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Lake Muzahi, Rwanda: limnological features and phytoplankton production

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Abstract

Lake Muhazi, a small lake of Rwanda (East Africa) was studied from 1986 to 1990. A dramatic decrease of the catch of *Oreochromis niloticus* (350 T y^{-1} in the fifties *vs* 30 T y^{-1} in 1982) suggested a loss of productivity or overfishing. In the same period, other ecological changes occurred: the submerged macrophytes regressed and there was a decrease in Secchi depth (0.65 m in 1987 *vs* 1.5 m in the fifties). Compared to other lakes of the same area, the plankton production seemed low. The results of the present study characterize lake Muhazi as a shallow lake with a rather unstable diurnal stratification and with slight differences in mixing regime between its eastern, deepest part and its western, shallowest part. Secchi disk depth does not vary seasonally to a large extent. The water has a rather high mineral content (conductivity of about 500 μS cm^{-1} at 25 °C) and low concentrations of dissolved N and P, except in the hypolimnion, where NH_4^+-N can be high.

Two species, *Microcystis aeruginosa* and *Ceratium hirundinella*, account for most of the phytoplankton biomass, which is about 50–80 mg chlorophyll *a* m^{-2} in the euphotic zone, usually with little seasonal variation. Daily gross production estimates amount to about 6 to 9.5 g O_2 m^{-2} d^{-1} with a significant difference between the two parts of the lake. Data on C:N and C:P ratio in the phytoplankton suggest that some N deficiency might occur in the eastern part. Moreover, the Zm:Zc ratio could also lead to rather low net production rates (0.21–0.25 d^{-1} for a mixed layer of 4 m)

In conclusion, the primary production of lake Muhazi is medium for African lakes and the hypothesis that decreased planktonic production could account for a reduced fish production should be discarded. Whereas the present yield of the fishery is only 20 kg ha^{-1} y^{-1}, the yield estimated from primary production ranges between 46 and 64 kg ha^{-1} y^{-1}. This could be reached through proper management. Finally, some hypotheses are given to explain the ecological changes which occurred in the lake.

Introduction

When compared to some other Rwandan lakes, the yield of the fishery of Lake Muhazi is low, at least for the most exploited species, *Oreochromis niloticus* L.: the catch per unit effort (CPUE) is 1.4 kg *vs* 27 kg in Lake Ihema (Plisnier *et al.*, 1988).

Lake Muhazi was originally inhabited by few species of fishes: one or two species of *Haplochromis* spp., still not formally described, *Clarias liocephalus* Boulenger, *Barbus apleurogramma*

Boulenger and *B. neumayeri* Fischer. Eight species have been introduced, such as *Oreochromis niloticus* (in 1935) and *Clarias gariepinus* Burchell. The available data on the subsequent exploitation of the lake are poor. High fish yield has been reported after the *Tilapia* introductions, during the forties: 350 T y^{-1} (Damas, 1953). It decreased thereafter with time, to reach *ca* 30 T y^{-1} in 1982 (Plisnier, 1990). The lack of detailed data about efforts and catches makes it difficult to assess the causes of this drop. Nevertheless, several facts indicate overfishing as one of the reasons: use of beach seines until the fifties, and utilization of small-mesh size gillnets, even in Tilapia breeding areas. Beside probable overfishing, other ecological changes occurred as well: the vast submerged macrophyte beds (with *Chara* spp., *Potamogeton* spp., ...) reported by Damas (1953) have almost totally disappeared nowadays. This might be partly the result of grazing by *Tilapia rendalli* Boulenger, which usually feeds on large water plants. Another likely cause is the decrease in water transparency; Damas (1954b) mentions a Secchi depth of 1.40–1.50 m in the eastern part of lake Muhazi, while only 0.85 m is reported by Plisnier (1989). This may be a consequence of soil erosion, as the catchment area became heavily cultivated (Ford, 1990).

A project of study and management of Lake Muhazi started in 1985. The maximum sustainable fish yield (MSY) was first estimated, in the absence of relevant information, by means of the MEI (morphoedaphic index) of Henderson & Welcomme (1974): this gave an estimate of 101 kg ha^{-1} y^{-1}. A more detailed study was then undertaken for one species of *Haplochromis* which represented some 78% of the fish biomass of the lake (Plisnier, 1990). The production of this fish was evaluated at 74 kg ha^{-1} y^{-1} and its MSY (maximum sustainable yield) at 24 kg ha^{-1} y^{-1} (Beverton-Holt model, 1957, in Sparre *et al.*, 1989). Still unknown are the population dynamics of *Clarias* spp. and *Oreochromis niloticus* which might actually be an hybrid with *Oreochromis spilurus niger* (syn. *Tilapia nigra* Boulenger) Günther. More fish introductions have been carried out recently (*Protopterus aethiopicus* Heckel, to exploit the large biomass of water snails) and others are being considered.

Another way of assessing the lake fishery potential or the fish production was through primary productivity (Melack, 1976; Oglesby, 1977; Mc Connell *et al.* 1977; Downing *et al.* 1990). According to the few available data before the present study, the primary production of Lake Muhazi seemed lower than in other lakes of the same area: chlorophyll *a* in L. Muhazi was on average about 20 $\mu g\ l^{-1}$ (Plisnier, 1989), compared to 70 $\mu g\ l^{-1}$ in L. Ihema (Descy & Théâte, 1984). There is a possible relationship between low primary production and reduced fish production. For investigating this, a study was undertaken in late 1987, in order to measure phytoplankton production and to assess possible nutrient limitation of algal growth. From estimates of primary production, potential fish production was derived by means of simple equations. In a second step, we verified whether the planktonic resource was efficiently utilized by *Oreochromis niloticus* by regular examinations of the fish gut content. The present paper deals with the first part of the study and is a synthesis of field observations carried out during a five year period, from 1986 to late 1990.

