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

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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-inforced 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 induce 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.

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 pseudoeutrophic, 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 & 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 & Podsetchine, 1994).

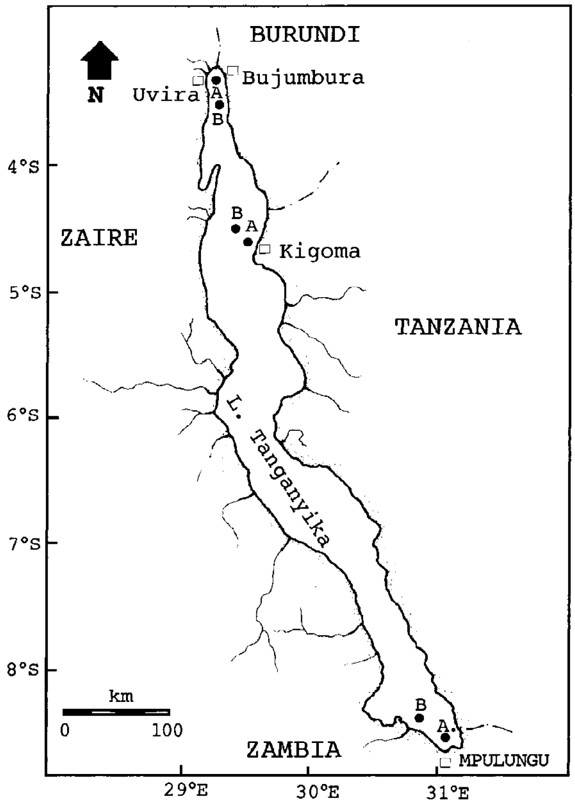


Figure 1. Location of sampling sites in Lake Tanganyika off Bujumbura/Uvira, Kigoma and Mpulungu (A = regular sampling, B = intensive sampling).

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 (Plisnier et al., 1996).

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^{3-}-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^{3-}-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. 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 turbidimeter 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

Physical and chemical variables

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 & 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 10–15 m 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).

