Hydrobiologia **368:** 41–59, 1998.

Temporal changes in phytoplankton structure and composition at the Turkwel Gorge Reservoir, Kenya

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Received 10 June 1997; in revised form 2 December 1997; accepted 9 December 1997

Key words: reservoir, phytoplankton, diversity, primary production, seasonality

Abstract

Temporal changes in phytoplankton chlorophyll *a*, composition, diversity, biomass (density and fresh weight) and primary production were investigated at the Turkwel Gorge Reservoir (Kenya) over a two year period (1994 and 1995). The phytoplankton properties investigated revealed a seasonal pattern that was very distinct in 1994 and muted in 1995. The wet season was characterized by higher levels of chlorophyll *a*, biomass and primary production and a lower diversity. A prominent seasonality in 1994 was found to be the result of a higher river inflow volume as compared to 1995. Chlorophyll *a* changes showed some positive correlation to changes in total nitrogen and total phosphorus. Diversity changes were inversely correlated to changes in total counts ($R = -0.84$ and -0.96 for 1994 and 1995 respectively). Individual species density changes varied from a distinct seasonal pattern to a nearly uniform density. While the diatom *Achnanthes* dominated the wet season in 1994, coccoid blue green algae were dominant during most of 1995. Throughout the study period, most biomass was due to the diatoms but with a lower percentage of total biomass in 1995 (40%) as compared to 1994 (88%). The wet season biomass in each year was dominated by the diatoms. Dominance of the intervening period changed irregularly between diatoms, dinoflagellates, green algae and blue green algae. The range of variation in chlorophyll *a*, total biomass and primary production were; 4.9 to 36.8 μg l^{-1}, 440.14 to 11172.70 mg m^{-3} and 1.85 to 9.67 g O_2 m^{-2} d^{-1} in 1994 and 4.9 to 11.5 μg l^{-1}, 486.46 to 1351.39 mg l^{-1} and 3.08 to 5.41 g O_2 m^{-2} d^{-1} in 1995 in the same order.

Introduction

The history of phytoplankton investigation in Kenya can be traced to the net sample collections of Bogert (Von Daday, 1907; Ostenfeld, 1908) and Cunnington (West, 1907) from the Kenyan side of Lake Victoria. These works form some of the earliest descriptions of tropical limnology. Since then, great advances have been made in the understanding of phytoplankton composition, ecology and their photosynthetic activity in the country (Talling, 1966; Melack, 1979; Hecky & Kling, 1981; Harper, 1991; Patterson & Wilson, 1995). These works have gone a long way in promoting the understanding the unique features of tropical limnology. Whereas phytoplankton periodicity in temperate latitudes follows a typical seasonal pattern (Sommer, 1989; Reynolds, 1989) dominated by the solar energy cycle (Patterson & Wilson, 1995), this pattern in the tropics is less apparent and is mainly under the control of weather and related changes. Because lake hydroclimate conditions in Africa cover a great span of variation (Lemoalle et al., 1981), phytoplankton biomass and species composition similarly vary widely.

Knowledge on phytoplankton dynamics of tropical reservoirs has only developed gradually, partly because reservoir construction in the tropics is a recent economic venture and also because the state of phytoplankton research in the tropics is far behind when compared to the same in temperate regions. In recent years, a renewed interest in reservoir limnology has been stimulated by conclusions that reservoirs are structurally different from lakes (e.g. Thornton et al., 1982; Ryder,

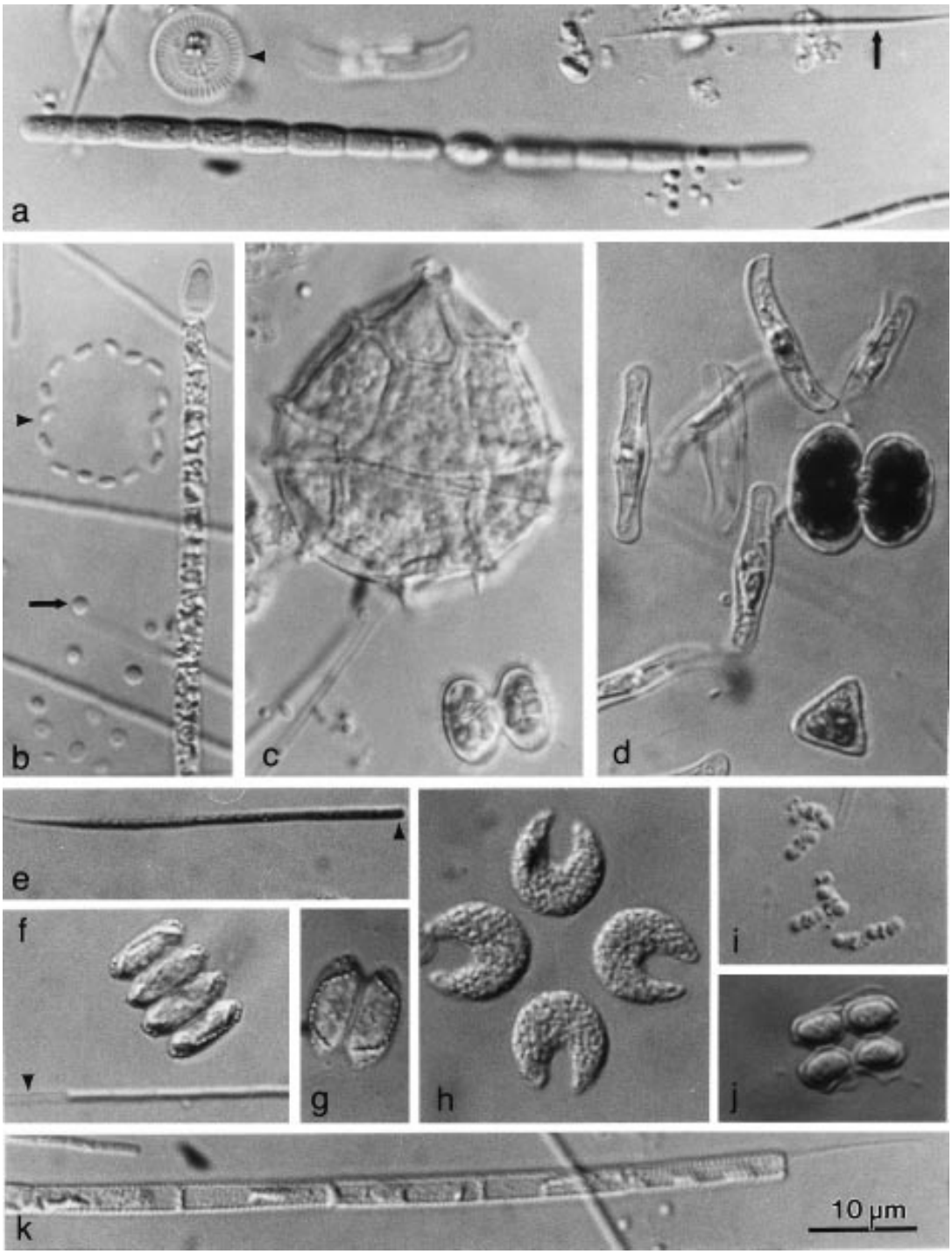

Plate 1.