Description of the site studied

Lake Muhazi (Fig. 1) is a shallow lake located in the upper part of the River Akagera basin, which is itself a part of the Upper Nile basin. The lake is situated about 20 km NE Kigali, at 1443 m above sea level. Its surface area is 34.6 km^2, its shape elongated (length 37 km, mean width: 0.6 km) and it has many narrow side-arms at the outlet of the numerous tributaries (Fig. 2). Mean depth is 7.6 m. Two different parts were already distinguished by Damas (1954a). The western part, toward the lake outlet, is narrow (less than 100 m wide at some places), located on schist and surrounded by steep hills; the maximum depth is less than 10 m and decreases slowly toward the outlet. The eastern part lies on granitic soils, is wider, deeper (up to 13.8 m according to Damas,

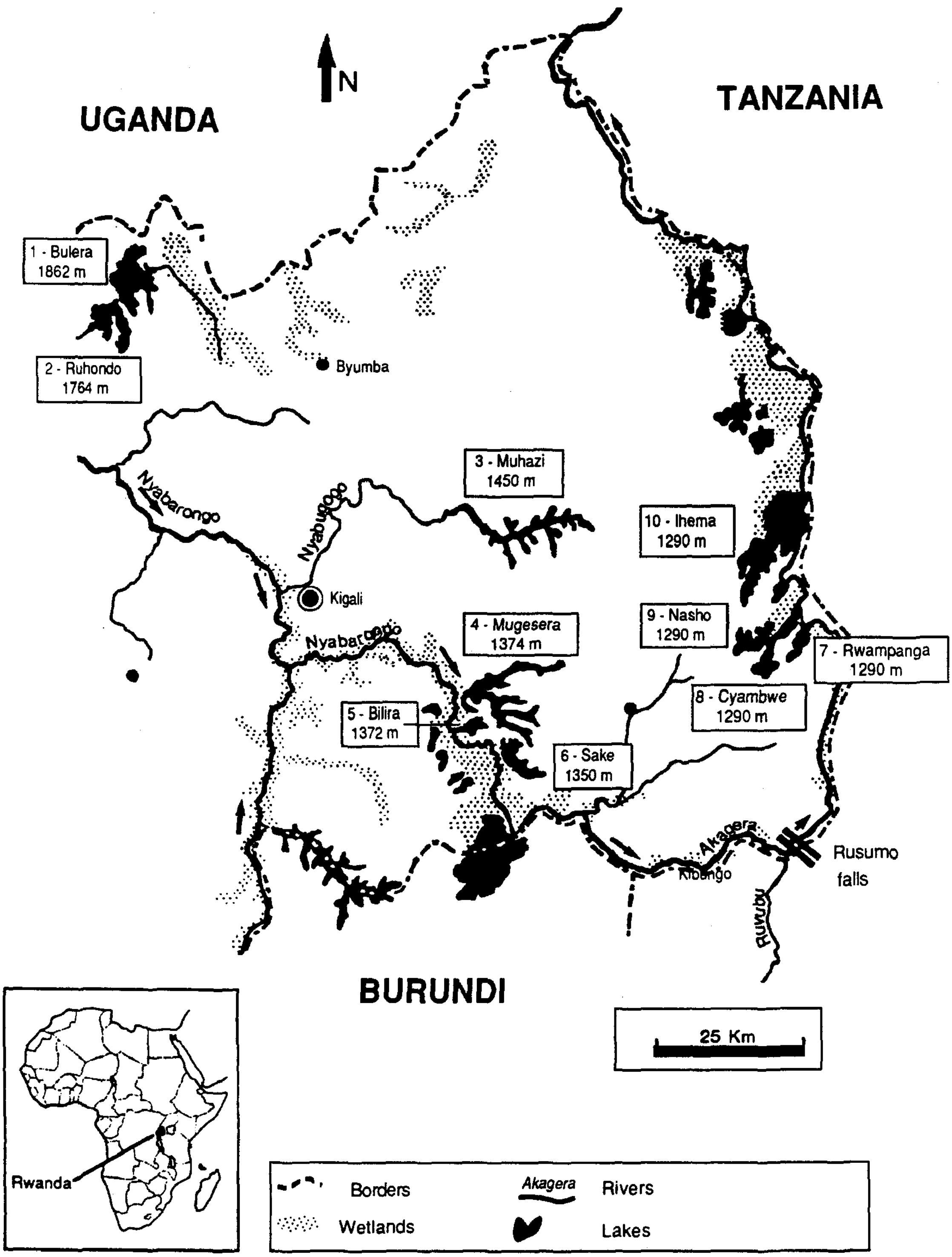

Fig. 1. Map of Rwanda, showing the situation of the various small lakes. Lake Kivu, a great Rift Valley lake located in the west of the country, is not shown here.

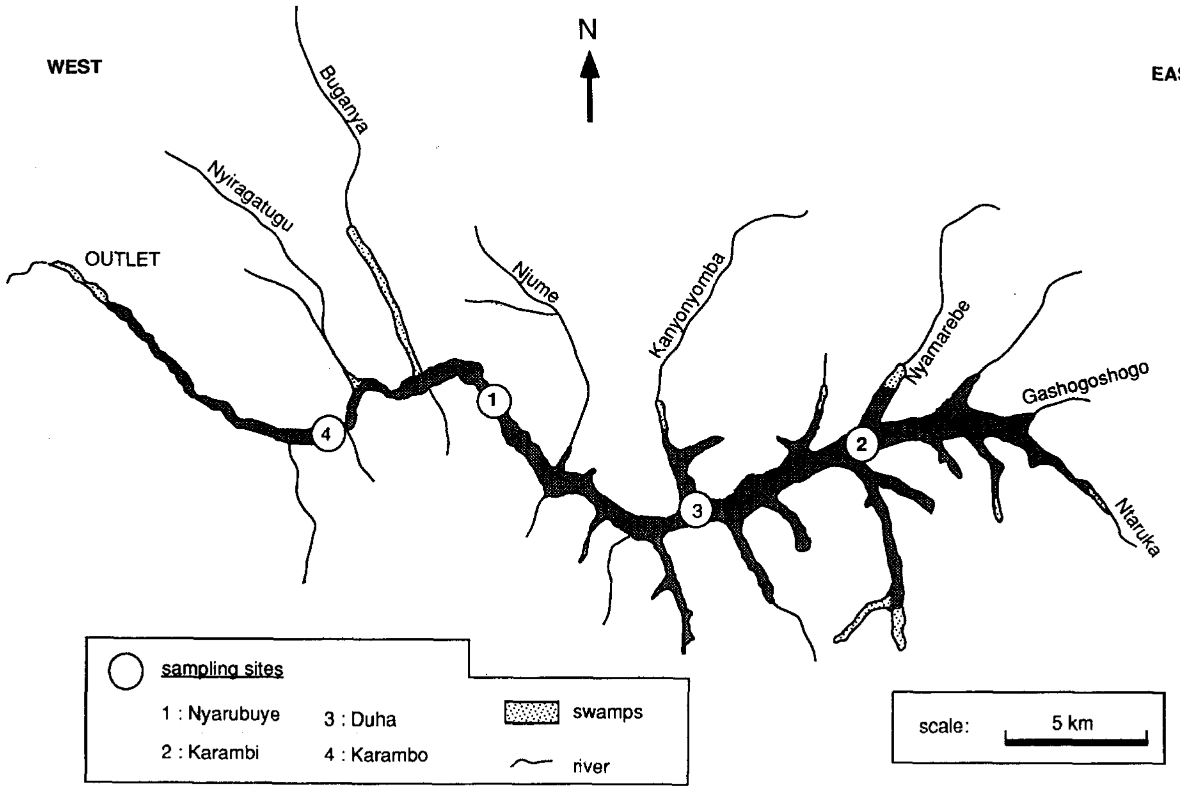

Fig. 2. Map of Lake Muhazi, with the location of the main sampling stations.

