien des ressources génétiques nécessite d'autres approches. Les espèces (et les lacs) varient considérablement dans leur vulnérabilité aux pressions anthropogènes. Des refuges occupant des zones appropriées des lacs et de leurs bassins versants semblent fonctionner de manière efficace, une fois financés et gérés. Leur succès dépendra principalement de la nature internationale des perspectives coût-bénéfices.

Mots clés:
Lacs anciens; Biodiversité; Conservation; Développement; Réserves; Zone côtière aménagée; Conservation et développement.

Introduction

By far the highest biodiversity in lakes occurs in a very few ancient basins (Martens et al., 1994; Rossiter and Kawanabe, 2000; Kawanabe et al., 1999; Knaap and Munawar, 2004). Remarkable and unique faunas have evolved in these. For example, for Lake Tanganyika of the 1400 described animal and plant species half are endemic (Coulter 1991). In this paper we refer as particular examples to the great Rift Lakes, Baikal in Russia, and Tanganyika and Malawi in Africa.

Considerable advances have been made in recent decades by national and internationally-assisted research on the biota and their evolution; biodiversity conservation, human impacts and social issues have also been studied (Lindqvist et al., 1999; Ribbink et al., 2001; Timoshkin, 2001; West, 2001; Lowe-McConnell, 2003). Major changes have occurred, and important long-term trends are evident in the past 50 year. Catchment development and agriculture expansion have caused erosion, siltation and pollution (Cohen et al., 1996; Kozhova and Izmest'eva, 1998; Allison et al., 2000). In L. Baikal and Tanganyika, there are direct urban and industrial inputs. In Africa in general, steep rises in fishing effort are related to soaring human populations.

Here we are concerned less with describing changes and threats in the ancient lakes (key references are given), than with proposing certain concepts we believe are presently important.

The deep Rift Lakes Baikal, Tanganyika and Malawi, are a huge, world-scale, water resource (probably over a third of all unfrozen freshwater). They are located strategically to supply dense populations. Water quality is closely linked to ecosystem health and biodiversity. The vital importance of these facts to humanity in this century does not seem well appreciated.

Conservation and development

We suggest three major flaws exist in common approaches to conservation and development in the ancient lakes.

1. Economic and demographic driving forces render management theory largely irrelevant.

In the Tanganyika and Malawi basins, rational planning has continually been outpaced by the growing momentum of rapid demographic increase and consequent spread of intensive development. Important are the kinds of catchment development and fishing that takes place under subsistence regimes. Both are driven by growing, labour-intensive under-capitalised effort, not restrained by considerations of sustainability. In fact, exploitation tends to persist well beyond an economic cut-off point (Coulter, 1999). The results for the lakes are accelerated siltation and overfishing, occurring most acutely in near-shore zones where biodiversity is highest (Cohen et al., 1996; Rossiter and Kawanabe, 2000). Long-term trends indicate that subsistence activities will in all likelihood continue to intensify, leading to resource depletion followed by extinction of species. In these circumstances, sustainable development theory becomes irrelevant.

In Lake Baikal, providing that industrial and urban inputs can be diminished, the major concern is to ensure high standards of catchment management. Important aspects are the control of fires and of tree felling around the lake, especially in the parks and reserves, along with mitigation of agricultural disturbance effects. Currently, there are economic constraints in maintaining the parks and reserves.

2. Lack of continuity

More international interest in the ancient lakes is needed to ensure survival of their biota. This paper is addressed to SIL because we believe independent scientists play an important role in the fate of ancient lake biodiversity. The interest of politicians, development policy makers and international donors is usually temporary in nature. The duration of their involvement in a policy or project may be merely the interval between successive elections, thus implementation is often frustrated by lack of continuous commitment. Commonly, crisis management takes the place of long-term policy. In consequence, many internationally assisted projects that are excellent in intent and achievement have poor follow-up and therefore weak outcomes with little real progress made.

At a local level, trained personnel responsible for management and/or research are confused and often lose commitment to project objectives by interruptions and switches of policy and financing. Moreover, conservation is vulnerable to shifts in fashions of thinking, and in the past decade socio-economic utilitarian views have become predominant (Coulter, 2003).

3. Attempted reconciliation of competing interests by non-viable compromises

A widespread view exists that conservation must go hand-in-hand with development, even in such sensitive diversity hotspots as the ancient lakes. It has now become almost axiomatic that conservation should be associated with development in a process called “sustainable development” (for review see Lee, 2001). We suggest that this concept, which is ambiguous and manages to identify two distinct aims with an ideal outcome, is inappropriate in the context of the ancient lakes. It will not ensure survival of their faunas.

It is difficult for the lake countries to give priority to biodiversity where it is of little economic importance. The short term linkages between biodiversity and the livelihoods of local people are weak, financial benefits from conservation seem limited, and consequently ecosystem degradation is not perceived as a problem. Therefore, integrated conservation and development programmes that are self-sustaining are not feasible.

In general, belief in development theory based on exploitation dynamics has given place to self-management concepts by ‘empowerment of resource-users’ through ‘community participation’ and ‘livelihood security’. Management driven by such social paradigms depends essentially upon political considerations (Lowe-McConnell, 2003). The dangers in persisting with these expedient concepts unsupported by secure evidence are obvious. Meanwhile, there is a plethora of (expensive) planning, but a dearth of implementation.

Strategies

Evidence indicates (Ribbink et al., 2001; Cohen et al., 1996; Coulter, 1999; Coulter and Mubamba, 1993) that it is possible to conserve representative habitats and faunal assemblages in these large lakes by setting aside refuges or reserves (including vital sectors of catchment), provided that pervasive gross pollution is controlled and ecologically harmful species are not introduced. This proviso points up the need for general management measures to maintain lake health outside the reserves. The Lake Malawi Cape McClear National Park, established over 30 yr, demonstrates a case where a complex littoral fauna may remain apparently unaltered by intensive fisheries further offshore; habitat specialization results effectively in separate faunal zones (A. Ribbink pers.comm.).

A recent assessment of biodiversity in L. Tanganyika (Allison et al., 2000) considered three general conservation strategies - direct protection (lake reserves), economic substitution (promoting alternative livelihood activities) and linked incentives (e.g. eco-tourism). The assessment recommended that conservation strategy should be based primarily on maintaining and extending existing land/lake parks, while admitting that funding to support reserves will almost certainly have to come from external sources. The socio-economic part of the same study takes the view, that biodiversity will only be managed by poverty alleviation and livelihood diversification.

The Baikal administration distinguishes between parks (controlled public access) and reserves (primarily conservation), but together they constitute a core system of ecological refuges which should go far to ensure survival of this acknowledged World Heritage – provided the refuges are managed well.

In the Tanganyika study (Allison et al., 2000), it was proposed to adopt principles of coastal zone management (CZM) to provide integrated conservation and development regimes outside the reserves. In such a scheme, appropriate protection would be given to specific areas within a wider strategy including human-development needs. Policy in each CZM area would differ according to development opportunities (e.g. fishing), or proximity to population centres, or if they border conservation reserves. But the major goals in a CZM area would be reconciliation of different interests.

Conclusions

The concept we advance for the survival of these ancient endemic biotas is two-fold:

(i) setting aside core conservation areas of representative habitats (land and lake) where a large fraction of the biodiversity occurs, and

(ii) establishing coastal zone management areas in the remainder, as appropriate to local circumstances.

Basic requirements are;

- greater specific international interest in the biodiversity values of the ancient lakes and their present jeopardy, e.g. interest such as has been given to tropical forests. This needs more active advocacy by scientists. The potential exists for large benefits to biodiversity and evolutionary science but will require more active advocacy by scientist.
- recognition of the above fundamental flaws in present approaches to conservation and development;
- international willingness to pay for the upkeep of core reserves in the ancient lakes as well as management costs, compensation for local loss of commercial opportunity (eg. fishing) and support for local research. Schemes to accept responsibility along these lines are already well-explored and operating in some areas of outstanding terrestrial biodiversity in the world (Wilson, 2002). In these cases, long-term continuity is provided through funding and technical management by a politically independent multilateral body working along with national scientists and managers.

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Summary

On the limnology of Lake Tanganyika

The central theme of this thesis was to study and analyse the variations of physical, chemical and biological properties of Lake Tanganyika, an exceptionally large tropical rift lake, in order to better understand its functioning. This has led to a number of key findings:

One of the most fundamental physical aspects regarding Lake Tanganyika's regimes is the permanence of stratification. High water temperatures and clear seasonal variations in temperature structures, with marked thermal stratification, classify the lake as meromictic. Generally, the characteristic responses of any stratified lake to wind include an aperiodic circulation and interface tilt or set up, and subsequent periodic oscillations in the density layers when the wind ceases. Meteorologically induced changes in stratification, internal motion and related vertical mixing mechanisms may allow nutrients to the surface layers for primary production.

Multi-year observations elucidating the behaviour of the vertical distribution of naturally occurring limnological constituents in the upper water layers of Lake Tanganyika revealed the existence of well-established vertical gradients corresponding to the lake's meromictic condition (Chapter 2 and 3). Lake Tanganyika is not homogeneous and physical and chemical structures are demonstrated to be unstable during an annual cycle. A nutrient-poor, warm, oxygenated epilimnion above a metalimnion varying in thickness lying in turn on top of colder, nutrient-rich anaerobic conditions in the hypolimnion.

Major differences were found to occur between northern and southern basins. In the north basin, oxycline, nutricline and thermocline structures are positioned closely together and vertical mixing is confined to the water mass above the thermocline at 20 – 100 m. In contrast, significant oxygen levels in the south are noticeably at far greater depths within the water column. At times mixing extends down to at least 300 m, pushing nutriclines well below the thermocline. Judging from an on average weaker stratification, this also indicates that mixing in the south basin is more substantial, extending to greater depths.

Frequent measurements reveal a wide variety of short and long term fluctuations in the thermal properties of the upper water layers of the lake. Apart from (local) differences within the basins, the largest changes in spatial and temporal dynamics in epilimnetic distributions of constituents depended mainly on hydrodynamical events initiating internal wave patterns and related mixing events.

The consistent presence of internal waves could be inferred from fluctuations in temperature, pH, conductivity, turbidity, total phosphorus, phosphates, ammonia, nitrates and nitrites. The change of epilimnetic values for most limnological variables toward hypolimnetic values coincided with the internal wave pattern. I.e., the wax and wane of internal wave patterns and upwelling events can be inferred from yearly spatial and temporal fluctuations of chemical and physical characteristics of the lake. In particular, changes in pH and conductivity provided an excellent way to examine the movements of the metalimnion.

We were able to elaborate on the existence of a yearly limnological cycle. Generally, at the beginning of the hot, dry season (May-August), strong southerly winds displace the epilimnion downwind, depressing the thermocline while upwind upwelling occurs. Conversely, during September – October, at the onset of the calm, wet season, cessation of the winds allows the density imbalance throughout the lake to return to equilibrium. The epilimnion tilts back due to gravity and after having oscillated, long-period internal gravity waves or seiches (28-33 days) are set upon the thermocline that were dissipating, but persisted throughout the whole year.

Upward movement or tilting of thermal gradients generally lead to stratification weakening while downward movement lead to a strengthening of gradients. The seasonal oscillations of thermal structures in the upper water layers along the north-south axis as a whole around a central positioned node explained why the vertical physical structures away from the lake's both ends showed less response to hydrodynamical forcing by the ruling southerly wind patterns.

The first back tilt of the thermal structures or collapse of the upwelled region following the cessation of the trade winds, generated a large amplitude progressive surge of water noticeable along the thermocline that appears to be related to a rise of a weakened thermocline in the north around October (henceforth referred to as secondary upwelling) and subsequently to local mixing events in the south (November). This phenomenon coincided with lowered oxygen concentrations in the upper water layers and may account for the occasional large fish kills and algal blooms seen inshore. Subsequently, after having been reflected from the basin boundaries the surge's energy dissipated and as of December, it assumed the character of the internal seiche.