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Plate 1. Some common phytoplankton taxa of Turkwel Gorge Reservoir, Kenya. a – *Aphanizomenon* cf. *manguinii*; *Cyclotella* cf. *stelligera* (arrowhead); *Koliella spiculiformis* (arrow); b – *Cylindrospermopsis raciborskii*; *Cyanonephron styloides* (arrowhead); *Aphanocapsa koordersi* (arrow); c – *Peridiniopsis cunningtonii*; *Cosmarium* sp.; d – *Achnanthes catenata*; *Tetraedron triangulare*; *Cosmarium* sp.; e – *Koliella spiculiformis* after cell division as indicated by the rounded filament end (arrowhead); f – *Scenedesmus grahneisii*; *Planktolyngbya undulata* with sheath (arrowhead); g – *Scenedesmus grahneisii* with well developed C-shaped incrustation on the cell wall surface; h – *Kirchneriella dianae*; i – *Cyanocatena planctonica*; j – *Crucigeniella apiculata*; k – *Aulacoseira granulata*.

1978; Ryding & Rast, 1989; Wetzel, 1990). Within the tropics, reservoirs have been shown to be comparatively more productive and with unique water quality problems (e.g. severe deoxygenation and eutrophication; Adeneji et al., 1981). As these water quality problems can have an impact on the utilization of reservoir resources, a close monitoring of reservoir limnology has been recommended (Adeneji et al., 1981).

In Kenya, several reservoirs have been built, the most important being those principally for hydropower generation. Cognizant of the country's past experience with eutrophication related biological problems, especially the explosive growth of aquatic weeds, the preconstruction environmental studies recommended a regular monitoring of the ecology of these reservoirs. However, very limited limnological attention has been paid to Kenya's reservoirs. Studies that have paid some attention to reservoir plankton include a report by Uku & Mavuti (1994) on the plankton diversity and biomass in a number of shallow lakes and reservoirs in the country. Dadzie & Odero (1989) links the decline in the fishery of Kamburu reservoir to changes related to plankton changes and the establishment of an upstream reservoir (Masinga). The subject of phytoplankton periodicity and controlling environmental factors has hardly been touched.

Phytoplankton periodicity still remains one of the most discussed topics of freshwater research, mainly because of the many unresolved issues on phytoplankton ecology. In recent years, the application of the short term or intermediate disturbance theory as a basis of explaining phytoplankton diversity changes has renewed research interest on the subject of phytoplankton diversity and changes (e.g. Reynolds et al., 1993; Sommer, et al., 1993; Padisak, 1993, 1995; Calijuri & Dos Santos, 1996). Although most of these research findings have been in support of intermediate disturbance as the cause of high phytoplankton diversity, more information is still needed if this explanation has to win universal acceptance.

In the study of the science of reservoirs, phytoplankton ecology is of special importance because they play a dominant role in its primary production. A combined effect of abiogenic turbidity and a wide fluctuation of water level as is the case with many reservoirs restricts the development of attached algae and rooted macrophytes (Ryder, 1978; Kimmel & Groeger, 1984). Long term investigations on phytoplankton changes in some of Africa's reservoirs have revealed that a progressive change in species composition which start after impoundment (e.g. Viner, 1969; Adeneji, 1973; Hammerton, 1976) may be superimposed on the annual seasonal pattern of change. These changes are often characterized by a progressive invasion by species previously absent at the inflowing river (e.g. Petr, 1975).

Phytoplankton studies on some of Africa's large and better studied lakes have shown some qualitative changes that are the result of several years of cultural eutrophication (e.g. Ochumba, 1987; Hecky, 1993; Mugidde, 1993). Since the smaller lakes and reservoirs are more susceptible to human impact (Crisman & Streever, 1996), these systems are better suited for an early detection of deleterious water quality changes. One important biological consequence of eutrophication is an excessive algal growth. Although the problem of algal blooms is cosmopolitan, it has been shown to be more severe at formative stages of man made lakes (Adeneji et al., 1981). Lethal levels of toxins produced by Cyanophyte algal blooms have been reported for a number of Africa's man made lakes (Adeneji et al., 1981). Because a limited number of species have been shown to be responsible for the undesirable consequences of algal blooms, a close monitoring of phytoplankton changes in man made lakes especially at the early stages of their filling can serve as an advance warning of potential problems.

This paper describes the phytoplankton composition, temporal periodicity, diversity and production changes at Turkwel Gorge Reservoir in an early stage of its existence. Attempts are also made to relate these changes to the reservoir hydroclimate. This being the first phytoplankton investigation of the reservoir, these findings form a useful baseline for an estimation of potential higher level productivity and assessment of the impact of changes in reservoir catchment land use