1954a) and characterized by long side-arms, most of which are clogged by swamps (mainly *Cyperus papyrus* L., with *Typha angustifolia* L. and *Miscanthidium veraceum* Stapf) retaining silt and nutrients carried by the tributaries.

Hypotheses on the formation of the lake have been reviewed by Damas (1954a); it is uncertain whether the flooding of the valley resulted from sediment buildup at the lake outlet or from subsidence of an ancient watershed.

Most of our results were obtained at four sites (Fig. 2) distributed from the east to the west; two of them were followed throughout the period of study, *Karambi* (east, visited once a month) and *Nyarubuye* (west, visited every two weeks); the other sites, occasionally studied, are located in the central area (*Duha*) of the lake or in the western part, close to the outlet (*Karambo*). During the major rainy season of 1990, weekly investigations were made at these four points.

Materials and methods

Physical and chemical factors

Current limnological methods were used for measuring the main physical and chemical variables, usually at 1 m intervals over the water column. Water samples were taken with a 3 l opaque Van Dorn bottle.

Temperature, oxygen, conductivity and pH were determined either with an HORIBA system combining the various probes or with separate instruments (WTW meters for temperature, conductivity and pH; oxygen-meter ANKERSMIT A111); O_2 probes were calibrated against the Winkler method (A.P.H.A., 1965). Alkalinity, nitrate (Cd-Cu reduction method), nitrite, dissolved phosphorus (molybdate method with extraction by hexanol or n-butyl-acetate) and dissolved silica were measured according to Golterman &

Clymo (1969); total P on filtered and unfiltered water was determined by spectrometry after persulfate hydrolysis (Wetzel & Likens, 1979). All spectrophometric measurements were performed on a BAUSCH & LOMB Spectronic 21 spectrophotometer allowing measurements in 1 or 5 cm cuvettes. The detection limit of N and P forms was about 1 $\mu g\ l^{-1}$; (10 $\mu g\ l^{-1}$ for ammonia nitrogen, determined according to H.M.S.O. (1982 a)).

Occasional measurements of major elements were made by atomic absorption spectrometry for cations (Ca^{2+}, Mg^{2+}, Na^{+} K^{+}), on filtered samples preserved with HCl, nephelometry for sulfate (A.P.H.A., 1965) and titrimetry for chloride (H.M.S.O., 1982 b).

On some samples, dissolved organic carbon was measured on filtered water preserved with phosphoric acid by means of a carbon analyser DOHRMANN DC-80.

The water transparency was estimated by the Secchi disk. In addition, on some occasions, a vertical attenuation coefficient was measured by immersing a photocell fitted with blue, green and red filters (according to Vollenweider, 1974), allowing readings of relative light intensity over the water column, against a similar cell integrating surface variations of light.

Biomass production of phytoplankton and particulate nutrients

Phytoplankton biomass was estimated by chlorophyll *a* concentration, corrected for phaeopigments (Lorenzen, 1967). At the beginning of the study, acetone 90% was used as extraction solvent; it was replaced by methanol, in order to achieve better passive cold extraction (Marker *et al.*, 1980). In 1988, we adopted the method of Pechar (1987), an extraction in hot acetone-methanol 5:1, which combines high extraction yield with good stability of pigments.

Primary production estimates were obtained from oxygen concentration in light and dark bottles incubated at various depths (typically between 0.25 and 5 m beneath the water surface), with an exposure time of 3–6 h around midday. As far as possible, incubations in the eastern and western parts of the lake were carried out simultaneously or at subsequent days. An alternative technique used during the major rainy season 1990 was based on subsurface incubations of polycarbonate containers fitted with neutral filters allowing fixed light intensities to reach the samples, collected at the mid-euphotic zone. On one occasion, during the dry season 1989, parallel ^{14}C-measurements based on a 4 h exposure were carried out at the same depths, at four sites: the results allowed intercalibration between O_2 production and CO_2 assimilation. The radioactivity measurements were performed by liquid scintillation counting (corrected for quenching) on filters (Millipore HA 0.45 μm) preserved by drying after filtration and kept frozen until the addition of the scintillation cocktail. Dark fixation was substracted from carbon uptake in the light.

Daily production was calculated as follows: For six times during the rainy season 1990, records of surface irradiance integrated over 15 min were obtained for the daylight period, by means of a LI-190SB sensor connected to a data logger. The photosynthesis-light curves were obtained and daily production calculated using Vollenweider's (1965) equation (Descy *et al.*, 1987). For all measurements referred to in this paper, we applied Talling's simplified equation for daily integral production in East African lakes (Talling, 1965):

$$\Sigma\Sigma P = (n\ P_{max}/k_{min})\ f(I)\ 0.9\ ,$$

where $\Sigma\Sigma P$ is the integral daily production (g O_2 $m^{-2}\ d^{-1}$); n is the phytoplankton biomass (chlorophyll *a*, mg m^{-3}); P_{max} is the light-saturated photosynthetic capacity (g O_2 g chl$a^{-1}\ h^{-1}$); k_{min} is the vertical attenuation coefficient (m^{-1}) of the most penetrating wavelength; $F(I)$ = 'light factor' $ln\ 2(I'_0/I_k)$; I'_0 is the mean subsurface irradiance of the exposure ($\mu E\ m^{-2}\ s^{-1}$) and I_k is the irradiance at the onset of light saturation ($\mu E\ m^{-2}\ s^{-1}$).

As most photosynthesis measurements yielded low P_{max} values (see below), a more reliable estimate of this parameter was obtained by retaining only O_2 production of 4 h incubations, which gave an average of 19.8 ± 5.5 mg O_2 mg chla^{-1} h^{-1}. As a consequence, daily production estimates were calculated with an average P_{max} value of 20 mg O_2 mg chla^{-1} h^{-1}. The data of 22 incubations for which light monitoring was available allowed the determination of the $f(I)$ factor. Despite a large range of variation of irradiance (500 to 2500 μE m^{-2} s^{-1}) during the incubations, a mean of 2.42 ± 0.28 was obtained, which is close to Talling's value (2.6) for East African lakes (Talling, 1965).

Nutrient content of the phytoplankton was determined from the material obtained by filtration of sedimented water samples (fixed with Lugol's iodine) on precombusted GF/C filters. Organic matter (as carbon) and nitrogen were measured with a Carlo Erba NA1500 elemental analyser. Phytoplankton phosphorus was derived from the difference between total P and total dissolved P, assuming that particulate P is only phytoplankton P.

Results and discussion

Physical characteristics.