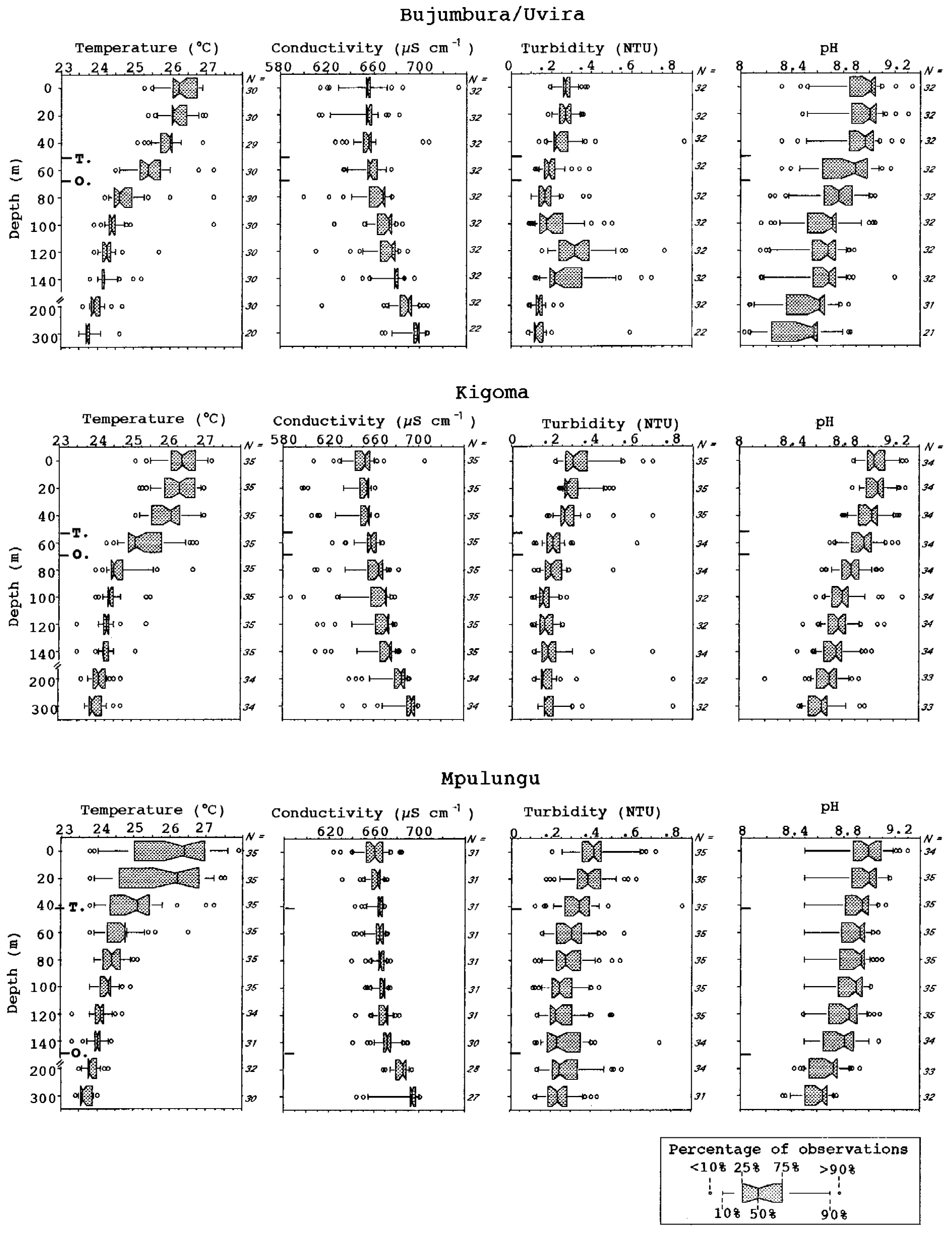


Figure 2. (A) Medians and percentiles of temperature, conductivity and pH. Samplings were made at intensive sampling stations. Depth of thermocline (T.) and oxycline (O.), calculated as the planes of strongest variation, are indicated. Sample size is indicated in italic.