Although the upward movement of nutrient-rich waters as a result of the seasonal cycle of patterns of seiches, surges and mixing is evident throughout the year, the actual nutrient loading into the epilimnion and euphotic zone is hampered by the stratification structures within the lake (Chapter 5).

Low or absent internal nutrient loading in the south was observed during the calmest periods of the year, indicating that hydrodynamically forced internal seiche movement and upwelling events throughout the lake must be intense enough for significant nutrient amounts to surface and mix into the productive layers of Lake Tanganyika.

Inferred from the occasional decreasing oxygen contents of the lower thermocline boundaries in northern regions, we observed that cross-thermocline mixing of reduced matters is expected to occur throughout the year. However, they seemed only detectable in the upper water layers during periods where temperature and oxygen gradients were strong and situated at similar depths. I.e., the response to water displacements in terms of nutrient supply to the epilimnion seems to be governed by the position and differences in strength of the thermocline, oxycline and nutriclines. At downwind regions, these gradients were strongest and closest to each other showing rather similar dynamics throughout the year. Secondary upwellings here resulted in nutrient increase within the euphotic zone. In contrast, at upwind regions the oxycline and hence the nutriclines are situated far deeper below the thermocline. While the upwelling events in terms of water movement were more evident here, the upward nutrient flux seemed less prominent than at the most northern regions.

In general chlorophyll-a concentrations are found to be similar throughout the lake (ca. 1-1.5 µg l^{-1}). Increased concentrations (up to 10 µg l^{-1}), defined as a measure of phytoplankton responding to increased availability of nutrients, were found following periods of unstable or weak thermal stratification. The most clear yearly reoccurring events were not only the upwelling in upwind regions of the lake (May-August), but also the secondary upwelling noticeable at downwind regions (October).

During the peak concentration of chlorophyll-a, two additional lake phenomena were observed:

Firstly, in Northern regions during May and June chlorophyll-a maxima were found just above the thermocline and below the euphotic zone following periods of deep thermal stratification, impoverished epilimnetic waters and low seiche activity. Secondly, near the lake surface, two types of very dense phytoplankton blooms (*Anabaena* sp.,Cyanobacteria) were observed in the central and southern parts of the lake. These were found as either covering a broad area or proliferating along kilometres-long straight bands (Chapter 3 and 4).

The formation of shallow mixed layers and weak vertical stratification of the upper waters appear not to be the only prerequisites for phytoplankton to proliferate. This implies rather different mechanisms determining phytoplankton peaks at times when the upper waters are characterised by strong mixing, or when there is absence of mixing. In both cases, it does underscore the importance of hydrodynamic conditions in influencing biological activity in Lake Tanganyika, either in securing internal nutrient loading or by controlling the spatial distribution of phytoplankton biomass.

Lake Tanganyika's waters are regarded to be very transparent. However, throughout two years of monitoring, the dimensions of the photic zone were far greater than previously reported and are also showed to be unstable. In particular, the light penetration is highly variable, both spatially and temporarily, with 1 % of incident PAR reaching depths of ca. 20 m down to 70 m (year average ca. 40 m), with additional vertical shifts of 25 m per week during certain times. Very low background fluorescence by humic substances and detrital particles allowed even UV-A to penetrate depths down to 15 m. This also partly explains the decrease of phytoplankton pigments in the upper water layers to a fraction of the original, within a matter of hours during clear days.

Despite Lake Tanganyika's clarity, it does not automatically follow that its productive layer is overall well illuminated. Algae mixing throughout the epilimnion are, due to the highly variable position of the thermocline, exposed to quite an extreme range of light intensities; from detrimental (sub)surface levels to levels well below the light compensation depth. Interestingly, throughout most of the year, virtually no correlation between available light and epilimnetic quantities of chlorophyll-a was found, and certain algal communities seemed to be well adapted to very poor light conditions, even at depths below the light compensation point. Thus, although the available PAR is an important factor in regulating algal biomass in Lake Tanganyika it appears sufficient to sustain higher amounts of chlorophyll-a.

Wedderburn numbers (a dimensionless number describing watercolumn stability and stratification strength under wind forcing), prove very useful to model links between hydrodynamical forcing (e.g., wind patterns, shear stresses), internal thermal structure dynamics (e.g., seiching and mixing) and the internal loadings of plant nutrients (Chapter 5). There are clear indications of an inverse relation between Wedderburn numbers and mean euphotic concentrations of dissolved inorganic nitrogen and soluble reactive phosphorus. At low Wedderburn numbers (< 1), internal nutrient inputs became significantly detectable. These factors, as well as the secondary upwelling event downwind, coincided with an increase in chlorophyll-a, but were not associated with increased primary production. Generally in the north, up to 4 times higher primary production rates were observed than in the south. Also, primary production in the north was highest during the dry season when thermal structures intensified and deepened. Besides the probability that during this period, rates may have been affected by entrainment of hypolimnetic water, ameliorated underwater light conditions or other external nutrient sources (e.g., from nearby river systems), our measurements showed a weak relationship between chlorophyll-a concentrations and primary production rates in Lake Tanganyika .

Interannual differences in yearly recurring trends in Wedderburn numbers were observed. Those years characterised by weaker winds, notably bring about surface warming. This causes stronger thermal gradients on one hand, but also brings about less intense upwelling events and seiching throughout the lake on the other. As a consequence, internal nutrient loadings promoting phytoplankton may be hampered during calm years. Although the soluble reactive phosphate loadings in the south remained rather conservative over the years, the dissolved inorganic nitrogen concentrations in the euphotic zone were higher during those years when lower Wedderburn numbers over a longer period were encountered.

During a lake-wide scientific cruise, the physical, chemical and biological properties of the pelagic waters in Lake Tanganyika were studied to examine the spatial environmental variability and its relation with fluctuations in major plankton species' abundance and community assembly at times of a dry season (Chapter 6). A wind-driven formation of a gradual change in physical and chemical properties of the productive zones along the north-south axis of Lake Tanganyika was observed. Dissolved oxygen, turbidity, conductivity, phosphorus and chlorophyll-a increased, whereas temperature and pH showed a marked decrease towards the south, indicative for the upwelling events towards the south. A transition zone (6 to 7 ^{o}S latitude) was observed, where vertical water column structures changed from northern to southern conditions. This did not include the river Rusizi affected regions north of 4 ^{o}S latitude. Here, the more turbid waters were characterised by a lowered conductivity and pH containing more chlorophyll-a. High spatial heterogeneity in nutrient supply (especially phosphorus) caused through differences in degree of mixing appear to have directly affected the plankton community assemblages.

During the dry season, differences in phytoplankton were observed between north and southern basins. Northern waters displayed reduced internal nutrient loading, lower phytoplankton biomass, and smaller sized zooplankton with the Cyclopoids (predominantly *Mesocyclops aequatorialis aequatorialis*) playing an important role. The mixed environments in the south displayed increased phosphorus availability, higher phytoplankton biomass and larger sized zooplankton, dominated by Calanoid grazers (predominantly *Tropodiaptomus simplex*). It is therefore plausible to argue for the occurrence of two rather different food web structures, when the yearly hydrodynamical forcing patterns uphold the striking differences in physical, chemical and biological properties of the northern and southern regions.

In order to better understand the relative importance of the internal regeneration or nutrient loadings to the Lake's overall yearly budgets, the contribution of external influxes of constituents through terrestrial run-off, river inflow and atmospheric deposition were investigated (Chapter 7).

The physico-chemical characteristics of the three largest inflowing rivers (Rusizi, Burundi; Malagarasi, Tanzania; and Lufubu, Zambia) and the wet atmospheric depositions at the LTR stations in Bujumbura, Kigoma, and Mpulungu, showed some remarkable differences in their respective annual fluctuations. Overall basin altitude and morphology appear to be important in determining riverine chemistry, while biomass burning and atmospheric transport processes affected local rains. Riverine nutrient loading rates were at their highest during the end of the rainy season (April-May), with the Rusizi providing by far the most and Lufubu the least of the total input. Additionally, the highest atmospheric nutrient deposition rates occurred in the north, nearby more populated and industrialized Bujumbura. Here, high rates were most significant at the beginning of the rainy season. Rivers deposited most of the soluble silicates and total phosphorus while the rain, proving also to be a significant phosphorus source, provided most of the dissolved inorganic nitrogen.

Net fluxes through wet deposition and riverine input were calculated to potentially induce a new yearly production of 45 to 60 g C m^{-2} (roughly 10 % of annual primary production). When these sources are combined at their peak (February-May), they together are expected to be most important to the productive water layers of the northern regions. This is because during this period, internal nutrient loading is likely to be low, while primary production rates are still relatively high in the lake.

In Lake Tanganyika, as in other large, and deep clearwater lakes, primary production of phytoplankton is expected to be the major source of energy for higher pelagic trophic levels, including fish. Knowledge of the trophic structure of the lake and the transfer efficiencies in the food chain is, and has been of interest for assessing the fishery potential, as well as providing a useful comparison with other lakes. Prior to this study, it has been suggested that primary production estimates were insufficient to meet the respiratory demand of the plankton community, let alone maintain the rather productive pelagic fishery (ca. 60 kg ha^{-1} yr^{-1}). Notably, Tanganyika's food web structure and functioning has been likened to marine systems. For example, it has been assumed that the lake's pelagic zones, as in marine regions, plankton biomasses are low, but that production rates are high, with efficient carbon transfers between the constituents of the food web structures, consequently leading to relatively high proportions of primary production being channelled into fish biomass.

In order to better understand the system structure and fish production efficiency, sources of carbon for phytoplankton, bacterioplankton, and zooplankton and pelagic fish production were evaluated in a comprehensive multi-year study (Chapter 8).

With the collection of new data on phytoplankton production (^{14}C and simulated in situ methods), bacterioplankton production (leucine incorporation method), zooplankton production (calculated from seasonal population samples, carbon contents distribution development stages) and fish production (hydro acoustics, length frequency analyses, and otoliths study) new insights were gained on the plankton relating to fish production. In this study, the estimates for primary productivity (426-662 g C m^{-2} yr^{-1}) were 47-128 % higher than previously published values. Bacterioplankton production was found to amount to about 20 % of the primary production while zooplankton biomass (1 g C m^{-2}) and productivity (23 g C m^{-2} yr^{-1}) were 50 % lower than previously reported, suggesting that the carbon transfer efficiency from phytoplankton to zooplankton is low, in marked contrast to earlier speculations. Similarly, planktivorous fish biomass (0.4 g C m^{-2}) and productivity (1.4-1.7 g C m^{-2} yr^{-1}) indicate low carbon transfer efficiencies from zooplankton into planktivorous fish production.

In a deep tropical lake, such as Tanganyika, relatively low transfer efficiencies are not unexpected. This is because of the generally high metabolic losses due to the high temperatures and presumably high costs of predator avoidance. The total fisheries yield in Lake Tanganyika in the mid-1990s was 0.08-0.14 % of pelagic primary production, i.e. within the range of typical values in lakes. Thus, we can assume that no special mechanisms need be invoked to explain the productivity of fisheries in Lake Tanganyika.

In Lake Tanganyika, wind-driven changes in the physical, chemical and biological properties of the pelagic zone, is an important factor affecting both food web structure and functioning of its basins. The construction of dynamic food web structures in Lake Tanganyika under different degrees of hydrodynamical forcing is essential for understanding short and long-term changes in the trophic status of Lake Tanganyika, and ultimately determining total fish catches, which has socio-economic implications for this highly populated region.

Of particular interest and concern will be to monitor the effect of the global warming over the next 50 -100 years on Tanganyika's trophic status and related fishery yield. Recent research findings claim that higher temperatures and lower wind stress have intensified the water column stability over the last few decades, in turn diminishing internal nutrient loading promoting phytoplankton growth and consequently bringing about a decline in pelagic fish catches.