Mean annual surface temperature of Lake Muhazi, calculated from weekly measurements, is about 24.5 °C, with a fluctuation of 1.5 °C (Fig. 3). Vertical profiles usually show a temperature gradient of about 2 °C between surface and bottom. Even if this gradient seems weak, stratification occurs during the day, with a depth of the mixed layer at around 4 m. This stratification is by no means stable, as shown by vertical profiles of pH and O_2 (Fig. 4), but mixing of the water column does not occur daily, as shown by diurnal temperature and oxygen measurements (Fig. 5). The deepest layers (6 m to 10 m) are generally oxygen-poor, the decrease taking place between 4 and 5 m. Even when complete mixing occurs, the combination of surface warming and rapid O_2 consumption (Fig. 5) can soon reestablish oxygen depletion at depth. Owing to the lower mean depth, mixing is more frequent in the western part of the lake than in the eastern part. Secchi disk depth reveals a slight, but constant difference between the eastern (0.80 m) and western parts (0.70 m) of the lake. Using the conversion factor obtained from *in situ* intercalibrations, corresponding coefficients of vertical attenuation of light are 2.4 m^{-1} (east) *vs* 2.7 m^{-1} (west); estimates of the euphotic zone (Ze) are 1.9 m (east) and 1.7 m (west). Variation in time is limited (*cv.* = 3–4%) and follows a periodic pattern, similar to lake Ihema, but of minor amplitude (Fig. 6). Secchi disk depth is related to rainfall and water level in the two lakes; however, in lake Muhazi, transparency is clearly more dependent on phytoplankton development than on inputs of suspended matter from the watershed during rainy periods. These inputs are limited by the small size of the drainage area and most of it is retained by the swamps near the outlets of the inflowing rivers (Gaudet, 1977). By contrast, other lakes located downstream in the Akagera river basin, like Lake Ihema, have a larger drainage area and, because of severe erosion (Ford, 1990) receive huge amounts of suspended matter in the rainy seasons.

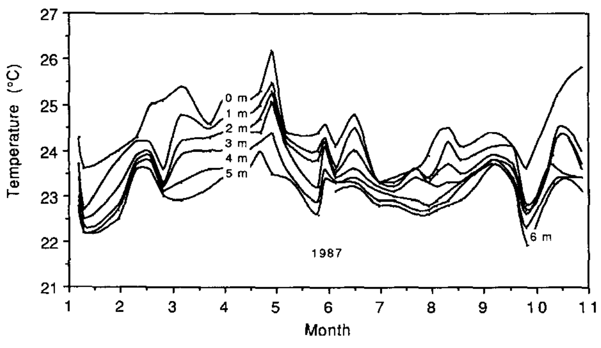

Fig. 3. Temperature at differents depths of Lake Muhazi during the year 1987.

Chemical characteristics

Major ion concentrations are high in comparison to other shallow lakes in Rwanda (Fig. 7; Table 1). Conductivity at 25 °C is close to 500 μS cm^{-1}; the dominant cation is Na^+ (1.8 meq l^{-1}),

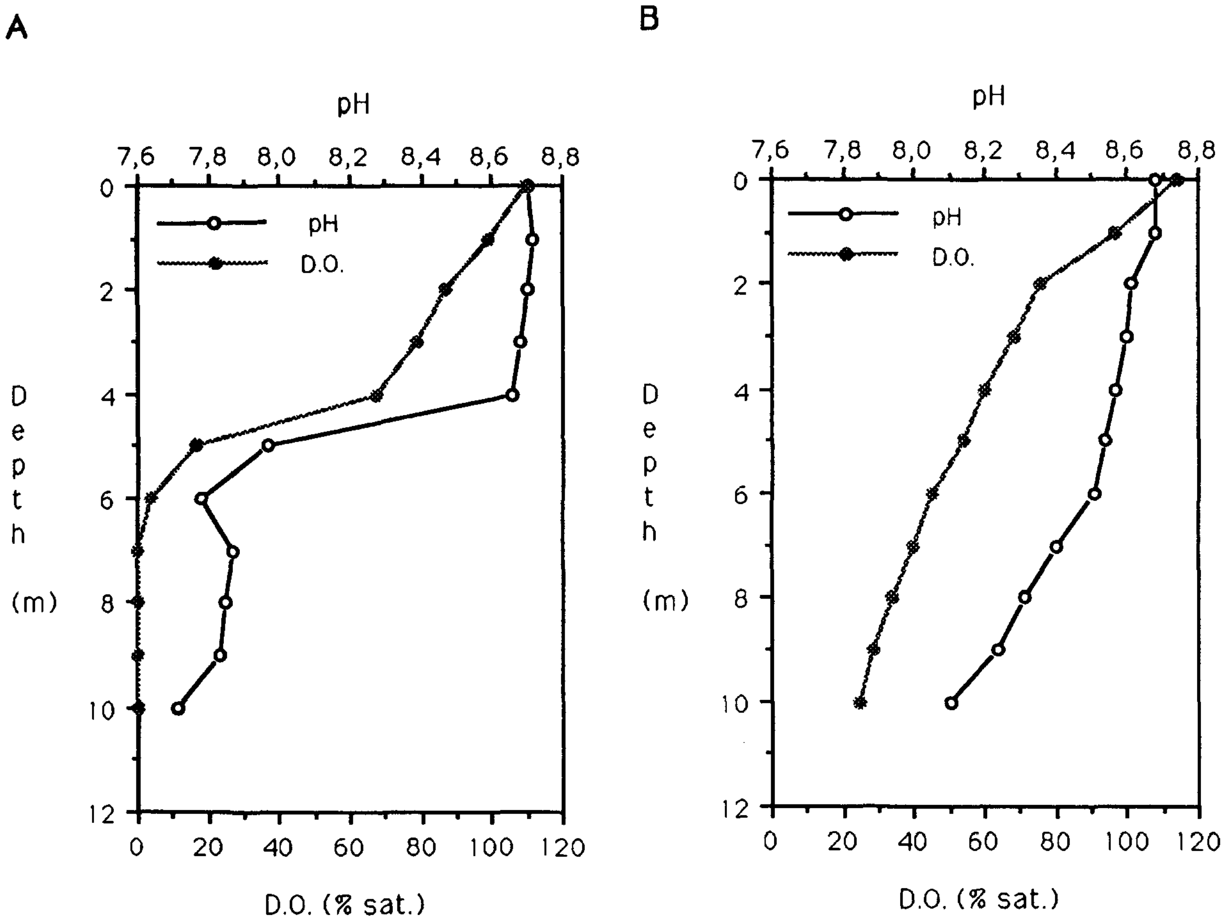

Fig. 4. Typical vertical profiles of pH and dissolved oxygen in Lake Muhazi, when stratified (A, at 9:30 a.m.) and after mixing (B, at 11:30 am.); the measurements were taken in the eastern part of the lake, on the same day, during the major dry season 1989.