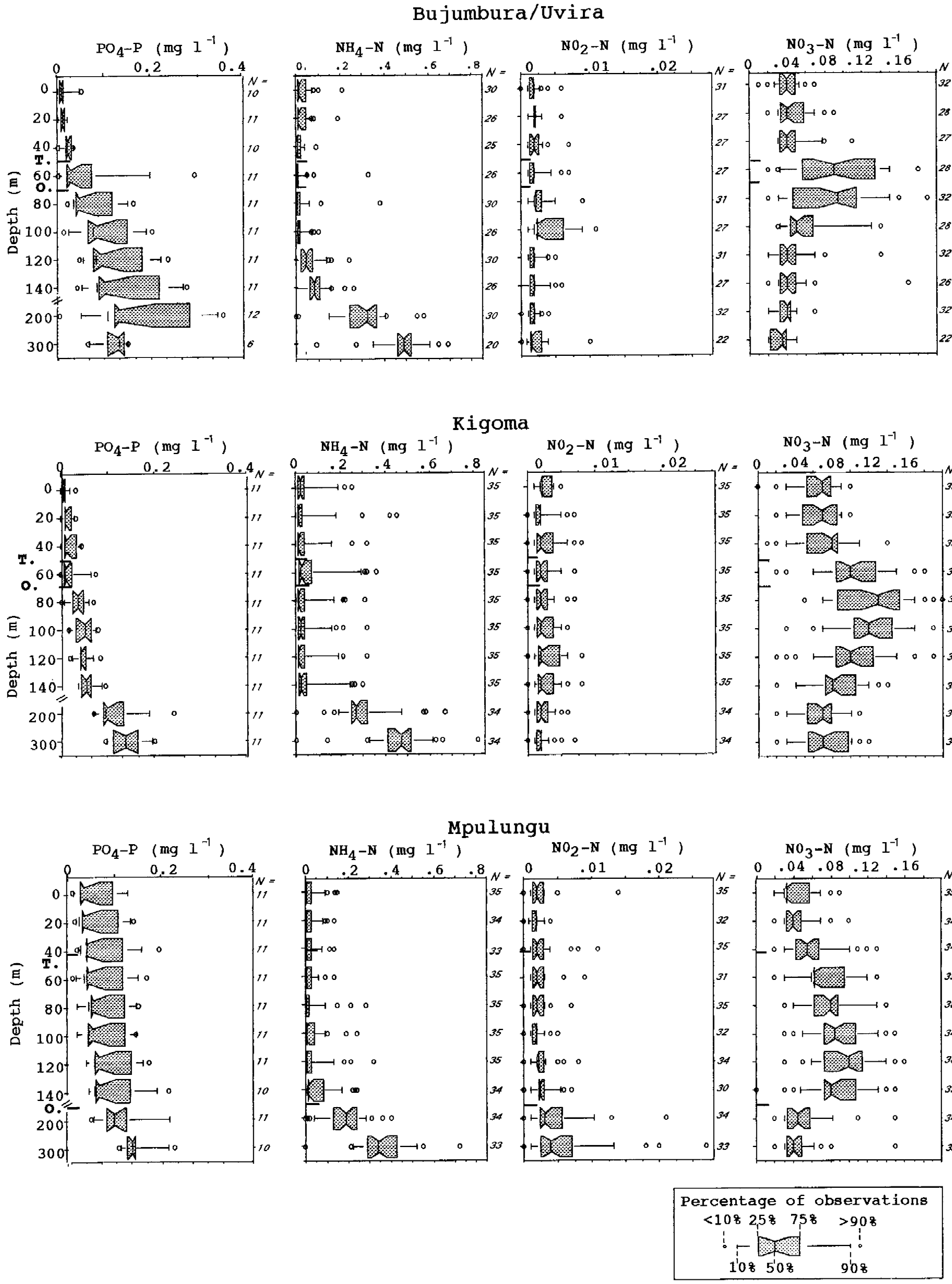
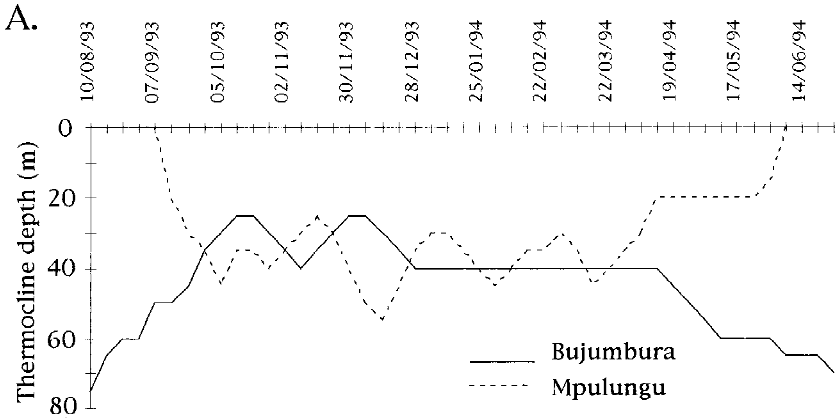


Figure 2. (B) Medians and percentiles of phosphate, ammonia, nitrites and nitrates. Samplings were made at intensive sampling stations. Depth of thermocline (T.) and oxycline (O.), calculated as the planes of strongest variation, are indicated. Sample size is indicated in italic.