Although an inverse relation between weather induced stratification strength and nutrient loading is documented here, increased nutrients did not noticeably lead to increased productivity (Chapter 9). Moreover, since the mid-1970s no feasible trend can be derived from the available phytoplankton production and Tanganyika's water transparency data, while total fish catches have not appreciably changed, or have in fact increased. While it is tempting, due to theoretical reasoning, to assume climate change is a major determinant of fish yields in

Lake Tanganyika, data currently available indicates rather that fishery intensification is the major factor affecting Lake Tanganyika's fish stocks.

Lake Tanganyika is a highly important environment, in terms of its wealth of biodiversity, containing multiple radiations of different faunal lineages (e.g. cichlid fishes, gastropods, crabs). It is also an extremely valuable resource providing cheap protein, transport, potable water and irrigation that form the basis of life for millions of riparian people. Survival of these unique faunas has to be managed along with vital resources use (Chapter 10). Acceleration of exploitation and catchment development in the light of a changing climate poses urgent problems that need better understanding. More international interest is needed to ensure survival of Tanganyika's biota.

Unfortunately, the interest of politicians, development policy makers and international donors is usually temporary in nature. The duration of their involvement in a policy or project may be merely the interval between successive elections, thus implementation is often frustrated by lack of continuous commitment. Commonly, crisis management takes the place of long-term policy. In consequence, many internationally assisted research projects that are excellent in intent and achievement have poor follow-up and therefore weak outcomes with little real progress made.

Basic requirements with greater specific and sustained (inter)national interest in the ancient lakes are needed, such as has been given to some tropical forests or coral reefs.

Résumé

Sur la Limnologie du lac Tanganyika

Les thèmes centraux de cette thèse de doctorat sont l’étude et l’analyse des variations dans les paramètres physiques, chimiques et biologiques d’un lac de graben tropical, le lac Tanganyika, dans le but de mieux comprendre son fonctionnement.

La stratification thermale bien nette liée aux températures élevées de ses eaux et les variations saisonnières prononcées de la température permettent de classifier ce lac comme méromictique. Normalement, parmi les réponses caractéristiques au vent de tout lac stratifié on note une circulation apériodique et l’inclinaison ou l’empilage de la couche intermédiaire, suivi d’oscillations périodiques dans les couches de densité après la cessation du vent. Des changements provoqués par la météorologie dans la stratification, le mouvement interne et les mécanismes de brassage verticaux y relatifs peuvent mener à une advection des nutriments à la surface, où ils sont disponibles à la production primaire. Ainsi, l’un des aspects physiques les plus fondamentaux à considérer dans le cycle du lac Tanganyika est la permanence de la stratification.

Des observations multi-annuelles de la distribution verticale des phénomènes limnologiques naturels des couches superficielles du lac Tanganyika ont permis de conclure que l’existence de gradients verticaux bien définis correspond à la condition méromictique du lac (Chapitres 2 et 3). Le lac Tanganyika n’est pas homogène et ses structures chimiques ne sont pas stables durant le cycle annuel. L’épilimnion pauvre en nutriments, chaud, oxygéné se trouve au dessus d’un métalimnion d’épaisseur variable (environ 1-300 mètres), situé à son tour au dessus d’un hypolimnion froid, riche en nutriments et anaérobique. Dans le bassin nord la position de l’oxycline, de la nutricline et de la thermocline est presque identique et le brassage vertical est limité aux masses d’eau au dessus de la thermocline à 20-100 m. Au sud, l’oxygène se rencontre dans la colonne d’eau à des plus grandes profondeurs. Le brassage s’y étend verticalement à plus de 300 mètres, poussant les nutriclines bien en dessous de la thermocline. Une stratification thermale moins grande indique également qu’au bassin sud, le brassage est plus substantiel, s’étendant à de plus grandes profondeurs.

De mesures réguliers ont permis de décerner toute une gamme de fluctuations à court et à long terme des caractéristiques thermiques des couches superficielles du lac. A côté des différences locales à l’intérieur des bassins, les plus grands changements de la dynamique spatio-temporelle de la distribution épilimnétique des composantes dépendent principalement d’évènements hydrodynamiques provoquant des ondes internes et le brassage y relatif.

La présence permanente d’ondes internes a pu être observée à partir de fluctuations en température, pH, conductivité, turbidité, phosphore totale, phosphates, ammoniaque, nitrates et nitrites. Le changement de valeurs épilimnétiques pour la plupart des paramètres limnologiques vers des valeurs de ceux de l’hypolimnion traduit le patron des ondes internes. Ceci implique que la dynamique des ondes internes et celle des remontées d’eaux profondes peut être étudiée à partir des fluctuations annuelles spatio-temporelles des caractéristiques chimiques et physiques du lac. En particulier, les changements du pH et de la conductivité sont des indicateurs efficaces des mouvements du métalimnion.

Nous avons été capables d’établir le cycle limnologique annuel. Généralement, au début de la saison chaude et sèche (mai-août), des vents forts du sud déplacent l’épilimnion vers le nord, déprimant la thermocline au nord et provoquant la remontée des eaux profondes au sud. En septembre-octobre, en début de la saison calme et humide, la cessation du vent permet le retour à l’équilibre des distorsions en densité. La pesanteur met fin à l’inclinaison de l’épilimnion et après oscillation, des seiches ou ondes internes de longue période (28-33 jours) sont communiquées à la thermocline. Ces ondes perdent de force, mais ne disparaissent pas durant l’année.

Le mouvement vers le haut ou l’inclinaison de gradients thermiques mène à une diminution de la stratification, tandis que des mouvements vers le bas la fortifient. Les oscillations saisonnières des structures thermiques des couches superficielles le long de l’axe nord-sud autour d’un nœud central expliquent pourquoi les structures physiques verticales éloignées des extrémités du lac démontrent une moindre réponse au forçage hydrodynamique par les vents du sud.

Le retour de l’inclinaison ou l’effondrement de la zone de remontée des eaux suite à la cessation des alizés provoque une onde progressive de grande amplitude apparente le long de la thermocline qui paraissait être liée à la montée de la thermocline affaiblie au nord autour d’octobre (dorénavant appelée remontée secondaire) et postérieurement aux effets de brassage au sud (novembre). Ce phénomène coïncide avec des teneurs baissés en oxygène des eaux superficielles qui provoqueraient des mortalités massives occasionnelles de poissons et la floraison d’algues observée dans la zone côtière. Par la suite, après être réfléchi par les limites du bassin, l'énergie de cette onde est dissipée et en décembre elle ressemble plus à une onde interne.

Quoique le déplacement vers le haut des eaux riches en nutriments résultant du cycle saisonnier de seiches, ondes et brassage soit apparent durant toute l'année, l'advection de sels nutritifs dans l'épilimnion et de la zone euphotique est limitée par la stratification (Chapitre 5).

De teneurs basses ou même l'absence de nutriments au sud furent observées durant la période la plus calme de l'année, indiquant que les mouvements forcés des seiches internes et la remontée d'eaux dans l'ensemble du lac doivent avoir suffisamment de poids pour permettre aux nutriments d'atteindre la surface et de se mélanger aux couches productives du lac Tanganyika.

En nous basant sur la teneur parfois basse en oxygène des limites inférieures de la thermocline de la zone nord, nous nous attendons à un brassage continu de matières réduites à travers la thermocline. Néanmoins, ils ne furent décelables aux couches supérieures que dans les périodes où les gradients en température et oxygène furent forts et situés à des profondeurs similaires. Ceci implique que l'advection de sels nutritifs à l'épilimnion semble dépendre de la position et des différences en force de la thermocline, de l'oxycline et de la nutricline. Ces gradients furent les plus forts et les plus proches en position aux régions à l'abri du vent, démontrant une dynamique similaire pendant toute l'année. La remontée secondaire des eaux provoquait une augmentation de nutriments dans la zone euphotique. Par contre, dans les régions sous le vent, l'oxycline et donc les nutriclines se trouvent plus profondément sous la thermocline. Les mouvements d'eau y furent plus évidents, mais le flux de nutriments vers le haut fut moins important que dans la plupart des régions du nord.

Généralement, les concentrations de chlorophylle-a furent assez similaires dans l'ensemble du lac (ca. 1-1,5 µg l-1). Résultant de la réponse du phytoplancton à l'augmentation des sels nutritifs, des concentrations plus élevées (jusqu'à 10 µg l-1) furent observées suite aux périodes de stratification thermique instables ou faibles. A part la remontée des eaux dans les zones à l'abri du vent (mai-août) comme phénomène annuel régulier, une remontée secondaire se notait également dans les régions sous le vent.

Deux autres phénomènes furent observés pendant le maximum de chlorophylle-a. Premièrement, dans la région du nord des maximums en chlorophylle-a furent observés juste au dessus de la thermocline et en dessous de la zone euphotique aux mois de mai et juin, après des périodes de stratification thermique profonde, caractérisées par l'appauvrissement des eaux éplimnétiques et la moindre activité de seiches. Ensuite, dans les zones centrale et méridionale du lac, deux types de floraisons très denses de Anabaena sp. (Cyanobactéries) furent signalés, celle couvrant une grande étendue et celle proliférant en bandes droites, longue de plusieurs kilomètres (Chapitres 3 et 4).

Une formation de couches mélangées peu profondes et une faible stratification verticale ne semblent pas être les seules préalables à la prolifération du phytoplancton. D'autres mécanismes provoquent des maximums en phytoplancton à des moments où il y a un fort brassage des eaux supérieures ou quand ce dernier est nul. Dans les deux cas, l'importance des conditions hydrodynamiques est évidente comme déterminante de l'activité biologique au lac Tanganyika, soit en assurant un chargement interne en nutriments soit en contrôlant la distribution spatiale de la biomasse en phytoplancton.

La grande transparence des eaux du lac Tanganyika est bien connue. Pendant les années de l'étude, l'étendue de la zone photique fut de loin supérieure à celle mesurée auparavant, mais instable, accusant des variations spatio-temporelles élevées, avec 1% de la PAR atteignant des profondeurs d'environ 20 à 70 m. (moyenne annuelle 40 m) et parfois fluctuant de 25 m par semaine. La très faible fluorescence de base émise par des substances humiques et des particules de détritus permet à l'UV-A de pénétrer à des profondeurs de 15 m. Ceci explique en partie la diminution drastique en quelques heures observée dans l'abondance des pigments de phytoplancton des couches superficielles.

La clarté du lac Tanganyika n'implique pas automatiquement une illumination homogène de ses couches productives. Due à la grande variabilité de la position de la thermocline, les algues présentes dans l'épilimnion sont exposées à une gamme extrême d'intensités lumineuses (variant des couches de surface désavantageuses jusqu'aux niveaux bien en dessous de la profondeur de la compensation de la lumière).

Il est intéressant à noter que pendant la plus grande partie de l'année il n'y avait pratiquement pas de corrélation entre la quantité de lumière disponible et les quantités épilimnétiques de chlorophylle-a; quelques communautés d'algues paraissaient bien adaptées à un manque de lumière, même aux profondeurs en dessous du point de compensation de la lumière. En dépit de l'importance de la PAR disponible dans la régulation de la biomasse algale du lac Tanganyika, elle semblait suffisante pour soutenir des quantités élevées de chlorophylle-a.

L'utilisation de nombres de Wedderburn a été d'une grande utilité pour modeler les liens entre le forçage hydrodynamique (p.e. patrons de vent, tension de cisaillement), la dynamique des structures thermiques internes (p.e. seiches et brassage) et le chargement interne en sels nutritifs (Chapitre 5). Il existe une indication nette d'un rapport négatif entre les nombres de Wedderburn, les concentrations moyennes euphotiques d'azote anorganique dissous et de phosphore réactif soluble. Aux valeurs Wedderburn faibles (< 1) le chargement interne en nutriments devient décelable. Ces facteurs, tout comme la remontée secondaire à l'abri du vent, coïncident avec une augmentation de chlorophylle-a, sans indication d'une augmentation de la production primaire. Au nord, les taux de production primaire furent généralement jusqu'à 4 fois plus élevés qu'au sud. La production primaire au nord fut maximale durant la saison sèche lors de l'intensification et l'approfondissement des structures thermiques. Ces taux peuvent également être influés par l'advection d'eaux hypolimnétiques, l'amélioration de la pénétration de la lumière ou d'autres sources externes de nutriments (p.e. des systèmes fluviaux avoisinants), mais la relation entre les concentrations de chlorophylle-a et les taux de production primaire paraît faible au lac Tanganyika.