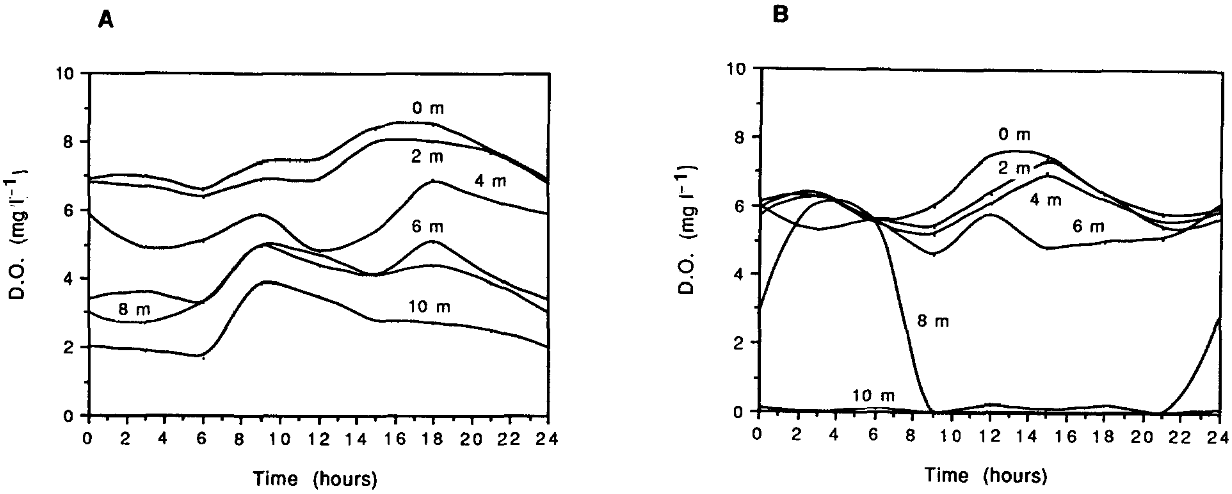

Fig. 5. Diurnal variations of dissolved oxygen at Karambi (eastern part of Lake Muhazi), at differents depths. A: 12-03-86; B: 10-04-86.

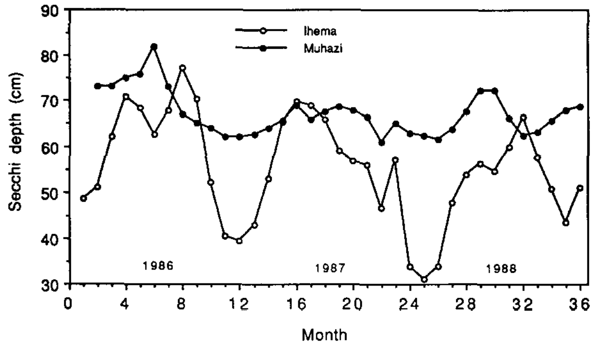

Fig. 6. Seasonal variation of water transparency (Secchi depth, average monthly values) in Lake Ihema and in Lake Muhazi, from 1986 to 1988.

Table 1. Concentrations of major ions (meq l^{-1}) in Lake Muhazi: data from Damas (1954) and Descy & Théâte (1990).

Ions	Damas, 1952	Descy & Théâte, 1990
Ca^{2+}	1.40	1.53
Mg^{2+}	2.06	1.53
Na^{+}	3.78	1.81
K^{+}	0.28	0.12
HCO_3^-	3.10	2.21
Cl^-	4.06	2.01
SO_4^{2-}	0.02	0.14
Si	0.27	0.25

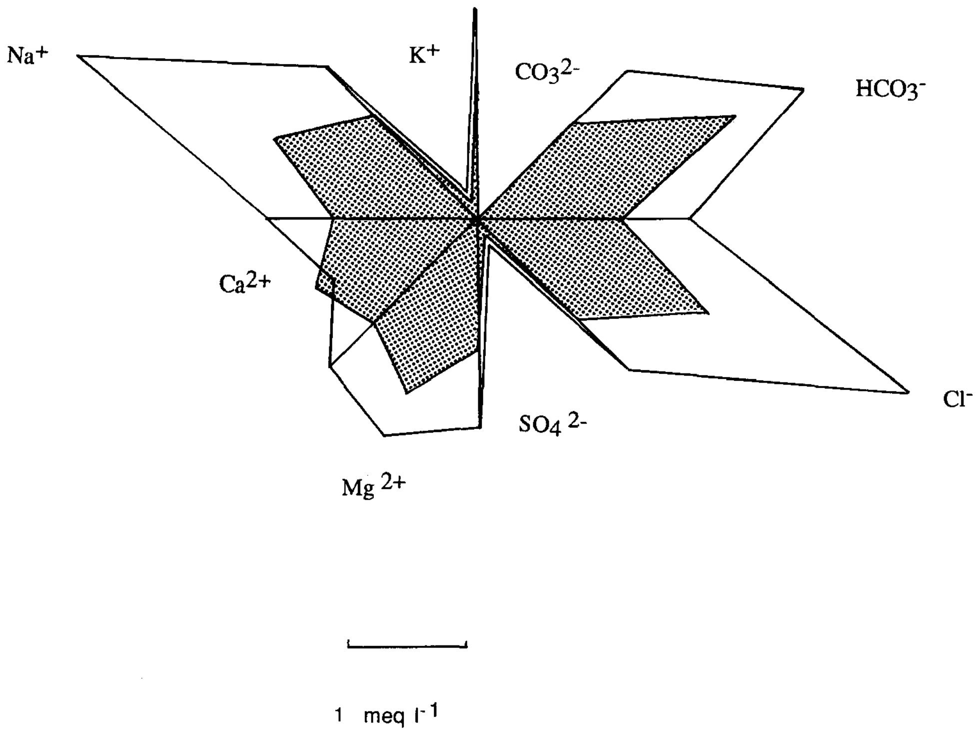

Fig. 7. Diagram of the concentrations of major ions in Lake Muhazi, from the data of Damas (1954) and to recent data (Descy & Théâte, 1990). The diagram is drawn according to Maucha (1936, in Symoens, 1968). Data from Table 1.

closely followed by nearly equivalent amounts of Ca^{2+} and Mg^{2+} (1.5–1.6 meq l^{-1}), whereas K^+ concentration is low (0.13 meq l^{-1}). Bicarbonate and chloride ions reach about 2 meq l^{-1}, while sulfate is low (0.1–0.2 meq l^{-1}). Mean silica concentration is 7.5 mg Si l^{-1}. This chemical composition, as mentioned by Damas (1954b), contrasts with other shallow lakes of the same region, which receive water from large swamp areas and have a lower mineral content. Lake Ihema, for example, has a conductivity of less than 100 μS cm^{-1}. Saline sources located along the shore of lake Muhazi, mostly in the eastern part of the catchment, could explain this peculiar composition. However, on the scale of tropical Africa, lake Muhazi is not atypical, but find a place in 'class I' in the system of Talling & Talling, 1965, close to lake Naivasha (Kenya). It was close to L. Tanganyika according the analyses of Damas (1954b); however, the site sampled by Damas was located in a region of the lake directly influenced by saline water inflows.