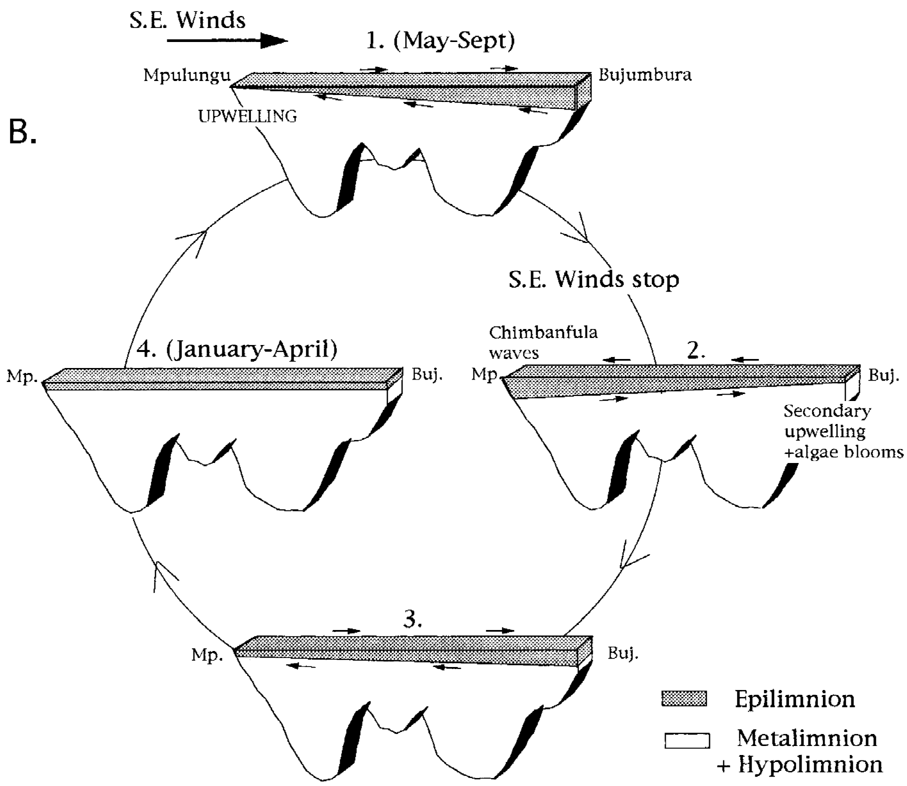


Figure 3. (A) Monthly means in thermocline depth at routine sampling stations (see Figure 1). (B) Schematic profile of water layers during an annual cycle. States 2 and 3 alternate before reaching stage 4. Internal waves are not indicated.

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 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. 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 was 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).

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 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.