Il y avait des différences interannuelles dans les nombres de Wedderburn. Les années caractérisées par des vents plus faibles démontrent d'une part un réchauffement de la surface créant des gradients thermiques plus forts et d'autre part une moindre remontée des eaux et des seiches partout dans le lac. Nous argumentons donc que le chargement interne en nutriments soit entravé durant les années calmes. Les teneurs en phosphates solubles réactives au sud sont restées relativement stables durant la période étudiée, tandis que les concentrations d'azote inorganique dissous dans la zone euphotique furent plus élevées dans un nombre d'années consécutives ayant des nombres de Wedderburn faibles.

Lors de campagnes scientifiques couvrant l'ensemble du lac, les paramètres physiques, chimiques et biologiques des eaux pélagiques du lac Tanganyika furent étudiés dans le but de caractériser la variabilité spatiale du milieu en relation avec les fluctuations de l'abondance des principales espèces et de la composition spécifique du plancton durant la saison sèche (Chapitre 6). Il fut observé que le vent provoque des changements graduels dans les caractéristiques physiques et chimiques de la zone productive le long de l'axe nord-sud du lac Tanganyika. L'oxygène dissous, la turbidité, la conductivité, le phosphore et le chlorophylle-a augmentaient, tandis que la température et le pH diminuaient vers le sud en raison de la remontée des eaux dans cette zone. Il fut observé une zone de transition (de 6-7^{o} latitude sud), où la structure verticale des colonnes d'eau changeait de celle observée au nord en celle typique pour le sud du lac. Ce phénomène ne se présentait pas dans les eaux nord de latitude 4 ^{o}S, qui sont sous l'influence du fleuve Rusizi. Les eaux turbides de cette région ont une moindre conductivité et pH et contiennent davantage de chlorophylle-a. Une hétérogénéité spatiale élevée de l'apport de nutriments (particulièrement de phosphore) provoquée par l'intensité du brassage influe sur les communautés d'organismes planctoniques. Tandis que le nord était sous l'influence d'un moindre chargement interne en nutriments, une biomasse plus faible en phytoplancton et des organismes de zooplancton de petite taille avec une prépondérance de Cyclopoides (surtout *Mesocyclops aequatorialis aequatorialis*), le sud montrait les effets de brassage, une plus grande disponibilité de phosphore, une plus grande biomasse de phytoplancton et une dominance de zooplancton de grande taille (dominé par *Tropodiatomus simplex*). Nous argumentons que le patron annuel de forçage hydrodynamique maintient la différence frappante en caractéristiques physiques, chimiques et biologiques entre les régions du nord et du sud ayant chacune sa chaîne alimentaire différente.

Dans le but d'estimer l'importance relative de la régénération interne ou du chargement en nutriments au budget annuel total du lac, la contribution de chacune des composantes externes, l'écoulement d'origine terrestre, les apports de rivières et le dépôt atmosphérique furent étudiés (Chapitre 7).

L'étude des caractéristiques physico-chimiques des trois plus grands fleuves affluents (la Rusizi au Burundi, la Malagarasi en Tanzanie et la Lufubu en Zambie) et des dépôts atmosphériques humides aux trois stations du projet LTR à Bujumbura, Kigoma et Mpulungu a permis d'observer des différences remarquables dans la fluctuation annuelle des paramètres.

Essentiellement, l'altitude du bassin et sa morphologie déterminent la composition chimique des eaux de rivières, tandis que les feux de brousse et le transport atmosphérique ont leurs effets sur les pluies locales. Le taux le plus élevé de nutriments dans les rivières fut mesuré en fin de la saison des pluies (avril-mai). Les apports de la Rusizi sont de loin supérieurs aux autres et celui de la Lufubu fut le moindre. Les dépôts en nutriments atmosphériques furent supérieurs au nord, près de la ville de Bujumbura peuplée et industrialisée. Ici, les taux élevés furent significatifs au début de la saison des pluies. Les rivières déposent la plupart des silicates solubles et du phosphore total, tandis que la pluie – également une source significative de phosphore – fournissait la plupart de l'azote inorganique dissous.

Ensuite, il fut calculé que les flux dus au dépôt humide et aux rivières pourraient causer une production annuelle de 45-60 g C m-2 (environ 10% de la production primaire annuelle). En février-mai, au moment du maximum des deux sources, ces deux facteurs sont considérés comme très importants pour les couches d'eaux productives des régions nord du lac. A ce moment, la stabilité de la colonne d'eau est très grande et peu de chargement interne en nutriments a lieu, la production primaire y est la plus grande de l'ensemble du lac.

Au lac Tanganyika, comme dans d'autres lacs clairs grands et profonds, l'on s'attend à ce que la production primaire du phytoplancton soit la source principale d'énergie aux niveaux trophiques pélagiques supérieurs, y compris le poisson. La connaissance de la structure trophique de lac et l'efficacité de transfert dans la chaîne alimentaire est d'un intérêt certain pour l'estimation du potentiel de pêche, ainsi que pour une comparaison avec d'autres lacs. Les études antérieures jusqu'à présent avaient suggéré que les valeurs de production primaire soient insuffisantes pour couvrir la demande respiratoire de la communauté planctonique, sans parler du maintien de la pêche pélagique assez productive (environ 60 kg ha-1 an-1). Etant donné les similarités entre le système du lac Tanganyika et les systèmes marines, ils furent prêts à attribuer des caractéristiques marines à la structure de la chaîne alimentaire du Tanganyika et son fonctionnement. L'on supposait que la biomasse en plancton de la zone pélagique fut faible et les taux de production élevés, comme dans le milieu marin. Selon cette opinion, les transferts de carbone sont très efficaces entre les différents niveaux de la chaîne alimentaire et une proportion relativement élevée de la production primaire serait convertie en biomasse de poisson.

Dans le but d'approfondir les connaissances de la structure du système et l'efficacité de la production en poisson, une étude de plusieurs années fut entamée sur les sources de carbone pour le phytoplancton, bactérioplancton, zooplancton ainsi que pour les poissons pélagiques (Chapitre 8).

De nouvelles données sur la production du phytoplancton (C14 et simulations in situ), du bactérioplancton (méthode d'incorporation de leucine), du zooplancton (calculées à partir d'échantillons saisonniers de la population, distribution des composantes de carbone dans les différents stades de développement) et du poisson (campagnes acoustiques, analyse de fréquences de longueur, otolithes) ont permis d'élucider le rapport entre la production de plancton et celle de poisson.

Dans notre étude, les estimations de la productivité primaire (426-662 g C m-2 an-1) sont de 47-128% supérieures aux estimations publiées antérieurement. Le niveau de production du bactérioplancton s'élevait à environ 20% de celui de la production primaire, tandis que la biomasse en zooplancton (1 g C m-2) et sa productivité (23 g C m-2 an-1) furent de 50% inférieures aux valeurs publiées, suggérant – contrairement aux spéculations antérieures - une faible efficacité du transfert de carbone entre le phytoplancton et le zooplancton. La biomasse des poissons planctivores (0,4 g C m-2) et leur productivité (1,4-1,7 g C m-2 an-1) suggère également une faible efficacité du transfert de carbone entre le zooplancton et les poissons pélagiques.

On s'attendait déjà à une efficacité relativement faible dans un lac tropical profond comme le Tanganyika, en raison des pertes métaboliques généralement élevées dues à la température élevée et aux coûts vraisemblablement élevés de l'évitement de prédateurs. Au milieu des années 1990, la production totale en poisson fut de 0,08-0,14% de la production pélagique primaire, bien dans la gamme des valeurs attendues pour un lac. Ainsi, il n'est pas nécessaire d'évoquer des mécanismes spéciaux pour expliquer la productivité de la pêche au lac Tanganyika.

Au lac Tanganyika, les changements des caractéristiques physiques, chimiques et biologiques de la zone pélagique dus au vent ont un impact sur la structure de la chaîne trophique et sur le fonctionnement de ses bassins. La structure de la chaîne alimentaire du lac Tanganyika soumise à des degrés variables de forçage hydrodynamique permet de mieux comprendre les changements à court et à long terme de l'état trophique du Tanganyika, qui déterminent les captures totales en poisson et donc le bien-être des millions d'habitants riverains.

L'étude de l'effet du réchauffement de l'atmosphère pour les 50-100 ans à venir sur l'état trophique et la production en poisson du Tanganyika est d'une grande importance. D'études récentes affirment que les températures élevées et le moindre cisaillement par le vent des dernières décennies ont intensifié la stabilité de la colonne d'eau, diminuant le chargement interne en nutriments, provoquant la croissance du phytoplancton et par conséquent ont diminué les captures des poissons pélagiques.

Nous avons décrit la relation inverse entre la force de stratification due au vent et le chargement en nutriments, mais une augmentation de nutriments ne résulte pas en une augmentation sensible de la productivité (Chapitre 10). La plus grande productivité fut trouvée au nord, tandis que le brassage par le vent est plus fort au sud. En plus, les données sur le plancton disponibles depuis le milieu des années 1970 ne montrent pas de différences nettes et les captures totales de poisson ont en fait augmenté ou n'ont pas changé sensiblement.

Même s'il y ait des raisons théoriques pour croire au rôle déterminant d'un changement climatique à la production halieutique du lac Tanganyika, il y a des signes assez nets actuellement, basés sur l'information disponible, que l'intensité de la pêche soit plutôt le facteur principal influant sur les stocks de poissons du lac Tanganyika.

Le lac Tanganyika représente une ressource extrêmement valable fournissant des protéines facilement accessibles, une avenue de transport et une source d'eau potable et d'irrigation, formant la base de vie aux millions d'habitants riverains. Le lac contient aussi l'une des plus grandes biodiversités lacustres du monde. La garantie de la survie de ces faunes uniques doit faire partie d'un programme intégré de gestion de l'utilisation des ressources vitales (Chapitre 10). L'accélération de l'exploitation et le développement du bassin versant posent de problèmes urgents requérant une meilleure compréhension en tenant compte du changement de climat. Il faudra davantage d'intérêt international pour assurer la survie de la biodiversité unique du lac Tanganyika.

Malheureusement, l'intérêt d'hommes politiques, rédacteurs de politiques de développement et donateurs internationaux est souvent de nature temporaire. La durée de leur engagement dans une politique un dans un projet peut simplement représenter l'intervalle entre deux élections. La mise en œuvre est donc frustrée par un manque d'engagement continu. D'habitude la gestion de crise prend la place d'une politique à long terme. En conséquent, beaucoup de projets de recherche, bénéficiant d'une assistance internationale, qui sont excellents dans leurs intentions et résultats ne sont pas poursuivis et n'aboutissent pas aux objectifs et progrès prévus.

Il faudra donc à court terme un plus grand intérêt (inter)national spécifique et soutenu aux lacs anciens et leurs risques actuels, tout comme celui accordé aux certaines forêts tropicales et récifs de corail.

Samenvatting

Over de limnologie van het Tanganyika meer

Dit proefschrift bestudeert en analyseert de fysische, chemische en biologische eigenschappen van het Tanganyikameer om tot een beter begrip te komen van het functioneren van dit systeem. De volgende bevindingen zijn hierbij opgetekend:

De vertikale verdeling van de limnologische parameters van het oppervlaktewater vertoont permanent goed ontwikkelde gradiënten, die uitwijzen dat het meer een meromictisch karakter heeft (hoofdstukken 2 en 3): Een nutriëntenarm, warm zuurstofrijk epilimnion boven een metalimnion (variërend in dikte), dat weer bovenop een kouder, nutriëntenrijke anaëroob hypolimnion ligt. De fysische en chemische structuren van het meer zijn niet stabiel gedurende het jaar.