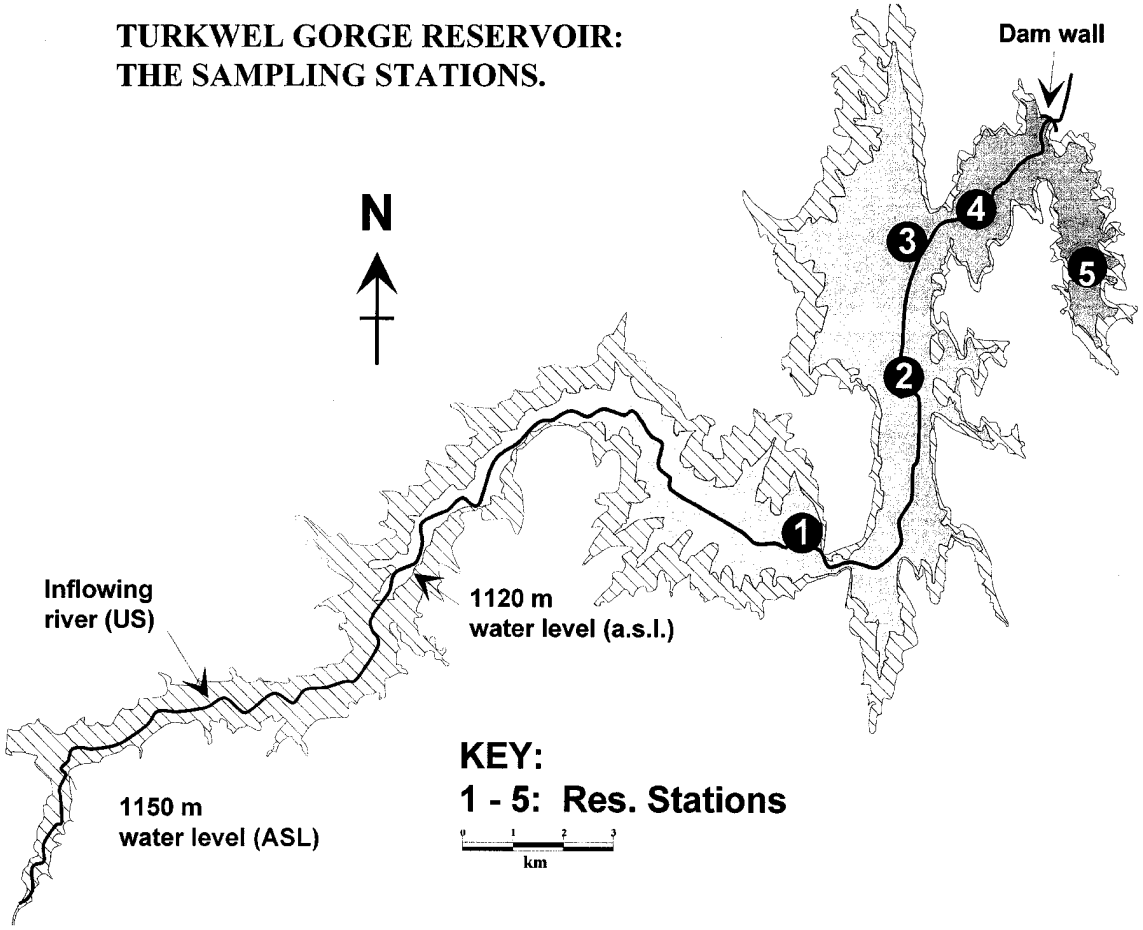

Figure 1. Turkwel Gorge Reservoir; sampling stations (modified from Kerio Valley Development Authority, 1988. Turkwel Multipurpose Project, Bush Clearing in Reservoir Area Tender Document, Figure 3).

patterns and an anticipated multipurpose use of the reservoir.

Materials and methods

Turkwel Gorge Reservoir (Figure 1) is located in Northern Kenya, some 500 km from Nairobi city. During the study period (November 1993 to December 1995), the reservoir maintained an area of between 16 and 17 km^2 and a mean volume of between 230 to 290 million cubic meters which represents less than 18% of the expected full capacity volume. This area and volume range has remained unchanged since 1992. The reservoir is surrounded by bush clad hills dominated by *Acacia reficiens*. The principle river draining into the reservoir is the Suam which rises from a crater in Mt Elgon. Its main tributaries are the Kanyangareng and Kunyao rivers which rise from the Karamoja hills in Uganda. The reservoir has a drainage area of 5900 km^2 which supplies an average of 568 million cubic meters of water per year.

At the reservoir, five sampling stations (R1 to R5; Figure 1) distributed along the long axis of the reservoir were selected for chlorophyll *a* and other water quality investigations. Detailed findings on the physical and chemical conditions and relations with the inflowing and outflowing river water will form the subject of a separate publication. Samples for phytoplankton identification and enumeration were collected from the first (R1), the middle (R3) and the last station (R5).

Water samples for chlorophyll *a* determination was obtained from each of the five reservoir sampling stations (R1 to R5) in 1994 and in the mid reservoir station in 1995. Chlorophyll *a* concentration (uncorrected) was determined as acetone extracts of filterable seston. A known volume of water was gently filtered through 47 mm diameter GF/C filters with the aid of a hand operated suction pump. A few drops of magnesium carbonate suspension was added during filtration (to aid in filter retention and as a precaution against the development of acidity; APHA; 1975; Vollenweider, 1974). Chlorophyll *a* extraction was carried out overnight in 90% acetone under freezing conditions. Sample extract optical density was next measured in a spectrophotometer as outlined in APHA (1975). Actual chlorophyll *a* concentration was estimated by the trichromatic method of Parsons & Strickland (1963). Phytoplankton identification was carried out in two stages. First, fresh net concentrated samples were examined under a compound microscope after every sampling trip. Secondly, samples for later identification were collected in 51 plastic containers and immediately fixed with Lugol iodine solution. A few samples were fixed with formalin. Fixed samples were left standing undisturbed in the dark for at least one week after which the supernatant liquid was carefully decanted to obtain a concentrate of about 500 ml. The concentrate was then transferred to a narrow measuring cylinder where repeated settling and decantation to a final volume of about 50 ml was obtained. Final light and scanning electron microscopy (SEM) identification was carried out at the Institute of Freshwater and Fish Ecology, Neuglobsow Germany. Identification was based on a number of references which included Geitler (1985); Komárek & Fott (1983); Krammer & Lange-Bertalot (1991); Prescott (1978) and Bellinger (1992). Confirmation of species identity was based on recent taxonomic descriptions of the species.

Samples for phytoplankton biomass (unit counts and wet weight) determination were collected in one liter plastic sample bottles and fixed with Lugol's iodine solution to achieve a volume by volume concentration of 0.5%. The preserved samples were left to stand in the dark for several days before concentration by decantation to a final volume of exactly 25 ml. The concentrates from the three stations were combined to produce a composite reservoir sample. From each composite sample, 10 ml of a well mixed sample was taken to Germany for enumeration. Prior to enumeration, the samples were diluted to the original sampling volume. Subsamples for enumeration were allowed to settle for at least 24 hours in 10 ml settling chambers before counting under an inverted microscope equipped with an ocular micrometer for cell dimension determination. The recording and processing of counts data to biovolumes was done with the aid of a computer software, Kip 6P4 (Hamilton, 1990). A counting precision of less than 10% (at the 95 percent confidence limit) was maintained for all samples (Lund et al., 1958; Venrick, 1978). Conversion of biovolume results to biomass was done assuming a specific gravity of 1.

Using the density results of the enumerated taxa, diversity indices for each month were determined by the computational function of the Shannon Weaver index:

$$H' = \frac{N\ln N - \sum_{i=n}^{i=k} fi\ln fi}{n};$$

where H' is diversity (in bits), N is the total individual count, ln is the logarithm to base *e*, fi is the frequency (total count) of species (or taxon) i, and k is the total number of taxa counted (Zar, 1996). The maximum possible diversity (H'max) for each month was calculated using the formula; H'max = ln k (Zar, 1996).

The rates of *in situ* phytoplankton photosynthesis was estimated by light and dark bottle technique (Vollenweider, 1974) at the mid reservoir station (R3). Opaque bottles were prepared by wrapping 300 ml biological oxygen demand bottles with a layer of aluminum foil followed by a double layer of black electrical masking tape. Water samples for filling paired transparent and opaque bottles were drawn from preselected depths with a Ruttner sampler. Bottle incubation at their respective depths were done for a half day period, usually between 0700 hr to 1200 hr. At the end of the incubation period, the bottles were rapidly withdrawn along the shaded part of the boat and dissolved oxygen immediately fixed by the Winkler technique (APHA, 1975). Acidification and titration was completed at the field laboratory within a period of one hour. Difference in DO between the paired light and dark bottles was used to plot a linear rate depth profile of photosynthesis for the half day exposure period. Areal rates of photosynthesis were established from the interpolation of the linear rate depth plots using the Simpson's formula (Vollenweider, 1974). Conversion of the rates of oxygen released to the rates of carbon assimilated was made with the assumption of a photosynthetic quotient of 1.2 (Vollenweider, 1974).