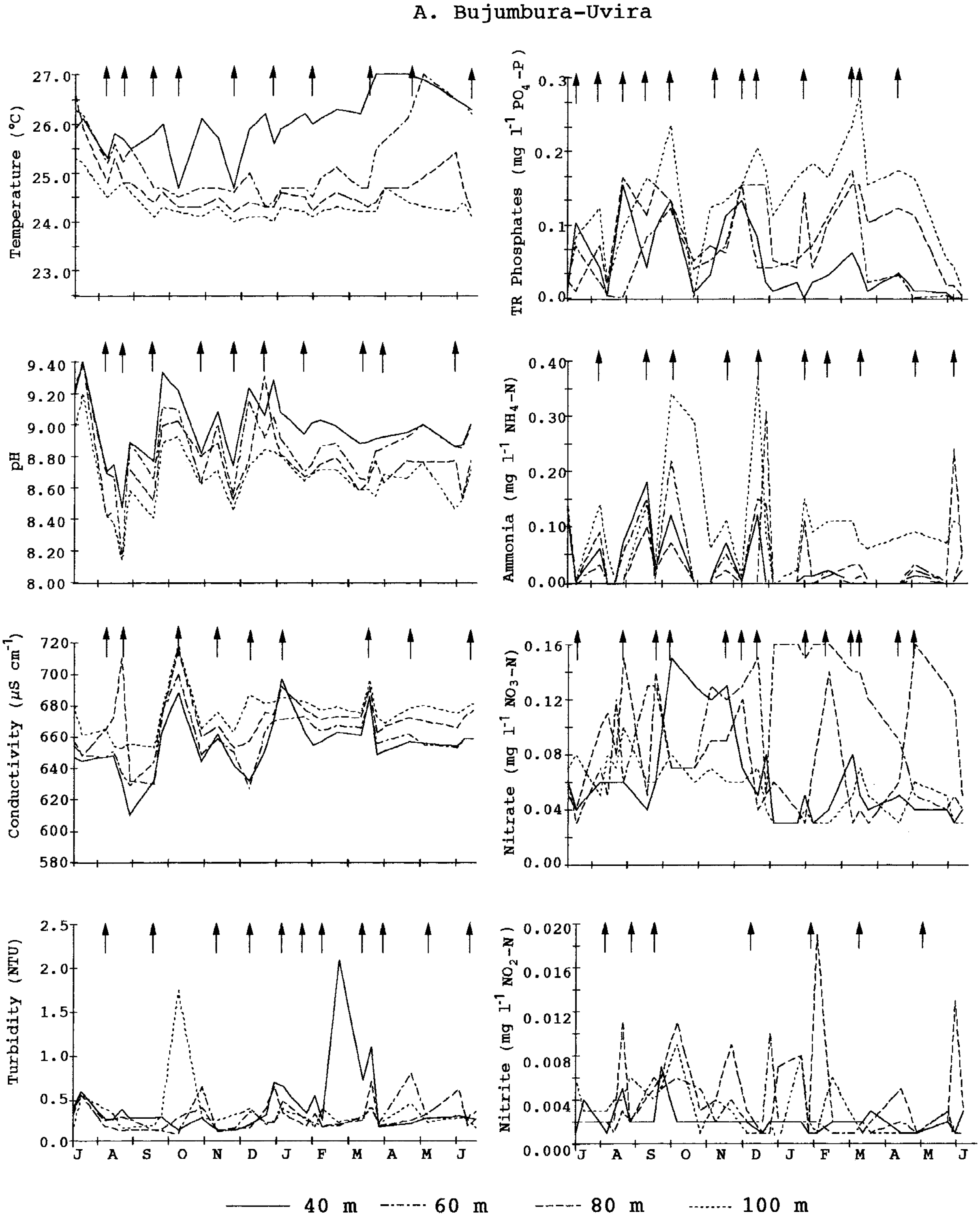


Figure 4a. Time series of temperature, pH, conductivity, turbidity, total reactive phosphorus, ammonia, nitrates and nitrites at the routine site of Bujumbura/Uvira in 1993–94 (4 depths drawn). Internal waves inferred from matching high values of conductivity, TRP, ammonia and nitrate and low values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