De vertikale opbouw van de waterkolom in het noordelijk en het zuidelijke bassin is verschillend. In het noorden liggen de oxycline, nutricline en thermocline vaak dicht bijelkaar en vertikale menging vindt veelal plaats in het epilimnion (20-100 m). Zijn doorgaans zwakkere stratificatie geeft aan dat mixing in het zuidelijke bassin omvangrijker is, zelfs tot op grotere diepte (300 m). Als gevolg hiervan worden de oxyclines en gerelateerde nutriclines op grotere diepte aangetroffen dan in het noorden.

Frequente metingen onthulden een afwisseling van kort- en langdurende fluctuaties in de thermale structuur van het meeroppervlak. Naast lokale verschillen in bassins waren de grootste veranderingen van epilimnetische bestanddelen in ruimte en tijd afhankelijk van hydrodynamische gebeurtenissen die, geassocieerd met het initiëren van interne golfpatronen, periodes van menging van waterlagen tot gevolg hadden.

Door het jaar heen blijven de interne golven detecteerbaar in de fluctuaties van temperatuur, pH, conductiviteit, turbiditeit, totaal fosfaat, fosfaat, ammoniak, nitraat en nitriet. Typische ‘epilimnion waarden’ voor verschillende variabelen schommelen in de richting van ‘hypolimnion waarden’, afhankelijk van het interne golfpatroon. Dus, de periodiciteit van de interne golfpatronen en die van de opwelling werden herkend in de schommelingen van de fysische en chemische kenmerken van het meer. Vooral veranderingen in pH en conductiviteit zijn goed bruikbaar om de dynamiek van het metalimnion te volgen.

Wij herkenden een jaarlijkse terugkomende limnologische cyclus. Met de start van het droge seizoen (mei - augustus), wanneer de in kracht toegenomen zuidenwind het epilimnion in beweging brengt en de temperatuurgradiënten benedenwinds naar beneden wegdrukt, vindt bovenwinds opwelling plaats. Bij de plotselinge afname van de windsterkte, aan het begin van de kalme regenperiode (september – oktober), probeert de opgebouwde dichtheidsonbalans over het meer weer naar de evenwichtsstand terug te keren. Het epilimnion beweegt zich terug door de zwaartekracht en begint te oscilleren, seiches (met een golfperiode van 28 tot 33 dagen) zijn dan goed waarneembaar op thermoclinediepte. Met afnemende amplitude blijven ze echter gedurende de rest van het jaar zichtbaar, tot het begin van het volgende droge seizoen.

Seizoensoscillaties van de thermale structuren langs de noord - zuid as van het meer rond een centraal gepositioneerde knoop verklaren waarom de vertikale fysische structuren dichter bij het midden van het meer een zwakkere dynamiek toonden dan aan de uiteinden ervan.

Het wegvallen van het opwellinggebied in het zuiden, direct na het wegvallen van de passaatwinden, genereerde een progressieve golf met hoge amplitude ter hoogte van de thermocline, die verantwoordelijk bleek voor de opwaartse beweging van een verzwakte thermocline in het noorden rond oktober (hierna secundaire opwelling genoemd) en vervolgens weer leidde tot perioden van sterke mixing in het zuiden rond november. Plotselinge afnames in zuurstofgehalte, omvangrijke vissterfte en algenbloei aan het oppervlak kenmerken deze turbulente periode. De golf verliest hierna energie en neemt meer het karakter aan van een interne seiche.

Het opwaarts kantelen van thermale gradiënten ging over het algemeen gepaard met een afname van de stratificatie, terwijl een benedenwaartse kanteling een versterking van gradiënten tot gevolg had. Hoewel de bewegingen van nutriënt-rijke waterlagen als gevolg van seizoenscycli van seiches, progressieve golven en mixing het gehele jaar door plaats vinden, bleek de stratificatie een barrière die een nutriëntentransport richting epilimnion belemmert (hoofdstuk 5). Bovenwinds vond verminderd transport van nutriënten plaats tijdens de rustigste perioden van het jaar. Interne golfbewegingen en opwelling moeten dus een bepaalde intensiteit hebben, willen ze nutriëntrijke lagen zover omhoog kunnen brengen dat ze mengen met het epilimnion en herkenbaar zijn.

In het noorden nam de zuurstof regelmatig af in waterlagen onder de thermocline. Dit impliceert dat er transport van gereduceerd materiaal door de thermocline heen plaats vindt.

Dit bleek echter veel duidelijker detecteerbaar aan het oppervlak op de momenten waarop de verticale temperatuur- en zuurstofgradiënten groot waren en dicht bijelkaar lagen.

De reactie op waterverplaatsingen gemeten aan nutriënten in het epilimnion wordt mede bepaald door de positie en sterkte van de thermocline, oxycline en nutricline. Benedenwinds waren deze gradiënten door het jaar heen het sterkst en lagen dicht bijelkaar. In deze regio resulteerde secundaire opwelling in een toename van de nutriënten in de eufotische zone, in tegenstelling tot het zuiden waar nutricline en oxycline zich doorgaans dieper manifesteren dan de thermocline. Terwijl de opwelling hier veel sterker was qua waterbeweging bleek het nutriëntgehalte minder prominent dan in de noordelijke gebieden.

Chlorofyl-*a* concentraties in het meer liggen rond de 1-1.5 µg l^{-1}. Hogere concentraties (tot op 10 µg l^{-1}), werden waargenomen volgend op periodes van instabiele of verzwakte stratificatie. De meest prominente jaarlijks terugkomende gebeurtenissen waar chlorofyl-*a* piekte waren de bovenwindse opwellingperioden (mei - augustus) en de secundaire opwelling benedenwinds (oktober).

Buiten deze perioden werden nog twee andere bloeiperioden gedetecteerd. Ten eerste, in het noorden, werd in mei - juni tijdens diepe stratificatie een verarmd epilimnion en lage seiche activiteit waargenomen met rond de thermocline - onder de eufotische zone - diepe chlorofyl–*a* maxima. Ten tweede werd aan de oppervlakte van het centrale en zuidelijke deel van het meer een omvangrijke algenbloei (*Anabaena* sp., Cyanobacteria) waargenomen, die verschillende vormen kon hebben: deze besloegen of een uitgestrekt gebied of profileerden zich als banden van enkele kilometers lang (hoofdstukken 3 en 4).

Mixing en de vorming van een zwakke stratificatie dicht aan het oppervlak blijken niet de enige vereisten voor versnelde fytoplanktongroei. Er zijn verschillende mechanismen, die het fytoplankton van het Tanganyikameer kunnen stimuleren, tijdens perioden van sterke mixing en afwezigheid van mixing. Hydrodynamische condities sturen de biologische activiteit in het Tanganyikameer, enerzijds door het verhogen van het gehalte aan nutriënten, anderzijds door het beïnvloeden van de verdeling van de fytoplanktonbiomassa in de waterkolom.

Tanganyika’s wateren zijn doorgaans erg helder. De dimensies van de fotische zone bleken echter veel groter en veranderlijker dan voorheen is gerapporteerd. Lichtpenetratie in Tanganyika is zeer variabel in ruimte en tijd, met een 1% van inkomende PAR meetbaar op diepten tot ongeveer 20 - 70 m (jaarlijks gemiddeld 40 m), regelmatig fluctuerend van 25 m per week tot 10 m per dag.

Vanwege de erg lage achtergrondfluorescentie van humusmateriaal en detritusdeeltjes kan UV-A een diepte tot 15 m bereiken. Dit verklaart waarom tijdens zonnige dagen fytoplanktonpigmenten in de oppervlaktewateren in een paar uur tijd kunnen afnemen tot een fractie van hun oorspronkelijke aantallen.

De helderheid van het Tanganyikawater bleek niet automatisch te betekenen dat de productieve waterlagen te allen tijde goed belicht waren. Door de grote variabiliteit van de ligging van de thermocline worden algen blootgesteld aan een extreme variatie van lichtintensiteiten, uiteenlopend van schadelijke waarden aan het oppervlak tot lichtniveaus beneden de lichtcompensatiediepte.

Door het jaar heen werd vrijwel geen correlatie gevonden tussen de beschikbare hoeveelheden licht en chlorofyl-a in het epilimnion. Algenkolonies leken goed aangepast aan verminderde lichtomstandigheden, zelfs beneden de lichtcompensatiediepte.

Wedderburn nummers (dimensieloze nummers die de stabiliteit en stratificatiekracht van de waterkolom bij verschillende windkracht uitdrukken) waren geschikt om de relaties te modelleren tussen hydrodynamische sturing (wind patronen, shear stress), interne thermale structuren (seiches en mixing) en de hoeveelheden interne plantnutriënten (hoofdstuk 5). Er zijn duidelijke aanwijzingen voor een inverse relatie tussen deze Wedderburn nummers en de gemiddelde concentraties van opgeloste vormen van stikstof en fosfaat in de fotische zone. Bij lage Wedderburn nummers (<1), werden significante hoeveelheden nutriënten gedetecteerd.

Deze perioden, net als bij de secondaire opwelling benedenwinds, vielen samen met een toename in chlorofyl-a, maar konden niet gerelateerd worden aan hogere primaire producties. Over het algemeen waren in het noorden de primaire productieniveaus tot viermaal hoger dan in het zuiden van het meer. Ook bleek primaire productie in het noorden het hoogst tijdens het droge seizoen, juist wanneer thermale structuren intensiveren en dieper zinken.

Naast de mogelijkheid dat tijdens deze periode de primaire productie positief beïnvloed kan zijn door opname van nutriëntenrijk hypolimnionwater, verbeterde lichtcondities onderwater of externe nutriënten afkomstig van nabij gelegen riviersystemen, vonden we over het algemeen een zwakke relatie tussen chlorofyl-a concentraties en primaire productie.

De Wedderburn nummers varieerden van jaar op jaar. Tijdens de jaren gekenmerkt door zwakkere winden was het oppervlaktewater warmer. De thermale gradiënten versterkten zich, en over het hele meer werd een afname van opwellingintensiteit en seiching waargenomen. Dit impliceert dat tijdens kalme jaren nutriëntgehalten en fytoplanktongroei lager zijn. Hoewel de opgeloste fosfaathoeveelheden in het zuidelijke opwellinggebied niet veel veranderden, waren opgeloste stikstofconcentraties in de eufotische zone tijdens de jaren met kleine Wedderburn nummers hoger.

Langs de noord - zuid as van het meer werd een door de wind veroorzaakte graduele verandering waargenomen in de fysische en chemische kenmerken van de productieve zones. Opgeloste zuurstof, turbiditeit, conductiviteit, fosfaat en chlorofyl-a namen naar het zuiden toe en de temperatuur- en pH-waarden namen af.

Een transitiezone waar de verticale structuur van de waterkolom veranderde van de noordelijke naar zuidelijke condities (gelegen op 6 - 7^o ZB) gaf aan tot waar de invloed van het opwelling evenement in het zuiden zich doet gelden. Dit omvatte dus niet de door de Rusizirivier beïnvloede gebieden ten noorden van 4^o ZB. Daar zijn troebelere wateren gekenmerkt door een lagere conductiviteit en pH en hogere chlorofyl-*a* concentraties.

Een grotere mate van heterogeniteit in nutriëntconcentraties (vooral fosfaat) veroorzaakt door verschillen in de intensiteit van menging lijkt een direct invloed te hebben op de planktonleefgemeenschap. Tijdens het droge seizoen werden de noordelijke wateren gekarakteriseerd door lagere nutriëntenniveaus, een lagere fytoplankton biomassa en kleiner zooplankton, met cyclopoiden (voornamelijk *Mesocyclops aequatorialis aequatorialis)* in de hoofdrol. De turbulente wateren in het zuiden werden gekarakteriseerd door een toegenomen beschikbaarheid van fosfaat, hogere fytoplankton biomassa en groter zooplankton, dat gedomineerd werd door calanoide grazers (voornamelijk *Tropodiaptomus simplex*).