Table 1. Mean reservoir levels (n = 5) of some selected physical and chemical parameters at the Turkwel Gorge Reservoir between 1992 to 1995.

Month	Inflow $m^3 \times 10^6$	Secchi depth m	Median pH	DO mg l^{-1}	Cond. μS cm^{-1}	T. Alk. mg l^{-1}	NO_3 μg l^{-1}	Total nitrogen μg l^{-1}	Total phosphorus μg l^{-1}	Silica mg l^{-1}
Nov	14.36	2.40	7.5	7.2	180	88	35.6	234.0	12.3	8.24
Dec	6.91	1.84	7.7	8.0	187	99	60.0	161.9	5.6	10.34
Jan	0.00	1.45	7.9	6.8	190	102	53.3	224.3	15.7	9.10
Feb	0.00	1.45	7.8	6.8	181	99	31.1	216.5	15.7	9.66
Mar	4.39	0.88	7.6	7.4	199	107	20.0	202.8	20.1	8.02
Apr	44.78	1.03	8.0	7.2	200	105	37.8	275.0	14.6	3.69
May	92.52	0.28	8.0	8.4	189	104	62.2	423.2	21.2	2.70
Jun	51.28	0.70	8.7	9.0	170	83	37.8	284.7	22.4	0.94
Jul	78.66	0.78	8.4	8.5	167	89	46.6	317.9	21.2	1.31
Aug	63.02	0.96	7.5	5.8	170	84	22.3	181.4	16.8	2.41
Sep	22.54	0.92	7.1	5.3	165	87	15.6	150.2	20.1	3.60
Oct	23.31	1.80	7.2	6.6	166	86	13.3	129.4	12.3	5.02
Nov	66.86	2.16	7.1	6.4	167	89	31.1	120.8	8.9	5.20
Dec	11.31	1.45		5.6	165	87	33.3	181.4	17.9	7.00
Feb	0.00	1.88		6.1	167	98	22.3	221.2	13.4	7.59
Apr	29.50	1.23		6.3	175	95	44.4	274.3	16.8	7.64
Jun	33.88	1.1		6.9	180	100	66.7	336.0	24.6	8.78
Aug	31.70	0.9		6.5	170	94	111.1	281.6	17.9	8.40
Oct	32.96	0.85		6.6	155	88	46.7	303.9	19.0	10.31
Dec	3.66	0.8		5.5	140	82	84.4	266.8	69.31	1.82

Results

Chlorophyll a

Changes in the levels of chlorophyll *a* (Figure 2a) showed a seasonal change that was related to the river inflow pattern. The resumption of river inflow into the reservoir in March 1994 (beginning of the wet season) led to a rapid increase in chlorophyll *a* levels at all reservoir stations to a maximum of 36.8 μg l^{-1} in May. Subsequently, there was a progressive decline to the lowest level (4.9 μg l^{-1}) in September. During the period of high chlorophyll *a* measurements, a discernible upreservoir increase in chlorophyll *a* was common with the exception of May when a turbid inflow depressed the level at the station close to the river mouth (R1). However, there was no significant difference in chlorophyll *a* among reservoir stations in 1994 ($P = 0.91$; using the single factor analysis of variance test). Characteristic of all reservoir stations in 1994 was a wide variation in chlorophyll *a* concentration (Figure 2b). Mean chlorophyll *a* concentration (as the average of all 5 reservoir sampling stations in each month) ranged from 5.58 to 28.29 μg l^{-1}. Using the results of all stations, a mean chlorophyll a concentration of 10.65 μg l^{-1} was computed for 1994. A coefficient of variation (CV) of 42.49% was computed from the monthly mean results. In the following year (1995), chlorophyll *a* ranged from 4.93 to 11.54 μg l^{-1} resulting in a mean of 7.94 μg l^{-1} and a CV of 7.6% for the year. Vertical profiles of chlorophyll *a* measured in 1995 (Figure 2c & 2d) show a well developed decline with depth in all months except December which had nearly uniform levels at all depths.

Based on the 1994 results, chlorophyll *a* showed a negative correlation to Secchi depth ($P < 0.005$) and a positive correlation to dissolved oxygen ($P < 0.002$), nitrate nitrogen ($P < 0.05$), total nitrogen ($P < 0.001$) and total phosphorus ($P < 0.05$). Only a positive correlation with dissolved oxygen ($P < 0.02$) and total nitrogen ($P < 0.05$) was noted in 1995.

Phytoplankton composition and species diversity

A list of species identified during the study and a summary of their abundance rating is provided in Table 2. The table includes the abundance rating for the species composition for August 1996. A notable change in