Dissolved oxygen and pH usually have typical clinograde profiles, with a steep gradient between 4 and 5 m in periods of stable stratification (Fig. 4). In the mixed layer of the stratified water column, which extends down to 4 m, pH is about 8.5 and O_2 around 100% saturation or more. Under the mixed layer, both variables decrease sharply to about 7.5 for pH and to near-zero for dissolved oxygen. After periods of deep circulation, surface waters have lower values of both variables, while deep waters are re-oxygenated. At the east of the lake, oxygen at depths below 5 m fluctuates between 0 and 50% saturation according to the circulation pattern. As oxygen depletion is rapidly restored when stratification reappears, these 'deep' layers are inaccessible to fish most of the time.

The concentration of dissolved organic carbon, according to measurements made only in the dry season of 1989, is constant (*ca* 5 mg l^{-1}), over the lake and over the water column.

Nutrients in water

Dissolved inorganic forms of N and P are low in the mixed layer. Nitrate nitrogen, when detectable, rarely exceeds 10 $\mu g\ l^{-1}$ and nitrite nitrogen is never detected. Soluble reactive phosphorus (SRP) is mostly in the range 0–5 $\mu g\ l^{-1}$, the mean value at 1 m being lower than 1 $\mu g\ l^{-1}$ (*i.e.* 0.7 $\mu g\ l^{-1}$ for the rainy season 1990). These dissolved nutrient concentrations yield a high Si:P ratio (8,300). Measurements in the dry season 1989 yielded a mean TN:TP ratio of 10.5 for the hole lake.

Dissolved nutrients accumulate in the deepest layers when the water column is stratified. For SRP, an average value over the major rainy season 1990 is 21 $\mu g\ l^{-1}$ at 10 m to 11 m depth. Ammonia nitrogen appears just below the mixed layer and increases with depth, up to several hundreds $\mu g\ l^{-1}$ N (recorded maximum: 1420 $\mu g\ l^{-1}$ N).

Composition and biomass of the phytoplankton

The phytoplankton of Lake Muhazi is composed of Cyanobacteria (47–58%), Chlorococcales (27–32%), diatoms (15%), Euglenophyceae and dinoflagellates (1–3%). Estimates of biomass from the biovolumes show an overwhelming dominance of colonial coccoid Cyanobacteria (mostly *Microcystis aeruginosa* (Kütz.) Kütz., 75% of the biomass) and dinoflagellates (*Ceratium hirundinella* (O. F.. Müll.) Duj., 8.6% of the biomass). No marked seasonal variations take place. Few nitrogen-fixing Nostocales are present (two species of *Anabaenopsis* relatively abundant in the phytoplankton counts, but accounting for only 0.5% of the biomass). Chlorophyll *a* concentration usually has a maximum at 1 m in daylight. Average and extreme values for the years 1988 and 1989 are presented at Table 2. While no distinct seasonal pattern emerges from the data, the variation between the two parts of the lake is significant (positive *t*-test at the 0.95 confidence level). The spatial difference of phytoplankton biomass is constant over the period of observation. This east-west heterogeneity of phytoplankton abundance was also verified by chlorophyll *a* measurements carried out during the dry season

Table 2. Summary of chlorophyll *a* data ($\mu g\ l^{-1}$, mean values) of lake Muhazi (years 1988 and 1989); extreme values are between (), *C.V.*: coefficient of variation (%); *n*: number of measurements.

Year	Dry season	Rainy season	Annual	*n*	*C.V.*
Nyarubuye (western part)					
1988	46.8	38.4	41.6 (24–50)	16	22
1989	35.7	31.3	32.4 (19–45)	14	21
Karambi (eastern part)					
Year	Dry season	Rainy season	Annual	*n*	*C.V.*
1988	32.6	29.0	30.2 (14–46)	6	26
1989	23.3	23.0	23.2 (14–33)	9	20

1989. During three sampling series, 30 sites distributed all over the lake were sampled at 1 m. The west-east phytoplankton biomass difference amounts to at least 10 μg chl*a* l^{-1}. Biomass in the side-arms was usually similar to that of the open water.

The mean chlorophyll content of the euphotic zone reaches 66 mg m^{-2} (average 1988–1990 for the western sites). The vertical distribution of the biomass is mostly similar to the profiles presented in Fig. 8, *i.e.* almost homogenous throughout the water column, with maxima in the euphotic zone, and minima near the bottom. Three photosynthesis measurements were carried out with algae sampled at 5 m and incubated at the light intensities of the euphotic zone and showed that this phytoplankton was photosynthetically active. Moreover, photoadaptation could be seen in two experiments out of three. The algae sampled at depth showed a stronger photoinhibition than the surface plankton, as well as a higher O_2 production rate at the lower limit of the euphotic zone. These observations confirm the relative stability of the water column, at least over the time needed for photoadaptation to develop.

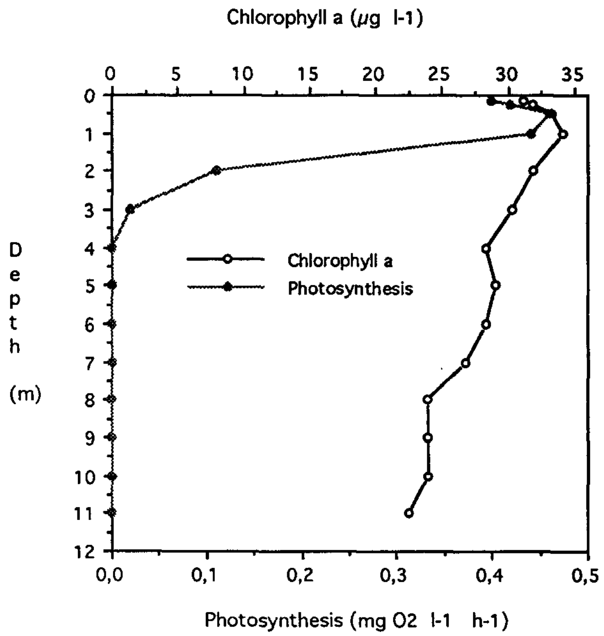

Fig. 8. Typical vertical profiles of chlorophyll *a* and photosynthesis in Lake Muhazi.

Photosynthesis and estimation of daily production

Typical photosynthesis-depth profiles were obtained in Lake Muhazi (Fig. 8). The photosynthetic capacity (P_{max}) of the phytoplankton of Lake Muhazi was calculated from light and dark bottle incubations (Table 3). These data are out of the common range for East African lakes (25 ± 5 mg O_2 mg chla^{-1} h^{-1} according to Talling, 1965), but similar to values found by many authors (review by Lemoalle *et al.*, 1981). However, a systematic decrease of photosynthetic activity is observed in our data for incubations lasting more than 4 h, which likely results from increasing limitation of photosynthesis by CO_2 depletion. This effect was confirmed, in 1990, by time-series of O_2 production in light bottles. For this reason, as explained in materials and methods, a constant P_{max} value of 20 mg O_2 mg chla^{-1} h^{-1} was used to calculate daily production (Table 4).