Zolang de jaarlijkse hydrodynamische sturing tijdens het droge seizoen de fysische, chemische en biologische structuren in het noorden en zuiden in stand houdt, zijn verschillende voedselwebstructuren in het meer waarneembaar.

Om de relatieve bijdrage van nutriënten te bepalen aan het budget van het gehele Tanganyikameer werden externe bronnen als rivieraanvoer en atmosferische depositie onderzocht (hoofdstuk 7). De fysische en chemische kenmerken van de drie grootste instromende rivieren (Rusizi, Burundi; Malagarasi, Tanzania; en Lufubu, Zambia) en de natte atmosferische depositie in Bujumbura, Kigoma en Mpulungu, lieten grote onderlinge verschillen zien in hun jaarlijkse dynamiek.

Hoogte, ligging en morfologie van een riviersysteem bleken grote invloed te hebben op de watersamenstelling, terwijl biomassaverbranding en atmosferische depositieprocessen lokale regens beïnvloedden. Rivierlading was het hoogst aan het eind van het regenseizoen (april - mei), met de Rusizi als de grootste en de Lufubu als kleinste bijdragende rivier. De grootste mate van depositie vond plaats in het noorden, nabij het dichtbevolkte en geïndustrialiseerde Bujumbura. Hier waren de concentraties beduidend hoger aan het begin van het regenseizoen.

De rivieren waren significante bronnen van silicaten en fosfaten terwijl de regen het meest van de opgeloste stikstof leverde. Netto nutriëntenhoeveelheden uit natte atmosferische depositie en die afkomstig van de rivieren zouden omgerekend een jaarlijkse productie van 45 tot 60 g C m^{-2} (ruwweg 10 % van de jaarlijkse primaire productie) tot stand kunnen brengen. Als deze bronnen samen pieken in februari - mei, is hun potentieel naar verwachting in het noorden nog hoger omdat daar dan het opgeloste nutriëntgehalte lager is.

In het Tanganyikameer is naar verwachting de primaire productie van het fytoplankton de hoofdbron van energie voor de hogere pelagische trofische niveaus, inclusief vis. Kennis van de trofische structuur en van de energieoverdrachtsefficiëntie binnen de voedselketen is cruciaal om het visserijpotentieel te bepalen, ook in vergelijking met dat van andere wateren. Voor aanvang van mijn studie werd gesuggereerd dat de geschatte primaire productie niet genoeg was om als basis te dienen voor een relatief productieve visserij (circa 60 kg ha^{-1} jr^{-1}).

Het Tanganyikameer wordt wat betreft zijn voedselwebstructuur qua functioneren regelmatig vergeleken met marine systemen. De pelagische zone, net als die van de meeste marine regio's, zouden zich kenmerken door kleine, maar hoogproductieve planktonbiomassa's, waar dankzij een efficiënte koolstofoverdracht tussen de schakels van de voedselketen uiteindelijk een relatief groot deel van de primaire productie zou kunnen worden vastgelegd als visbiomassa (hoofdstuk 8).

Echter, de primaire productie (426-662 g C m^{-2} jr^{-1}) bleek 47-128 % hoger dan bekend was. Bacterioplankton droeg voor circa 20% bij aan de primaire productie, terwijl de zoöplanktonbiomassa (1 g C m^{-2}) en de productiviteit ervan (23 g C m^{-2} jr^{-1}), ongeveer 50% lager waren dan voorheen gepubliceerd was. In tegenstelling tot eerdere speculaties, suggereert dit dat de koolstofoverdrachtsefficiëntie van fytoplankton naar zooplankton laag is. Gezien de biomassa van de planktivore vis (0.4 g C m^{-2}) en productiviteit (1.4-1.7 g C m^{-2} jr^{-1}) lijkt er verder ook een vrij lage overdrachtsefficiëntie tussen zooplankton naar de productie van planktivore vis te bestaan.

Voor een diep tropisch meer zoals Tanganyika komen relatief lage niveaus van energieoverdracht niet onverwacht. Door de hoge temperaturen en de waarschijnlijk hoge kosten verbonden aan het ontwijken van de predatoren, zijn de metabolische verliezen bij de prooivissen hoog. Gedurende het midden van de jaren 1990 was de totale visserijopbrengst 0.08-0.14 % van de pelagische primaire productie, hetgeen valt binnen de reeks van typische waarden voor meren. We kunnen dus concluderen dat het niet nodig is een afwijkend mechanisme te veronderstellen voor het verklaren van Tanganyika’s productieve visserij.

In het Tanganyikameer zijn meteorologisch en hydrodynamisch aangestuurde veranderingen in fysische, chemische en biologische eigenschappen van de pelagische zone belangrijk omdat ze de structuur en het functioneren van de voedselketen beïnvloeden. De veranderende opstructuur van de voedselketen bij verschillende intensiteiten van hydrodynamische aansturing verklaart de waargenomen korte- en lange-termijn verschillen in de trofische status van het Tanganyikameer. Dit verklaart de fluctuaties in de opbrengst van de visserij, die zulke verstrekkende sociaal-economische gevolgen heeft in dit dichtbevolkte gebied.

Het is belangrijk dat in de komende vijftig tot honderd jaar de invloed van de opwarming van de aarde op de trofische status van het Tanganyikameer en de hiermee samenhangende eventueel veranderende visserijopbrengst worden gemonitord. Recent onderzoek beweert dat de stabiliteit van de waterkolom al is vergroot door de hogere temperaturen en veranderingen in windpatronen en dat het gehalte aan nutriënten daarom al zo is verminderd, dat de fytoplanktongroei en zelfs de visopbrengsten afgenomen zijn.

Hoewel hier een omgekeerde relatie is vastgesteld tussen de sterkte van de stratificatie en de nutriëntlading, hebben toegenomen nutriëntconcentraties veelal niet geleid tot een hogere primaire productie (hoofdstuk 9). Daarnaast kan sinds het midden van de jaren 1970 geen duidelijke trend gevonden worden in fytoplanktonbiomassa en watertransparantie, terwijl de visserijopbrengst is toegenomen. Het is verleidelijk om op te theoretiseren dat de klimaatsverandering de belangrijkste factor is die de visvangst in het meer beïnvloedt. Toch laten de gegevens op dit moment zien dat het intensiveren van de visserij de belangrijkste doorslaggevende factor is geweest.

Het Tanganyikameer vormt een uniek ecosysteem, dat een ongekende rijkdom aan endemische soorten omvat (vissen, krabben, garnalen, sponzen, etc). Het is bovendien een extreem waardevolle bron van voedsel (dierlijke eiwitten), transport, drinkwater en irrigatie die de basis vormt voor het welzijn voor miljoenen mensen in regio. Het duurzame behoud van dit ecosystemen vraagt, naast een verstandig gebruik ervan, om een actief beheer (hoofdstuk 10). Een versnelling van het exploitatieniveau en door de mens teweeg gebrachte ontwikkelingen elders in het stroomgebied brengen urgente problemen met zich mee, die begrepen moeten worden in het licht van een veranderend klimaat. Helaas heeft de aandacht van politici, ontwikkelingsbeleidmakers en internationale donoren slechts een tijdelijk karakter. Hun interesse in een bepaald beleid of in een project is veelal niet langer dan de tijd die ligt tussen twee opeenvolgende verkiezingen. Door dit gebrek aan permanente betrokkenheid raakt de onmisbare financiële of technische assistentie bij de uitvoering van een houdbaar beheerssysteem in het slop. Steeds vaker lijkt daarom crisisbeheersing de plaats in te nemen van lange-termijn beleid. Dientengevolge hebben veel internationaal opgezette onderzoeksprojecten, ondanks de beste bedoelingen, nauwelijks of geen consoliderende vervolgfase en dus weinig lange termijn effect. De basisvereisten zijn een grotere specifieke en duurzame nationale en internationale interesse, zoals die bijvoorbeeld aan tropische bossen of koraalriffen gegeven wordt. Het unieke ecosysteem van het Tanganyikameer is dit zonder meer waard.

Acknowledgements

Me and my girlfriend, Petra Paffen, never imagined working both in Africa while studying aquatic ecology in the Netherlands. It was pure chance that our study friend Jeroen Creuwels noticed a vacancy for this project by the Dutch Ministry of Foreign Affairs, DGIS. As we conducted our studies at none-applied scientific universities (Groningen and Amsterdam), we had never even considered the possibility of starting jobs via our ministry in a UN organisation. At the time, we were trying to get PhD jobs in New Zealand and even Canada. We both applied and got employed by the UN. Thanks Jeroen, without your tip, our lives surely would have turned out quite differently. We surely would have missed this splendid opportunity to experience Africa as it is: heartbreakingly beautiful, wild, full of opportunity and wonderful resilient people, but also sadly troubled by lots of complicating factors. I do not believe I could have learned so much in so little time elsewhere.

We started our work in December 1993, at the project headquarters in Bujumbura. The country had already fallen into civil unrest since October. When we arrived, the city was still full of repatriating expatriates whose development projects all had ceased to exist and who were helping the embassy programmes to provide humanitarian relief, mostly by trucking blankets, food and medicine. While they were going out, more solid humanitarian relief programmes by UNHCR, WFP and other organisations were set up. I believe we where one of the very few development projects that continued their work in those years. We were lucky; the lake was safe enough to do so, in contrast to most parts of the city and the country as a whole. While everybody hoped that the worst of the situation was had, month after month, it never did during our stay around the lake (up to this date a UN security phase 3 and thus a curfew is still in place). In 1994 all hell broke lose in Rwanda and in 1996 Zaire also began to unravel, starting in the provinces neighbouring Rwanda and Burundi. From then on, all of the lake became the Wild West as trouble crosses borders easily.

Our start-up team at the fisheries department in Bujumbura and their colleagues from D.R. Congo were simply great. I would love to hear how things are now. Eduard Nikomeze, Bernard Ndimunzigo, Kalala Tshibangu, Bwebwa, Kakogozo, Jean Marie Tumba, Emmanuel Gahungu, Charley Butoyi, Sebastien Nyamushahu, Kimbadi, Roger Varayannis, Rugoreka, Sinanka, the managing, sub director of the Fisheries Department in Bujumbura, Boniface Nyakageni and our friend, project secretary and organiser of (almost) everything, Mamert Mamboneza. The unfortunate and far too early demise of Boniface, Mamert and Tschibangu has moved us deeply. We will always miss your warm sympathy. Our international colleagues of the Belgian project CPGL, who provided valuable help to the project, we thank you for sharing the vision "in heaven is no beer that's why we should drink it here" and the cheers and good times during hard living: Alain Vandelannoote, Luc de Vos and Luc Risch. Tuur (Luc de Vos) has also passed away. We miss your wicked smiles.

I remember our inventive and diving friend Jean Luc Kesh (alias Gaston lagaffe), our "Italian connection" and friends Raoul Balleto, Gabrielle and Antonella Maraviglia, our dear, Belgian friend Emanuelle Legrand and our Dutch friends Toin and Mieke de Leeuw. All get our love. Le petit Suisse will always be remembered as one of our greatest heroes, making Italian ice and serving cold beers during a civil war so far from home is way out. All of you have introduced Africa to us.

Things became hairy at times, bullets everywhere, the numerous roadblocks, the hippo attacks, the bodies and the occasional pirates, how crazy and unreal it sounds, it became almost a part of a regular Burundian day.
Anyway, after a near 300 morning calls of our regional UN security officer code name "whiskey" and a last "bien reçu whiskey, et bonne journée" from me as Romeo deux….we moved in February 2006 to our second duty station in Mpulungu.
After four days with all our stuff, a brand new four wheel drive and four dogs on the VIP deck of the passenger vessel Liemba, we set foot at the most southern harbour at the lake. Incredibly to us at the time, none of the bystanders offered some help with luggage or whatever. Apparently earning titbits or more, simply was not known, expected or cared for in Mpulungu.
At our arrival the harbour officials seemed unbending to rules we had never even heard of. Sent us straight to the capital at 1200 km distance to sort out matters. Twice, as we returned with papers that lacked something I cannot remember now. Luckily Gabrielle, Antonella and

their Burundian driver had already settled into Lusaka and supported any kind of help to find our way around the city and the city officials. It was truly wonderful to see you again, get some shelter and perspective.
Mpulungu was hot, dry and outback. Shoprite and cell phones had not yet arrived. There were only two, continuously overloaded, or simply broken, outgoing telephone lines connecting the region to the rest of the world. There was onions, cabbage and tomatoes. For all kinds of papers and real shopping, we had to drive to Lusaka. Mortal danger came not from civil war, but from snakes, mosquitoes and other disease.