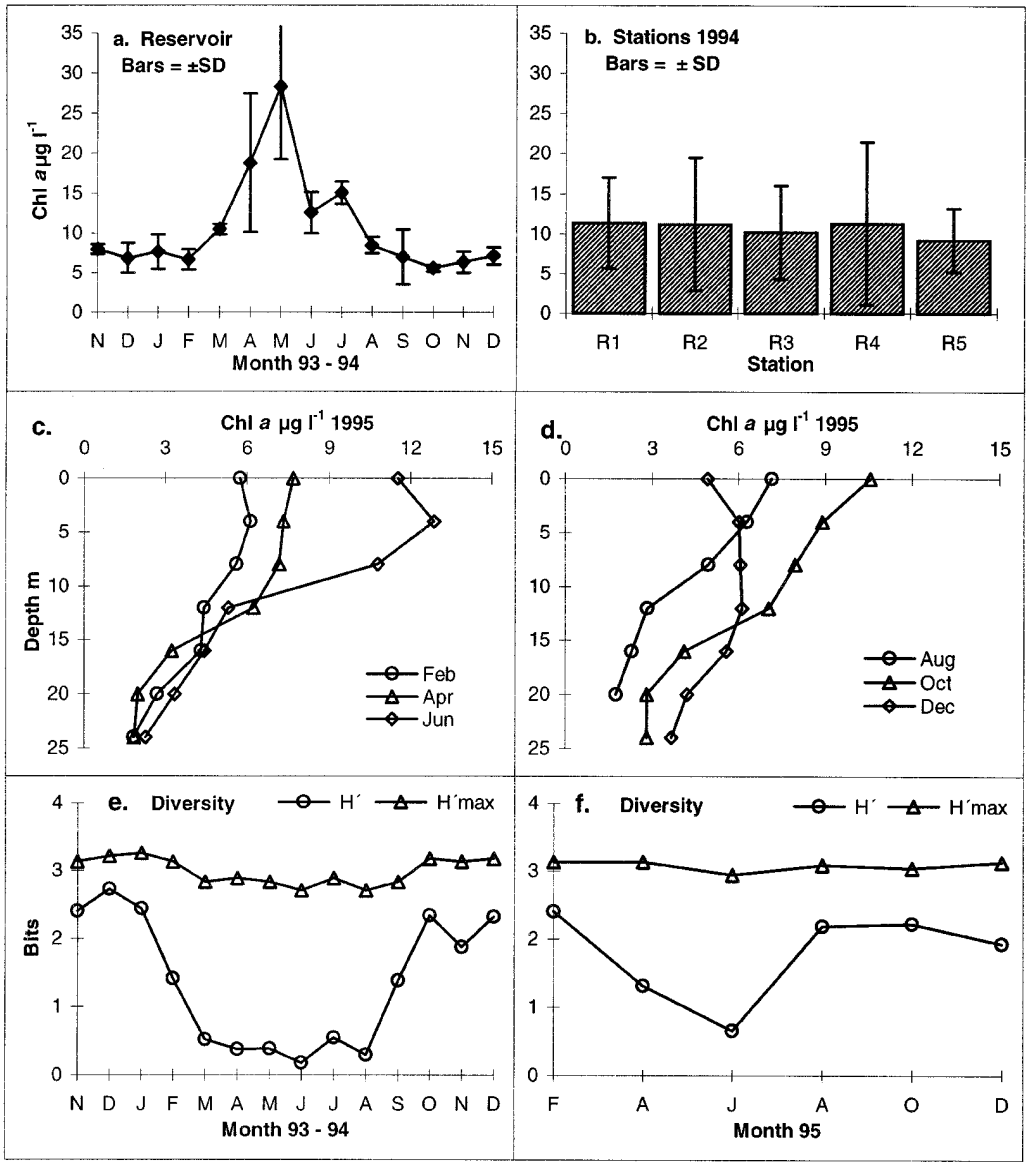

Figure 2. Temporal, spatial and vertical variation in chlorophyll *a*, and temporal changes in the Shannon-Weaver diversity index (H') and the maximum possible diversity (H'max) as established at different periods between Nov. 93 and Dec. 95 at Turkwel Gorge Reservoir.

abundance rating relates to the coccoid blue green algae whose abundance appears to have over the three years shown a progressive increase. On the converse, the abundance of the diatom *Achnanthes* appears to have suffered a progressive decline. The more common phytoplankton taxa are provided in Plate 1. Diversity indices (H') varied from 0.18 to 2.43 (Figure 2e) and from 0.66 to 2.40 (Figure 2f) for 1994 and 1995 respectively. In general, diversity declined with an increase in individual counts. The result was a negative correlation between the two ($R = -0.84$ and -0.96 for 1994 and 1995 respectively). The maximum possible diversity (H'max), in the two years only showed a slight decline during the period with high cell counts (Figure 2e & 2f).

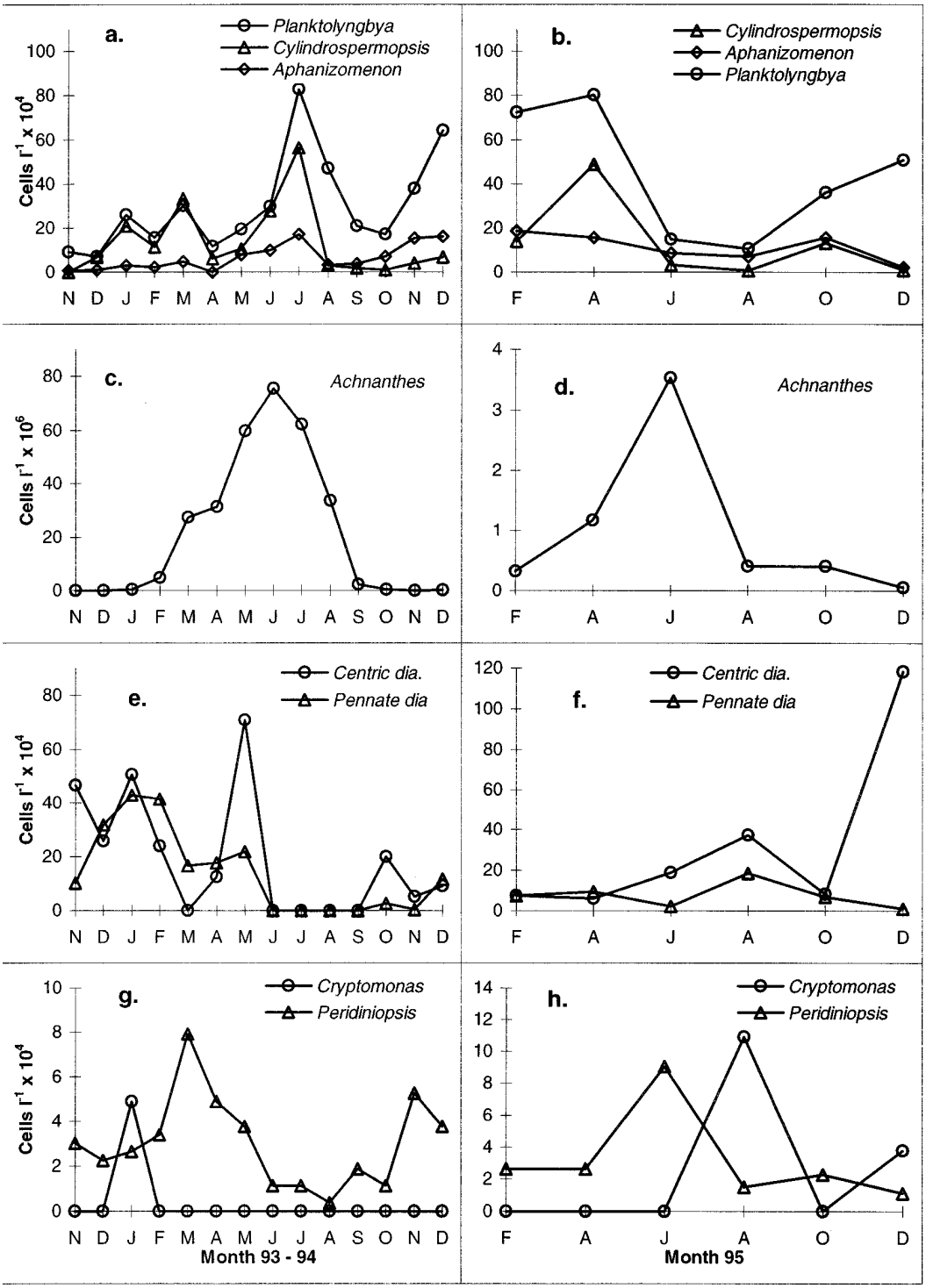

Figure 3. Temporal variation in total unit counts of common Cyanophyta, Bacillariophyta, Cryptomonadophyta, and Dinophyta at Turkwel Gorge Reservoir.