These estimates are in good agreement with the relationship found by Lemoalle *et al.* (1981) for African lakes ($\Sigma\Sigma A = 0.140\ \Sigma B$), and are in the same range as in Lake Ihema, according to Kiss (1976).

Elemental ratios and nutritional status of the phytoplankton

Data on elemental composition of the phytoplankton allow a comparison of the four sites of the lake during the survey of July 1989, at depths between 1 m and 5 m (Table 5). These re-

Table 3. Summary of P_{max} measurements (mg O_2 mg chla^{-1} h^{-1}, mean values) of lake Muhazi (years 1988 and 1989); extreme values are between (), *C.V.*: coefficient of variation (%); *n*: number of measurements.

Year	Dry season	Rainy season	Annual	*n*	*C.V.*
Nyarubuye (western part)					
1988	16.2	18.0	17.3 (4–30)	16	36
1989	14.4	16.8	15.8 (6–26)	10	28
Karambi (eastern part)					
1988	9.7	18.1	14.7 (4.9–24.6)	5	33
1989	17.1	14.1	15.4 (8.4–22.3)	10	23

Table 4. Daily phytoplankton production (GP, g $O_2m^{-2}d^{-1}$) in Lake Muhazi (Rwanda), calculated according to Talling (1965), with P_{max} = 20 mg O_2 mg chla^{-1} h^{-1} and $f(I)$ = 2.6.

Year	Dry season	Rainy season	Annual	*n*	*C.V.*
Nyarubuye (western part)					
1988	9.48	7.67	8.57	16	18
1989	8.05	6.74	7.30	14	16
Karambi (eastern part)					
1988	7.55	6.98	7.17	6	26
1989	6.39	5.70	6.10	9	19

Table 5. Measurements of particulate C, N, P (μatg l^{-1}) in lake Muhazi, July 1989.

Z (m)	C	N	P	C:N	C:P
Karambi					
0	46.9	2.4	0.37	19.5	126.8
1	36.0	2.0	0.66	18.0	54.6
2	35.2	4.1	0.49	8.6	71.8
3	32.0	3.9	0.44	8.2	72.7
4	28.9	3.8	0.49	7.6	60.0
5	28.7	3.7	0.43	7.8	66.7
Duha					
0	74.5	7.2	0.48	10.3	155.2
1	79.6	7.6	0.46	10.5	173.0
2	82.6	4.9	0.80	16.9	103.3
3	82.6	8.9	0.78	9.3	105.9
4	97.4	10.8	–	9.0	–
5	84.9	9.0	–	9.4	–
Nyarubuye					
1	42.4	3.85	0.44	11.0	96.4
2	33.9	3.08	–	11.0	–
3	30.5	3.10	0.30	9.8	101.7
4	25.3	2.70	–	9.4	–
5	26.5	3.00	0.40	8.8	66.3
Karambo					
1	32.2	3.4	0.43	13.4	74.9
2	36.5	3.3	–	11.1	–
3	25.0	2.7	–	9.3	–
4	32.8	3.2	–	10.3	–
5	38.1	3.9	–	9.8	–

sults indicate a deficiency for N rather than P at all sites: only two C:P ratios are above the threshold value of 133, suggesting P-deficiency, proposed by Healey & Hendzel (1980). By contrast, C:N ratios often exceed 8. Remarkably, N-deficiency seems stronger in the light-saturated zone than in the deeper layers. This could result from light limitation i.e. lower nutrient demand associated with reduced growth rate and DIC uptake or from higher N availability at depth *i.e.* presence of ammonia under the mixed layer. No clear difference was apparent between east and west, except for Karambi, the most eastward site, where C:N ratios in the euphotic zone were highest.

Analyses of C and N content of the phytoplankton of the euphotic zone over the rainy season 1990 are plotted in Fig. 9. Linear regressions allow separation of the algal fraction from detrital particulate matter. The regression equation on all data gives a C:N ratio of 7.2, which does not indicate a clear N deficiency. When data from the eastern site are considered separately, the slope is close to 10 and the Y-intercept is low (Fig. 9). As far as this approach, based on elemental ratios, is reliable (Healey & Hendzel, 1980; Hecky & Kilham, 1988), such results support N-limitation of algal growth in the eastern part of the lake throughout the studied period. By contrast, the C:N phytoplankton ratio at the western site is 6.6 (r^2 = 0.81), equal to the Redfield ratio.

Critical depth and growth conditions

Beside a possible nutrient limitation of phytoplankton growth at the eastern sites, the relative position of the depth of the mixed layer, Zm (4 m when the water column is fully stratified) and of the critical depth, Zc (Kirk, 1983) may limit growth. Simple calculations were based on mean values of k_{min}, on an average I_k of 200 μE m^{-2} s^{-1} (calculated for 20 incubations involving measurements of surface PAR) and using 0.09 as an estimate of *r* (respiration rate relative to P_{max}). Estimated Zc for a mean surface irradiance of 1000 μE m^{-2} s^{-1} is 4.8 m (west) to 5.4 m (east) on average, indicating that, even for this rather high mean daylight irradiance, net production and growth rate of algae circulating in the mixed layer should be low. Calculations of net production rate at each day of measurement, based on actual k and depth of the mixed layer, yielded low values (0.21–0.25 d^{-1}), inversely related to chloro-