Our harbour saviour was Luc Bupe Powels. Young, dashing and on bare feet, he translated our requests in local tongue and got our stuff deposited into the garden of the house of our Dutch colleagues. After their departure to Kigoma, we rented the same house and even built a swimming pool in its garden. Luc, Steph and his extended family and friends from the village of Kasama at some 300 km distance on the road to Lusaka, instantly became and still are, good friends. Just as the Dutch graduate students, Ralph and Tiesha Kohne that became coffee farmers on one of the first large coffee plantations (Isanya estate) that returned to the area around Mbala at the time. Our local, musungu neighbours where Beryl and Paul Nielsen, with whom we spent some joyful evenings and the ‘local’ Greek owners of so called industrial fishing companies, Andreas, his son Miltos, daughter Helena and colleague Dimitri. We were dumbstruck to hear that Dimitri died of a heart attack. Never heard so many truly adventurous stories of fishing in the region all the way up to Lake Edward. And always accompanied by quick and boastful laughs. We will always miss his splendid company and hospitality. Dimitri was a Hercules to his friends.

So, at second glance, our time at Mpulungu provided lasting friendships and incredibly wild adventures. We bought a boat, sought out our diving, fishing and golfing gears and had the time of our lives. The southern rift is a place of unknown wonders where otters, crocodiles and fish eagles pass the office windows at the fisheries department, you can have a football game with the village of Kasakalawe, find ancient humanoid bones at the Kalambo falls (now a protected prehistoric site) and rediscover one of the very first, steel, steam vessels ever to have travelled this magnificent lake. The Cecil Rodes was rediscovered at no more than 6 meter of depth during a diving trip by Phillip Nielsen, Michael and Petra during one of the boy’s school holidays. Its demise has been described in the account of warfare around the lake during the First World War as ‘being towed off the beach of Kassakalawe, where it was being refitted for war, after a brisk engagement with Rhodesian forces’. In fact the boys and Petra thought to find some helicopter with gold and diamonds from Zaire, but nevertheless thought to have had good fortune when they made their discovery. Petra still assumes its origins to date back from before the time that North Eastern Rhodesia was so called ‘pacified’ in 1900 and thereby is inclined to dispute the widely, acknowledged assumption that it was the Good Hope that was the first of such vessels on the lake in 1890.

As co-chair of Mbala golf course together with a few regional players we gave a great impulse to junior golf. We had several youngsters playing off scratch in 1998. Lessons were given and we turned out well and competitive. We became known throughout Zambia while playing some great tournaments; we grabbed the best prices on several occasions.

I like to remember the warm collaboration and support by our Mpulungu counterparts: Laurens Makassa, Charles Lukwesa, Rubin Shapola, Isaac Zulu, Edward Chipulu, S. Sichivu, Kenneth Kaoma, J. Chimanga, B. Kassikila, C. Sichamba, Mr. Chomba and Mr. Harris Phiri. We have been very sad to hear that their manager at the time, friendly, kind and just Leonard Mwape, had suddenly passed away.
It is impossible and would be unjust not to mention our warm felt thanks to our driver and brother Chisambo and Denis. Chisambo got all things you wished for. Driving up and down a thousand times to get the stuff and even found topsoil for our garden. Denis was always at his lodge to listen, share beers, number ones, experiences and wisdom. Denis made everybody connect just by being himself. We miss you both and love you.

Our many trips to Kigoma had us experience the lure of the great discoverers as Burton, Speke, Livingstone, Stanley and Jane Goodall. We have seen Kigoma during diving trips with the local diving bunch from Bujumbura and by visiting on project business. It was always cheerful and peaceful. We have no idea if Sally Ann is still living at her chimp peninsula, but send our warm regards nonetheless. Keep on laughing girl, your life is beautiful. Thanks to Astrid and her husband, also in tow for a Jane Goodall fund, and always helpful and good fun.

Our Tanzanian counterparts were many. We particularly thank E. W. Lyoba, D. Lyoba, M. Chatta, N. Challe, S. Muhoza, A. Kalangali, E. Kadula, O. Kashushu, W. Kisisiwe and M. Agustino. We remember Chitamweba as the driving force of it all. A striking figure, tall, sophisticated and very humorous. Thanks man, we thought we would never (but we did) forget the longest name of that Gaelic village you pronounced effortlessly during the 1995 Lake Tanganyika symposium in Kuopio.

Of course, our international colleagues at LTR are unforgettable: Firstly our Canadian, managing coordinator Dr. George Hanek who boxed us through all. He notoriously nurtured a rather fancy golf handicap. When we played together on numerous fantastic golf courses he must have “fired my ass” a thousand times. He could immediately bring flair and spice on to the golf course and in the project. I thank our Belgian, first scientific coordinator Eric Coenen who coached us through all; our British, second scientific coordinator Dr. John Craig who provided some common sense; our Finnish hydrodynamical officer Pekka Kotilainen (alias Mika Häkkinen) and of course Mervi Heinonen that stood fast; our Belgium, limnologist Pierre Dennis Plisnier who brainstormed the hell out of us; our Italian, fish biologist Pierro Mannini who incredibly could and probably can put matters into perspective; our zooplankton officer Heini Kurki who always provided shelter while we were in Kigoma and our Dutch associate professional officers, Els Bosma and Piet Verburg who helped us set up in Mpulungu when we swapped stations in 1996.

It is important not to forget to mention the crazy effort and goals we achieved by building a new, large, pelagic trawler and research vessel, the Tanganyika Explorer. She was built between 1994 and 1995 by Greek entrepreneurs at the harbour of Bujumbura while a large part of the town and the county were slashed and bombed night after night. The equipment was fitted in French and English while the Dutch, Danish and Finnish experts harmonised it all while. The Swahili speaking technicians were basically coordinated in Greek. It worked nevertheless, in record time she was in the water. The R/V Explorer was a magnificent asset to our research, as she enabled us to cruise the lake for months at a time. She was equipped with lots of wondrous tools, a lab and a wonderful, able, regional crew. Regards to our captain, Mr. Lukwesa, his first officer, Mr. Challe, the engineers, Mr. Robert and Mr. Suleiman and the main deckhand Pio.

We have conducted more than ten lake wide cruises on varying subjects between hydrodynamics and zooplankton to fish biology. All of them real exploratory as we sampled the most exquisitely, intriguing sites where no roads, footpaths or ranging vessels from the stations had ever sampled before. I remember lowering the oxygen sampler during the night above a location that was more than a thousand meter deep, while our spotlight hit a wall of Congolese mountain rock at no more than 50 meter distance. The waters were really calm and it was impossible to see either the stretch up or the stretch down. It was easy to imagine undiscovered phenomena and species on either side. We always wanted to return diving at these Congolese coasts, but never could at that time. Adventures came even in the middle of the lake; there were the pirates, the occasional rockets, vast swarms of jellyfish, clouds of insects that picked out our vessel as temporary resting place in the midst of a migration between Tanzania and Zaire, freakish storms, schools of Lates and Boulengerochromis attacking migrating fish larvae.
The whereabouts of the R/V explorer are not known to me these days. In 2006, she was seen towing barges across the lake….

Finland provided the most notable influence by enhancing scientific cooperation from diverse Finnish universities and scientific institutes. The Universities of Kuopio, Helsinki (including Lammi Biological station), and Turku and the Pirkanmaa Regional Environment Centre in Tampere provided a periodical but constant flow of materials, participating professors, senior scientists and students to visit us around the lake. The team with Ossi V. Lindqvist, Hannu Mölsä, Jouko Sarvala, Timo Huttula, Kalevi salonen and. Anu Peltonen were our scientific backbone in Finland. The Finnish connection remained after my return to the Europe. Though

at some seasons impossible to reach (especially when days become longer), it was their open mind, long breath, impeccable efficiency and underlying energy that provided the necessary solid ground to my efforts to establish and contain fruitful cooperation on this work. Thank you.

Surely the LTR project in whole wouldn't have worked without Jim Kapetsky, Scientific Coordinator (FAO), Dora Blessich and Mike Doeff, Project Operation Officers (FAO), and A. Bakun, J. Collins, A. Gribling and other officers of FAO involved with LTR for our "backstopping" support.

After returning to the Netherlands, it was the University of Wageningen that enhanced my continued work on this study. Other universities simply lacked the basis for appreciating the unique data and at the time, I was unable to convince them on it. As it turned out, Wageningen was the place to be for this kind of stuff. Its support and relations fitted perfectly. Rudy Roijackers, Martin Scheffer, Bart Koelmans, Marijke Kuijpers (daaaaaag lieverd) provided an office and all helped. Together with funding from the Centre for International Mobility (CIMO) of the Finnish Ministry of Education, extensive visits tot Finland (1 year in Turku and Helsinki) could be arranged, during which I published some of my work. I thank them but also the other colleagues of the Department of Aquatic Ecology and Water quality Management of the Wageningen University and Research centre (WUR, The Netherlands), I hope we will pick up some promising projects together again soon.

I am indebted to my friend Frits Roest. He has supported me on many occasions; helped introducing us to the FAO system, helped me into the Wageningen University and even found time, next to knocking up a wonderful Karl may book, to help me editing my thesis. Just by being honest and reflective he is one of the best project evaluators I know. I have great respect for his judgements.
Also Thanks to Martin van der Knaap, I hop you will make a quick start of the new Tanganyika Project. Me, Frits and also Martin van der Knaap still occasionally meet and catch up during our travels to Africa in the framework of the Great Lakes of the World initiative of the Aquatic Ecosystem Health and management Society (AEHMS)

The revisions and suggestions made by J. Coakley and Graeme Patterson (married now!), H. Bootsma, R. E. Hecky are greatly appreciated. Especially the talks with Dr. George Coulter from New Zeeland I found wonderful. He was one of the first to study the lake and actually wrote a comprehensive book about it. His "bible" (as we refer to it) is undoubtedly the most quoted work on Tanganyika. His knowledge provided valuable help, revisions and advice. I thank him dearly for his help and support.

While I thought to do it in a maximum of three years, it is 8 years since I started this endeavour. Lucky for other plans (that cost money), in 2003 I got a job at our Ministry of Wateraffairs. Thus I had to work on in the evenings. Meanwhile, Petra and I got settled, bought a house, got two wonderful boys and rolled into a family life as it is with two working parents in the Netherlands. Petra often tells me that it is this thesis and my other African work that has derived from it (AEHMS and the Foundation for the Development for Sierra Leone), that enables her to remember and reflect on our time around Tanganyika. Both of us are really happy this stage of our connection is now over and finally produced, but we will always appreciate the possibility given to go, stay and remain connected by this work. It was and is absolutely fabulous to have done this.

Yes, it is important to put these acknowledgements into the perspective they deserve. The LTR project and our lives around Tanganyika simply would have been impossible without the enormously positive and inexplicably kind help by all our local colleges and friends. There were so many people involved that it will be impossible to thank all accurately after all these years. So let it be known to all our local and international colleagues, friends, fishermen, captains, chiefs, drivers, secretaries, repairmen, fundies, neighbours, house and harbour personnel, divers, golfers, (flying) doctors, entrepreneurs, cooks, travellers, barmen and their clients that we thank you for your own, colourful contribution to our lives around the lake and remembrance of it. No one can exist alone, certainly not in Africa.

To end these acknowledgements, I would like to introduce you to a sample of local Tanganyika energy and humour. What follows is the translation of the theatrical play on fisheries by the local, Mpulungu theatre group Zapota (famous for their best male striptease act in Africa).