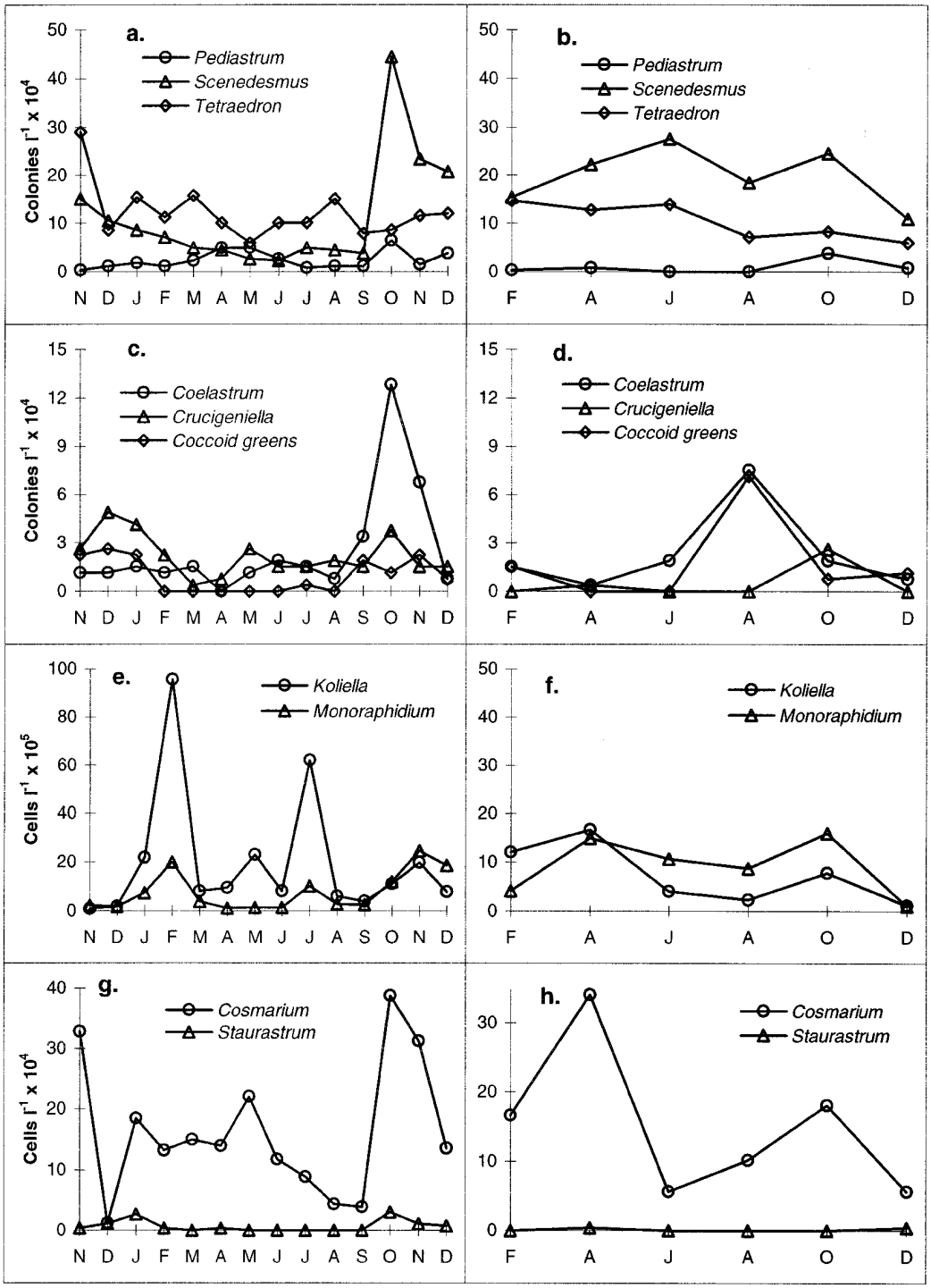

Figure 4. Temporal variation in total unit counts of common Chlorophyta at Turkwel Gorge Reservoir. (Left column: Month 93–94; right column: month 95.)

Table 2. Phytoplankton composition and abundance at Turkwel Gorge Reservoir, Kenya.

Taxon	1994	1995	1996
Cyanophyceae			
Aphanocapsa koordersi StrØm	+	+++	+++
Aphanocapsa sp.	–	+	+
Aphanizomenon cf. *manguinii* Bourr.	+	+	+
Chroococcus sp.	–	–	–
Cyanocatena planctonica Hind.	–	–	+
Cylindrospermopsis cf. *philippinensis* (Tayl.) Kom.	+	+	–
Cylindrospermopsis raciborskii (Wolosz.) Seenay. et S. Raju	–	–	+
Cylindrospermopsis sp.	–	–	–
Cyanonephron styloides Hickel	–	–	–
Microcystis sp.			
Planktolyngbya undulata Kom. et Kling	+	+	+
Pseudanabaena sp.	–	–	–
Cryptophycea			
Cryptomonas sp.	–	–	–
Euglenophyceae			
Phacus sp.	–	–	–
Trachelomonas sp.	–	–	–
Euglena sp.	–	–	–
Chrysophyceae			
Mallomonas sp.	–	–	–
Bacillariophycea			
Achnanthes catenata Bily et Marvan	+++	++	++
Aulacoseira granulata (Ehrenb.) Simons.	–	–	–
Cyclotella cf. *stelligera* Clev. et Grun.	+	+	+
Cyclotella sp.	–	–	–
Thallassiosira sp.	–	–	–
Stephanodiscus sp.	–	–	–
Fragilaria ulna (Nitzsch.) Lange-Bertal.	+	+	+
Nitzschia sp.	+	+	+
Dinophyceae			
Peridiniopsis cunningtonii Lemm.	+	+	+
Peridinium sp.	–	–	–
Chlorophycea			
Botryococcus braunii Kütz.	–	–	–
Chlamydomonas sp.	–	–	–
Coelastrum pseudomicroporum Korsch.	+	+	+
Coelastrum reticulatum (Dang.) Senn.	–	-	–
Cosmarium div. sp.	+	+	+
Crucigeniella apiculata (Lemm.) Kom.	+	-	+
Crucigenia sp.	–	–	–
Dictyosphaerium tetrachotomum Printz	–	-	–
Franceia droescheri (Lemm.) G.M. Smith	–	-	–
Golenkinia radiata Chod.	–	–	–
Kirchneriella dianae (Bohl.) Comas	–	–	–
Koliella longiseta (Visch.) Hind.		+++	+++
Koliella spiculiformis (Visch.) Hind.	+	+	+
Komarekia appendiculata (Chod.) Fott	–	–	–
Lagerheimia subsalsa Lemm.			
Micractinium pusillum Fres.			
Monoraphidium contortum (Thur.) Kom.-Legn.	++	++	++
Monoraphidium griffithii (Berk.) Kom.-Legn.	+	+	+
Monoraphidium irregulare (G.M. Smith) Kom.-Legn.	–	–	–
Nephrochlamys allanthoidea Korsch.	–	–	–
Nephrochlamys subsolitaria (G.S. West) Kosch.	–	–	–
Oocystis lacustris Chod	–	–	–
Pediastrum simplex Meyen	+	–	+
Planktopsphaeria gelatinosa G.M. Smith	–	–	+
Pseudodictyosphaerium jurisii (Hind.) Hind.	–	–	–
Pseudoschroederia antillarum (Kom.) Heg. et Schnepf	–	–	–
Selenastrum gracile Reinsch	–	–	–
Scenedesmus grahneisii Heynig	+	+	+
Scenedesmus div. sp.	–	–	–
Coenochloris sp.	–	–	–
Staurastrum div. sp.	+	–	–
Tetraedron minimum (A. Br.) Hansg.	+	+	+
Tetraedron triangulare Korsch.	–	–	–
Tetrastrum komarekii Hind.	–	–	–
Treubaria triappendiculata Bern.	–	–	–