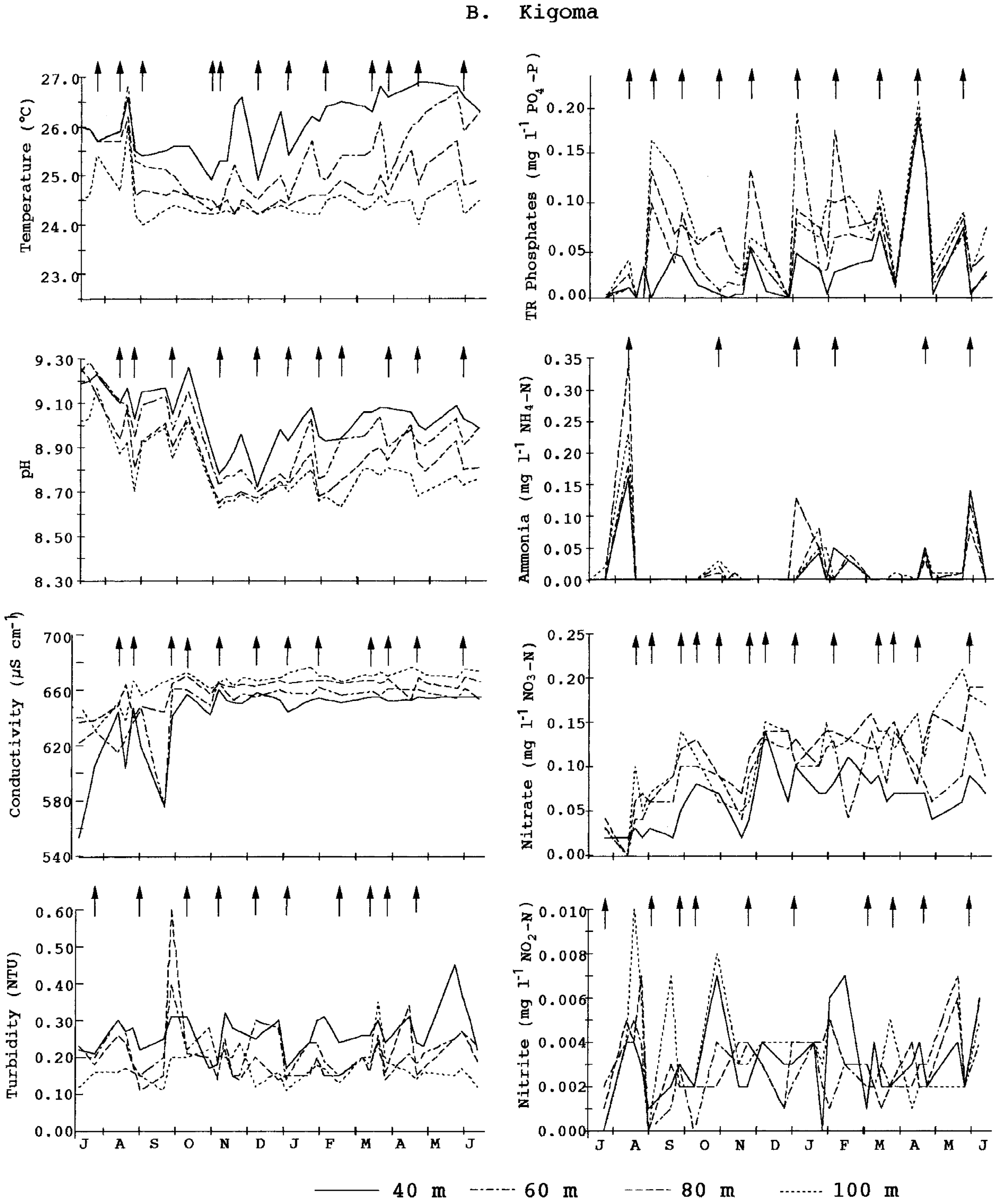


Figure 4b. Time series of temperature, pH, conductivity, turbidity, total reactive phosphorus, ammonia, nitrates and nitrites at the routine site of Kigoma in 1993–94 (4 depths drawn). Internal waves inferred from matching high values of conductivity, TRP, ammonia and nitrate and low values of temperature,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