You see, for implementing sustainable fishing practices or regulations following science-based fisheries management, workable contact and communication with the “real” stakeholders (e.g., the common fishermen) is a prerequisite. In Tanganyikan region this requirement has never been straightforward. Undesirably, among the Tanganyikan fishing villages and settlements, high illiteracy rates are common. Also, in these places, rather frantic and at times dangerous forms of scepticism have been demonstrated at times government officials came to visit to inform fisher folk on new measures.

Considering the success ZAPOTA had in disseminating crucial information on cholera or aids among the remote communities in Zambia, it was agreed to produce a theatrical play on causes and consequences of the current lake fisheries’ state.

It is all about being committed and bringing message across….

The play

“The Cause is mankind”

By ZAPOTA
Mpulungu theatre group (Zambia)

Scene 1: opens in Yakobo Kambole’s house at Kapoko village near Mpulungu. Orator: Maria Kambole hurriedly prepares nshima. She has been away for most of the day looking for food. She has been away with John Mfula her husband’s work mate but also her lover. Meanwhile Mr. Kambole has been playing a fool all along. But when he returns home very tired and hungry his patience is almost stretched to the limits when he doesn’t find his food ready especially now when he knows why…..

Maria: welcome dear.
Kambole: what’s that?
Maria: what? (She dares not to look at him)
Kambole: (vigorously pointing at sugar canes) that!
Maria: (with defiance) but you have seen it! Mhuuu!
Kambole: mhuuueee! Is that the way your mother taught you to answer me?
Maria: why do you always bring in my mother when…..
Kambole: shut up you! You are coming from Kasakalawe, that’s where you bought these sugar canes. Now tell me my supper is not yet ready, already. You know I am going on fishing. What have you been doing all day long to be frying Kapenta now? Where is all the money I gave you for relish (munani). (Kicks pan scattering everything all over the floor).
Maria: (freighting anger). Where do you think I….
Kambole: you daughter of a goat (he stands close threateningly, and then withdraws from her sniffing angry). Who brought you the sugar cane eh? Is it that Mfula son of a rat eater eh?
To tell you the truth Maria don’t think i am a fool. It is not me who brought poor catches on this Lake Tanganyika. You have been taught several times thinking they were telling lies. You know Maria; fish on this lake has been finished. Now thinking because I always come home with nothing it has been a passport for you to look for people with money eh!!! Fine!
Maria: (showing fear on her face) bu.. but.. but who told you I was going with Mfula? Is that good?

Kambole: there! There! Now! Suppose I call Mfula What reason are you going to give?
Maria: eeeeee!
Kambole: okay fine let me call him (exit)

(Meeting Mutale and Kambole)
Mutale: (in surprise) oh! God forbid what an obscenity now in this time of poor catches. Where do you think he will get any kapenta in this lake? Something must be done to punish Maria Kambole. She wants to spoil this village, like those unruly girls from our adjourning village who are wrongly brought up and do things to the disgrace of their elders
Villagers: (voices are heard from a far) (in a chorus)
Greetings to you all (after a pause)
Kambole: Greetings to you too.
1st villager: (in surprise) we have heard noises like you are quarrelling here, is it?
Maria: Nothing is happening here. Please can you all go back to your respective houses?
Mutale: Elders and people of this village called Kapoko having a problem of poor catches on this lake are a common man's concern (pause) old men of this village, mediators, native doctors have always convened to offer sacrifice but no sign of having good catches has shown so far, and this reminds me that we have got to be extra careful.
2nd villager: (triumphantly) elders of this village, I am glad that many of us here have learnt something from this lesson. There is need for our people with nets to open their eyes and say no to fishing and give a room for fish up to the rate of four (4) to six (6) months.
Kambole: (majestically) you see people from the government have been telling us several times. They promise paradise on every Jim and Jack (with emphasis) only a fool won't believe everything they say. It is for this reason that, let us all behold and look for our future, and at least we shall be liberated from this slavery.
3rd villager: Nonsense! You talk about things that you have no notion about? Have you ever seen one or two people from the government bring us fish in this lake? This is for god only.
Mutale: I feel I have done a lot of talking at this point in time. I ask anybody from this group who has got anything to say pertaining to this subject to stand up and do so… (Pause) feel free people this is a democratic society.
Muchawi: (stamming) bu.. bu..but..but, I heard from the group that Maria has been going about with John Mfula, is it true and what is your comment because Maria can not spoil Kambole's name when in this village Kambole is respected starting from the smallest to the biggest people.
Maria: (to Muchawi) who told I was going about with M..f..ula? is.. is it that no good meddling Mutale?
Kambole: There! There, now! Did he mention any names? Why do you mention Mutale? Common tell me why (he goes near her)
Mutale: Anyway, it seems Maria Kambole is over something isn't it? How can I involve myself in your affaires as if I am the one who has finished fish in the lake? Maria if you think Kambole is not a man just pack and leave him, god will give him another woman to marry.
1st villager: (murmurs of approval) I have also been seen a problem in this woman and something must happen to punish her.

END OF SCENE ONE
CURTAINS CLOSE

Scene 2: (the following afternoon Kambole and the people of the village went to the chief's palace) A spotlight then lights in the afternoon, Mutale from the auditorium emerges amid the tapping of his stick and then……..

Mutale: (to Muchawi) hey Muchawi !!, I bet we are not as late as everybody thought we would. Have you any slightest idea as to why the chief is summoning the whole village before this palace?
Muchawi: Oh no! I haven't but I suspect its something to do with Maria Kambole's wife of Yakobo Kambole.
Mutale: of course something must be done to punish her. She thinks that it is only this part of Kapoko where people are having poor catches. It is all over the lake shore even when you go to Chipwa, Nsumbu and so on!
Muchawi: (sharply cuts his pal) Shhhh! .. or that assembly will accuse us of having propped this story somewhere (they reach the left side of the stage, kneels down and claps three times they greet the assembly)
Villagers: (in a chorus) Greetings to you!
Kapaso: Shall we some silence over there! The chief is about to come, so when he comes let him find harmony among this people for he has news of great importance to you all (distant drums are heard, and then Kapaso nods his head). Those are royal drums aren't they! Let me find out.
(exit Kapaso) enter the chief, between 2 dancers who are dancing in the rhythm of the drums. Villagers kneel down as the chief reaches centre stage. He sits down on a thrown. Kapaso is behind the chief. The villagers greet the chief in a chorus).
Villagers: we greet you o chief lord our land..
Chief: (majestically) I respond (pause) elders and villagers of this land, the reason why I summoned you here is to let you know that this afternoon, this afternoon, I have a special announcement to be announced to you my people. First and not for almost I want to tell you that all along this lake was full of fish and now people are crying for fish. Yet they know the reason. I can tell you the story, before some of you where not born there were a lot of kapenta, buka buka and many more, But comparing to today so many have nets, tilly lamps all over the lake shore killing even small kapenta by using their small eyed nets. Do you believe that fish in the lake can live a long life?. No.no..no..no Now that you have no where to find kapenta or another fish in the lake Maria Kambole has tarnished her name because Yakobo Kambole goes fishing every day but comes home with nothing. And moreover if this system doesn't change I tell you my people hunger will continue killing us especially who are along the lake. I hope and still hoping that we are all together isn't it? Why can't we just come together as fishermen and see what to do. Do you want the government to send soldiers or what? Why can't we see that this is finished and that it exists for tomorrow?
Mutale: (murmuring) Mhuuuuu….mhuuuu…mhuuuu whats that!!
Kapaso: who's that uncultured villager; whenever the chief is holding the floor allow him to do so and thereafter he allows you to say something concerning the matter. Please Chief I call upon you and continue this issue before we leave this village
Kapaso: (again) I call upon you chief
Chief: (he shouts a slogan and villagers respond) my people, elders of this village, indunas, advisors and fishermen stricken villagers at large. Will you please give me your ears and get something from what I am telling you. I have not come here to quarrel with you but to teach each other how to keep this lake for ages and see what will be the outcome. But I heard one of you saying "mhuuuu it is a great lie…" Okay fine! Do you want the government to send soldiers? I am just adverting you as your chief because for tomorrow don't come and complain that you were not told. This Tanganyika Lake is yours and do not misuse it as it is now because even for the coming generation can come and also use it. People from the government and not so stupid for adverting you on how you should be catching fish in this lake. Therefore you must come and together as one and solve the problem. We are not like people in Tanzania or Zaire where they give room to the fish in this same Lake Tanganyika, but for us why can we not do the same. I think my people I have talked a lot. I am only allowing one person to ask me a question. Thank you (then sits down)
Mutale: (with happiness on his face) My chief, lord of the land, I have no question to ask but only thanking you for this special meeting. My chief everyone here is happy and when you go back tell the people from the government to come see you when you come again (drums are heard from the backstage and everyone freeze and introduce themselves)

THE END

Story by: Joseph Cossarm
Directed by: Stanely Chola and Cossarm Joseph
Coordinated by: Victor Langenberg

The Academic Board considers chapters 3, 5, 6, 7, and 9 as the actual proof that the candidate is capable of independently carrying out research. The Academic Board accepts that chapters 2, 4, 8 and 10 have been added to the thesis to create a more comprehensive overview of the limnology of Lake Tanganyika.

Curriculum vitae

Victor Theodorus Langenberg werd geboren op 10 juni 1966 te Uden, Noord Brabant. Na het doorlopen van de HAVO en het VWO aan het Kruisheren college te Uden, begon hij aan een studie biologie aan de Rijksuniversiteit van Groningen alwaar hij zijn propedeuse behaalde. Zijn eerste kennismaking met wetenschappelijk onderzoek was een visreproductie studie op Corsica. Na een grondige voorbereidingsfase op het NIOZ te Texel voerde hij in 1990 een stage uit op Curaçao waar hij als kikvorsman duikend onderzoek verrichte aan de regeneratie capaciteit van beschadigde rifbouwende koraalsoorten. Een overstap naar de Universiteit van Amsterdam leidde in samenwerking met het Natuurhistorische Museum te Leiden tot een stage in de Spermonde archipel te Ujung pandang, Indonesië. Daar onderzocht hij de invloed van de Jeneberang rivier op de aanwezige rifgemeenschappen. Na afronding in Amsterdam werkte hij kort bij een beginnend milieuadviesbureau ORCA te Groningen om vervolgens in 1993, via het ministerie van Buitenlandse zaken, in Afrika in dienst te treden als “associated Professional Expert” van de Voedsel en landbouw organisatie van de Verenigde Naties. Onder leiding van Dr. George Hanek hielp hij als visserijbioloog bij het opzetten van laboratoria in Burundi, Zambia, Tanzania en Zaïre en coördineerde hij wetenschappelijke monitoring op het Tanganyika meer. In 1995 nam hij als leidinggevende de coördinatie van een regionaal visserijonderzoekstation te Mpulungu, Zambia over. Bij terugkeer in Nederland in 1998 startte hij met de oprichting van het platform MEAL (Modelleren van Ecosystemen in Afrikaanse Meren) waar hij tot op heden met het helpen organiseren van correspondentiegroepen, workshops en conferenties, water experts bij elkaar brengt om met name de Afrikaanse expertise betreffende aquatische ecosystemen te vergroten. In 2000 is begon hij met zijn promotieonderzoek getiteld “Over de limnologie van het Tanganyika meer”. Onder leiding van Professor Sarvala en Professor Scheffer werkte hij verschillende publicaties uit te Wageningen, Turku en Helsinki. In 2003 trad hij als projectleider in dienst van het Rijks Instituut voor Kust en Zee van de Rijkswaterstaat en beoefende hij als senior adviseur het ambassadeurschap ten behoeve van de waterkwaliteit van de zoute rijkswateren in nationaal en internationaal verband. In 2007 accepteerde hij een zetel in het voorzitterschap van de stichting voor de ontwikkeling van Siërra Leone. Begin 2008 trad hij als senior adviseur in dienst van de unit Zee en Kust systemen van de zojuist opgerichte stichting DELTARES, te Delft.

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