Frequency: – present, $<$ 10,000 ind. l^{-1}; + = common, $<$ 500,000 ind. l^{-1}; ++ = abundant, $<$ 1,500,000 ind. l^{-1}; +++ = dominant, $>$ 1,500,000 ind. l^{-1}.

Phytoplankton density

Density changes in individual phytoplankton taxa varied widely. In general, high cell counts were characteristic of the wet season. Comparatively, higher cell counts were recorded in 1994 than in 1995. Density changes in the common phytoplankton are presented in Figures 3 and 4. Some irregularity in density fluctuation which was more pronounced in 1994 was common to most taxa. In general, temporal variability ranged from a nearly uniform density throughout the year to a distinct seasonal pattern with distinct peak and low count periods.

A nearly uniform density was exhibited by *Tetraedron* at the reservoir in 1994 (Figure 4a) and by a number of other taxa that included the pennate diatoms, *Pediastrum*, *Crucigeniella*, *Koliella*, *Monoraphidium* and *Staurastrum* (Figures 3f; 4b, 4d, 4f & 4h) in 1995.

The density of *Tetraedron* at the reservoir in 1995 (Figure 4b) showed a progressive decline to the end of the year.

Among the species showing peak density periods, *Achnanthes* was the only species that peaked at the same period in 1994 and 1995 (Figure 3c & 3d). This alga usually had a low density at the beginning of the year. A rapid increase in cell density coincides with the wet season inflow of flood water. Density increase progresses to a peak in June, followed by a steady decline to the end of the year. The peak density in 1994 (75.56 million cells per liter) was over 21 times its peak density in 1995 (3.53 million cells per liter).

Most of the remaining species showed more than one annual peak, especially in 1994. In most cases, density changes followed a wax and wane character peculiar to each taxon and on some occasions, each year. The most common feature was the existence of one main peak with the highest cell count and other smaller peaks. Taxa showing this temporal pattern include *Aphanizomenon, Cylindrospermopsis* and *Planktolyngbya* among the blue green algae, the centric and pennate diatoms, *Peridiniopsis* (dinoflagellate) and most of the green algae genera. *Aphanizomenon, Cylindrospermopsis* and *Planktolyngbya* exhibited a rise and fall pattern throughout the study period. Peak densities for the three genera were recorded in July 1994 (Figure 3a) and April 1995 (Figure 3b). However, the 1995 peaks were slightly lower.

Very low counts for the centric and pennate diatoms were registered between June and September 1994 (Figures 3e). Prior to the low count period, the centric forms showed a sharp rise and fall pattern with a maximum density in May while the pennate forms showed a more gradual change with a peak in January. The centric forms continued the wax and wane feature into 1995 (Figure 3f) with the highest cell density being recorded in December.

The green algae species *Scenedesmus*, *Coelastrum* and *Cosmarium* peaked in October 1994 (Figure 4a, 4c & 4g). Lower peak densities that occurred at different months were realized in 1995 (Figure 4b, 4d, & 4h). Individual counts for *Pediastrum*, *Crucigeniella*, coccoid green algae and *Staurastrum* showed a muted temporal fluctuation change in 1994 (Figure 4a, 4c, & 4g). Higher counts of these species were observed at the beginning and the end of the year except for *Pediastrum* whose peak density was recorded in May 1994. The coccoid green algae registered the highest density for the entire study period in August 1995 (Figure 4d). *Koliella* and *Monoraphidium* (Figure 4e & 4f) were among the species with the highest cell densities. The two genera exhibited a rise and fall pattern with *Koliella* having the greatest amplitude. In 1994, peak density for *Koliella* was recorded in February while that of *Monoraphidium* was recorded at the beginning and the end of the year (Figure 4e). Whereas *Koliella* had a comparatively higher density than *Monoraphidium* in 1994, the converse was the case in 1995 (Figure 4e & 4f).

Cryptomonas was rare during most of the study period and only made peak appearance at some periods. A short peak appearance of this species was recorded in January 1994 (Figure 3g) and in April 1995 (Figure 3h).

Using total individual counts as indices of dominance, a difference in dominance patterns of the wet and dry seasons of the year was evident. In summary, the driest months were characterized by low individual counts and a greater frequency of dominance changes while the wetter months had a higher cell count and a prolonged dominance by one species. Between November 1993 and February 1994 (dry season), successive changes in dominance were in the following order; centric diatoms (*Cyclotella*, *Stephanodiscuss* etc.), pennate diatoms (*Fragilaria* etc.) and *Koliella* sp. Taxa occupying a subdominant or lower positions during this period included *Cosmarium* and *Monoraphidium*. Total individual counts ranged from 2.10 to 18.03 million cells per liter. Between March to September (wet period) the dominant and subdominant species were *Achnanthes* and *Koliella* respectively. Total individual counts ranged from 3.54 to 64.15 million cells per liter. In the last 3 months of 1994, dominance was due to *Monoraphidium* with *Koliella* being subdominant.

Phytoplankton biomass

Dominance in terms of biomass presents a slightly different picture from density changes with larger cell size taxa assuming greater importance. During the period from November 1993 to January 1994, biomass dominance changes were in the following order; *Peridiniopsis*, pennate diatoms and the centric diatoms. Between February 1994 to September 1994, most biomass was due to *Achnanthes*. Important contributions at different times of this period were from *Peridiniopsis*, the centric diatoms, *Aphanizomenon, Cylindrospermopsis, Planktolyngbya* and *Tetraedron*. The period between October 1994 to December 1995 was characterized by a less regular change in dominance as compared to the previous period. In general, dom-