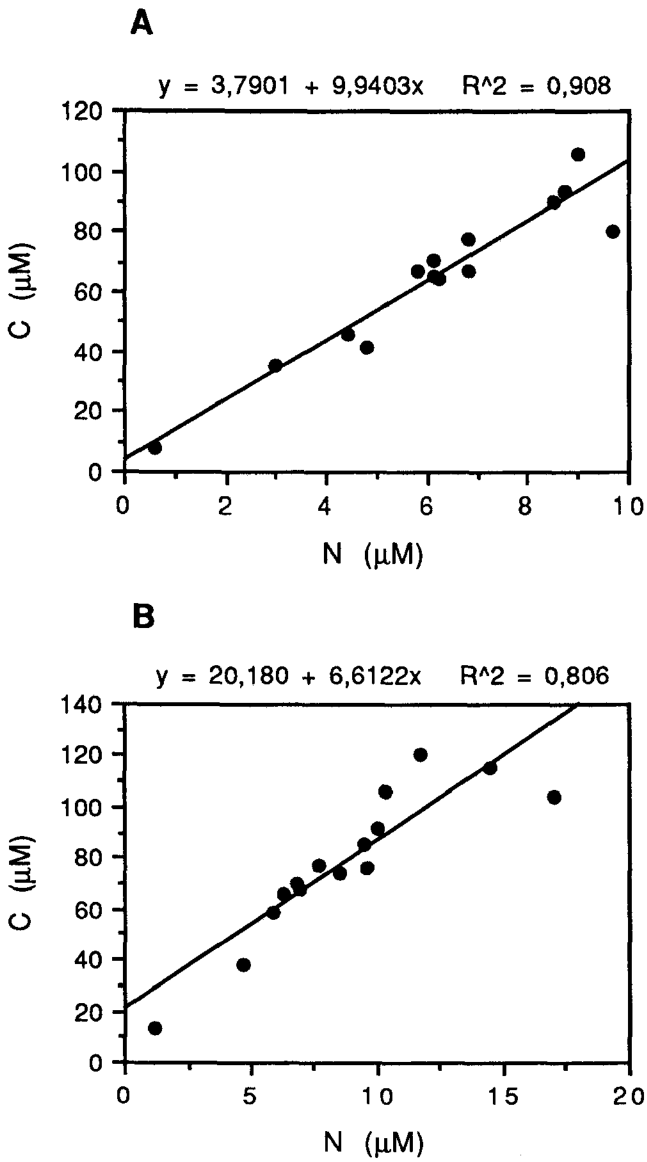

Fig. 9. Plots of particulate carbon *vs* particulate nitrogen in Lake Muhazi; A: Eastern part; B: Western part. The slope of the regression line gives an estimate of the phytoplankton elemental ratio.

phyll *a* in the mixed layer. So, the Zm:Zc ratio may play a role in limiting the phytoplankton biomass in lake Muhazi, which barely exceeds 20 mg m^{-2} of chl*a*, integrated over the mixed layer, (80 mg m^{-2} over the euphotic depth).

Conclusions

A first conclusion from our studies is that primary production of Lake Muhazi, considered as a whole, is in the range reported for African lakes (Talling, 1965; Beadle, 1981; Lemoalle *et al.*, 1981). This can be seen from Fig. 10, where various data of phytoplankton biomass *vs* daily production have been plotted. Lake Muhazi lies in the same range as typical tropical shallow lakes, where phytoplankton growth is mostly dependent on mixing frequency, which influences nutrient availability and the balance between photosynthesis and respiration. For instance, the significant difference of phytoplankton biomass and production between the western and the eastern parts of the lake probably results only from different depth and mixing pattern.

A second point is that the low fish yield of Lake Muhazi (*ca* 20 kg ha^{-1}, Plisnier 1990) is not the consequence of a limited phytoplankton resource. Indeed, using our estimates of phytoplankton gross primary productivity and the equation of Melack (1976), which seems the most reliable for estimating fish yield of tropical lakes inhabited by filter-feeding species, the annual fish yield of the lake should be 46–64 kg ha^{-1}. Hence, it is quite clear that a higher fish yield could be achieved by proper management practices. Among these are the exploitation of haplochromines, which represent the major part of the present biomass, restoration of the population of *Oreochromis niloticus* (through a study of its dynamics, protection of the breeding areas, regulation of the catches, reintroduction of pure strains). Contrary to what has been done until recently, introductions of new species should be considered only after a complete assessment of the consequences on the present fish community and on the ecosystem.

A comparison of the present state of the lake with the data of Damas (1953) shows that the ecology of the lake has changed. Some hypotheses may explain those changes: Drainage of the wetlands, and soil erosion resulted in an increased input of suspended matter to the lake during the rainy seasons (Ford, 1990). As a consequence, the submersed aquatic vegetation experienced

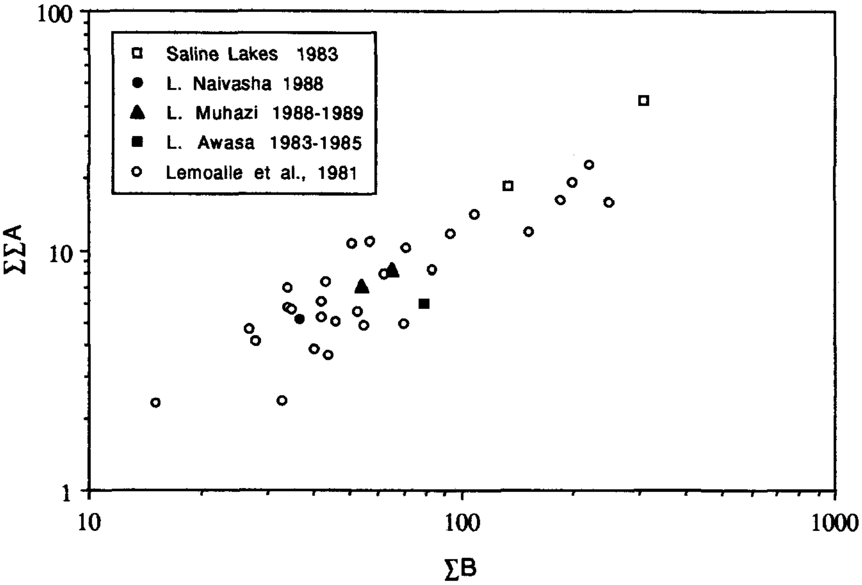

Fig. 10. Relationship between daily gross production (ΣΣA, $gO_2\ m^{-2}d^{-1}$) and the chlorophyll content in the euphotic zone (mg chl*a* m^{-2}) in various African lakes, modified from Lemoalle *et al.* (1981); note logarithmic scales. Dots: data already reported by Lemoalle *et al.*; empty squares: data from Kalff (1983); black square: data from Kifle & Belay (1990); black circle: value estimated from Harper (1991); black triangles: this study.

light-limitation; *Tilapia rendalli*, which feeds on macrophytes, overgrazed them and became stunted; the nutrient loading increased due to inputs from the tributaries. The phytoplankton quickly responded to those changing conditions and increased. This contributed to low water transparency and the submersed macrophytes disappeared; O_2 depletion of deep layers increased. *Oreochromis niloticus*, which feeds on planktonic algae, could find optimal conditions but was soon overfished. *Haplochromis* spp., which were present before the *Tilapia* introductions, became the dominant fraction of the fish biomass. The decrease of *O. niloticus* resulted in reduced grazing on large phytoplankton species, which dominate the algal community of the lake. Most of the algal production (as much as 90%) is not used by pelagic consumers (the zooplankton is dominated by small rotifers and *Chaoborus* larvae) and is lost by sedimentation and by decay in the water column. If these hypotheses actually describe the evolution of the lake, the process could be reversed by better management, including sustaining the populations of filter-feeding *Oreochromis*: a greater part of the primary production would be transferred to the higher trophic levels and, with the reduction of phytoplankton biomass, ecological conditions of the lake (*i.e.* water transparency, oxygen in the hypoliminion) should improve.

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