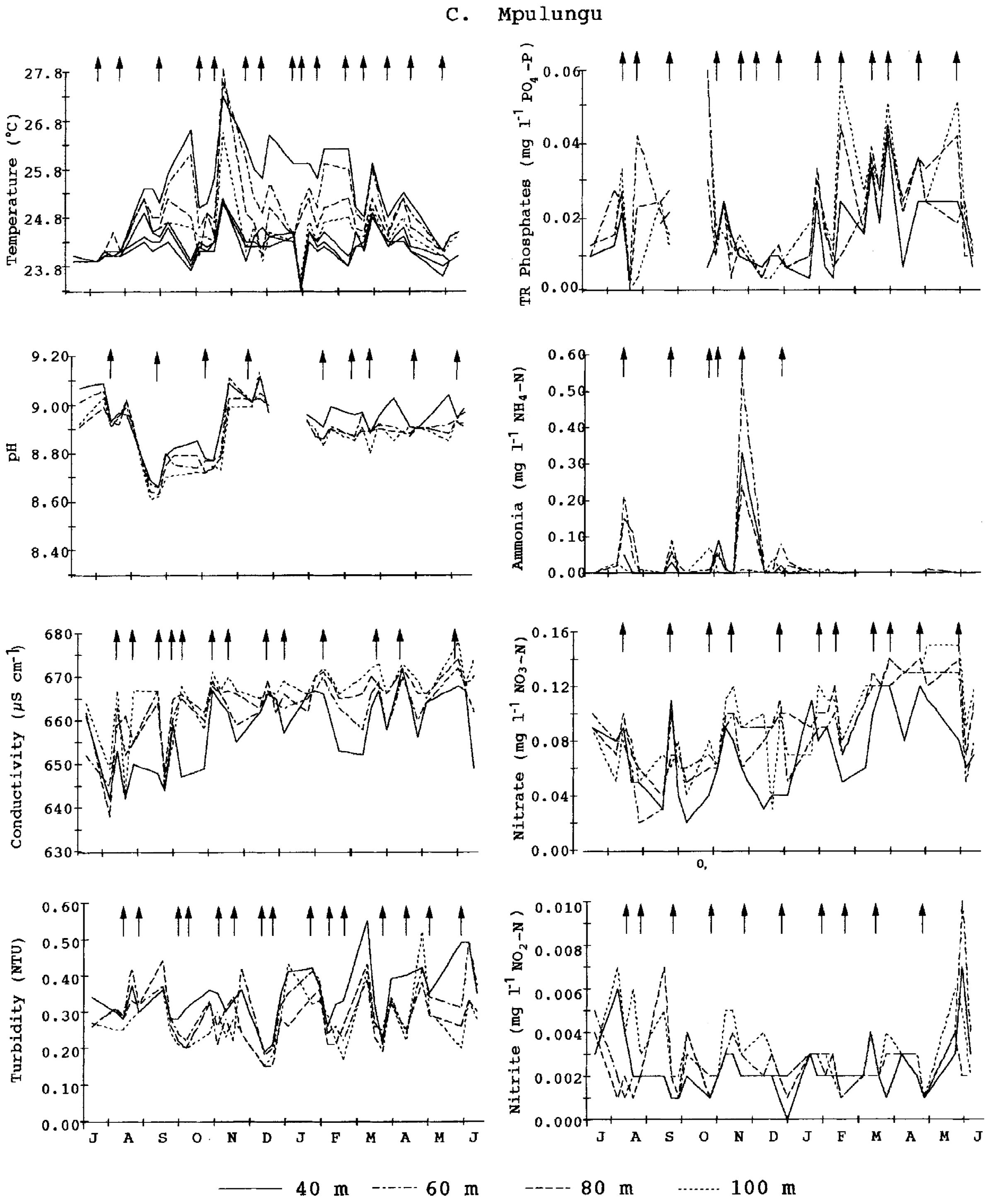


Figure 4c. Time series of temperature, pH, conductivity, turbidity, total reactive phosphorus, ammonia, nitrates and nitrates and nitrites at the routine site of Mpulungu in 1993–94 (4 depths drawn). Internal waves inferred from matching high values of conductivity, TRP, ammonia and nitrate and low values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

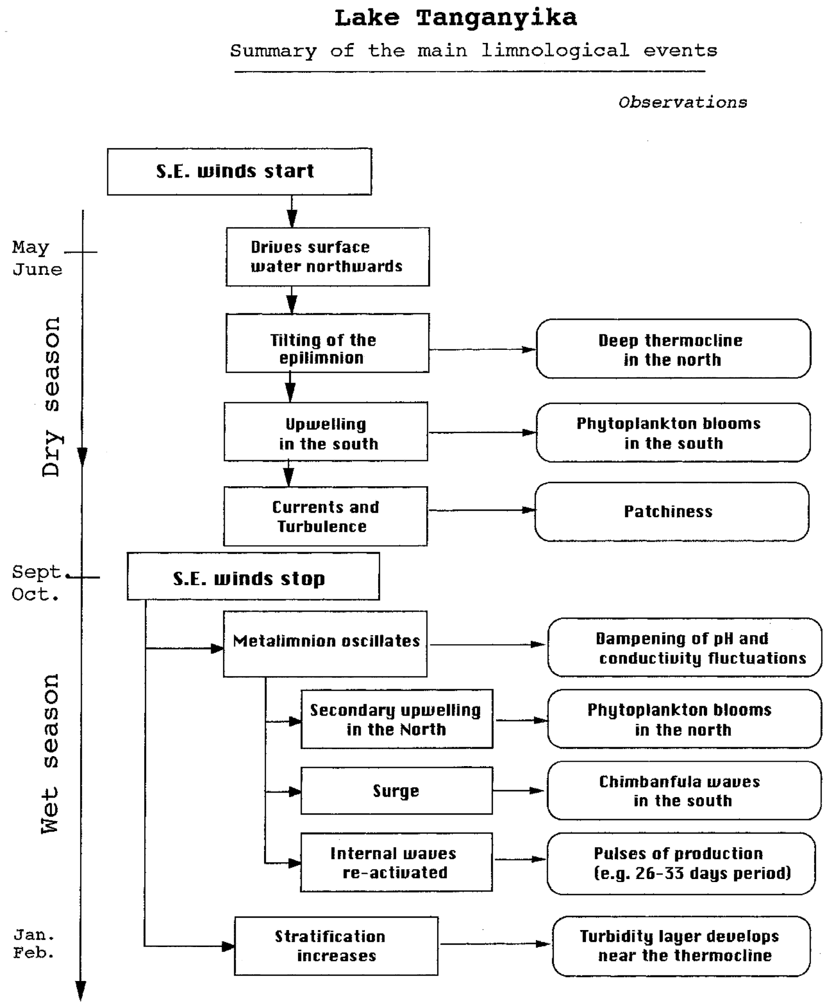


Figure 5. Seasonal hydrodynamic cycle of Lake Tanganyika and its consequences.

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 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 HCO_3^- 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 & 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 were 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 is not significantly influenced by river inflows in Lake Tanganyika as these waters are generally colder and sink rapidly 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 & 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 & 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 & 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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