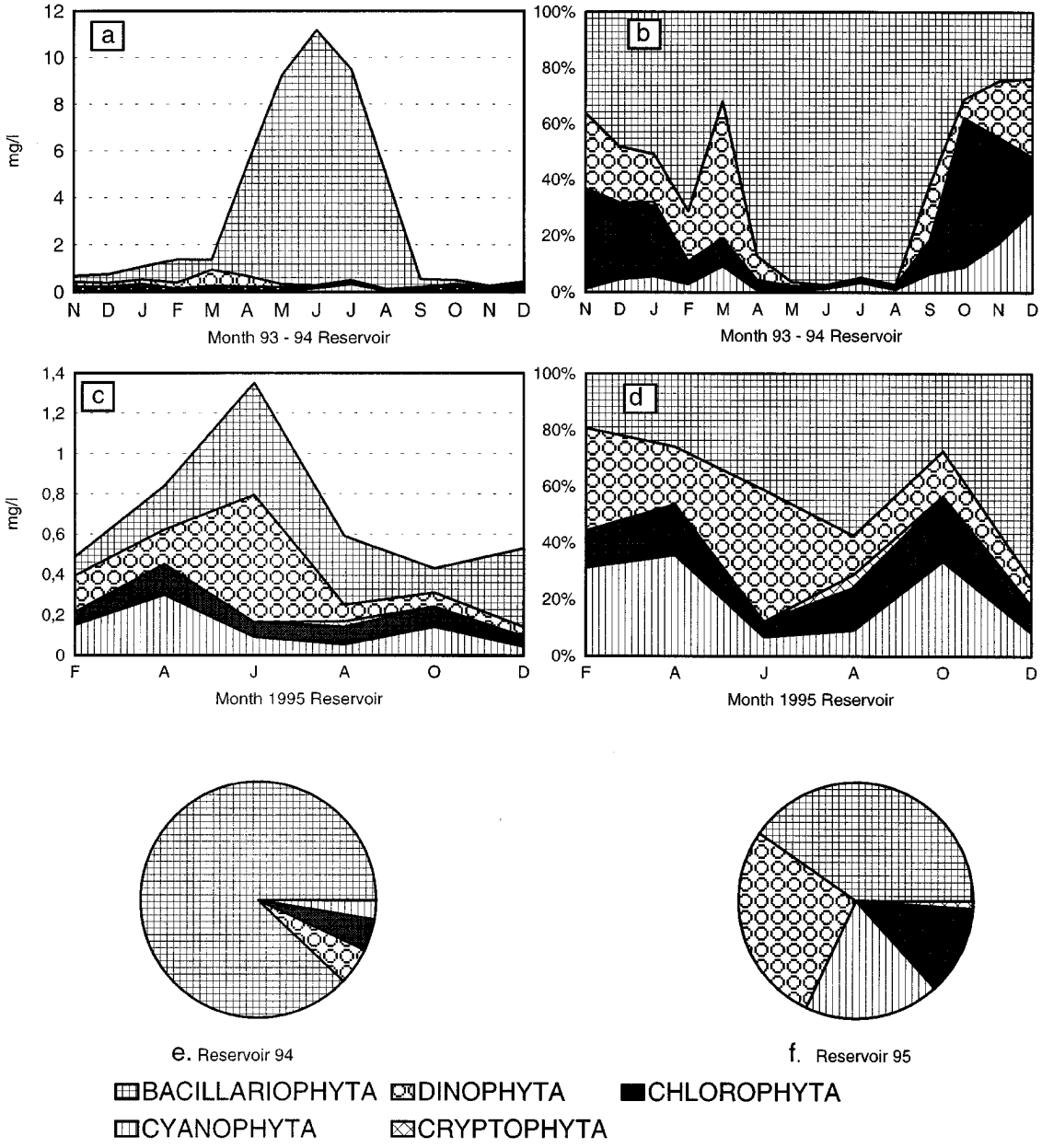

Figure 5. Temporal variation and the percentage distribution of biomass among the main phytoplankton divisions at Turkwel Gorge Reservoir.

inance changed between *Cosmarium*, *Peridiniopsis*, *Aphanizomenon*, *Cylindrospermopsis* and the centric diatoms.

Total biomass of the algal divisions represented in the phytoplankton showed different patterns of change (Figure 5). The Bacillariophyta (Figure 5a) showed the greatest amplitude of change. Beginning in March, its biomass rose rapidly to a maximum in June from whence it rapidly declined to about the previous levels. Bacillariophyta biomass was negatively correlated to silica levels and its biomass decline coincided with the period with the lowest reservoir silica. Chlorophyta biomass was the least variable with higher levels at the beginning and at the end of the year. Dinophyta biomass peaked in March with very low levels in the mid year period. Cyanophyta biomass showed a pro-

gressive increase to a peak concentration in July. The Cryptophyta only made a short peak appearance in January. In terms of percent contribution to the total biomass (Figure 5b), the diatoms contributed the highest percentage in all months with the exception of March, October, and December in which the greatest percentage of total biomass was due to Dinophyta, Chlorophyta and Cyanophyta respectively (Figure 5b). Overall, 88% of the mean biomass for 1994 (Figure 5e) was due to the Bacillariophyta with the Dinophyta, Chlorophyta and Cyanophyta having 5, 5 and 2% respectively (Cryptophyta, less than 0.1%).

Total biomass changes of the different divisions in 1995 was less regular (Figure 5c & 5d). Cyanophyta registered two peaks in April and in October. Chlorophyta biomass varied only slightly with minor peaks in April and October. Peak Bacillariophyta biomass was noted in June and December respectively. Peak Dinophyta and Cryptophyta biomass were recorded in June and August respectively. The Bacillariophyta contributed the highest percentage of biomass in the months of June, August and December. Dinophyta and Cyanophyta led in February and April respectively. In October, the biomass levels of the Bacillariophyta, Cyanophyta and Chlorophyta were almost equal with the Dinophyta biomass being lower (Figure 5d). Compared to 1994, biomass was more equitably distributed among the algal divisions in 1995 (Figure 5f). Only 40% of the mean biomass was due to the Bacillariophyta with the Dinophyta, Cyanophyta, Chlorophyta and Cryptophyta having 28, 18, 12 and 1 percent respectively (Figure 5f).

Total biomass for 1994 ranged from 440.14 (December) to 11172.70 mg m^{-3} (June) with a mean of 3360.85 mg m^{-3}. Much lower measurements were recorded in 1995 with a range from 486.46 (February) to 1351.39 mg m^{-3} (June) and with a mean of 702.2 mg m^{-3}. An assessment of the temporal relations between biomass and some environmental conditions at the reservoir for 1994 revealed positive correlation to river inflow volume ($r = 0.68$; $P < 0.01$), DO ($R = 0.73$; $P < 0.002$), nitrate nitrogen ($R = 0.93$; $P < 0.001$), total phosphorus ($R = 0.67$; $P < 0.01$), and chlorophyll *a* ($R = 0.87$; $P < 0.001$), and a negative correlation to Secchi depth ($R = -0.78$; $P < 0.001$). Biomass changes in 1995 did not show a significant correlation to any of the investigated parameters.

Phytoplankton primary production

Primary production rates for 1994 varied from 1.85 (September) to 9.67 g O_2 m^{-2} d^{-1} (May) with a mean of 4.94 g O_2 m^{-2} d^{-1} (Figure 6). This computes to a carbon assimilation range of 0.58 to 3.02 g C m^{-2} d^{-1} and a mean of 1.56 g C m^{-2} d^{-1}. Primary production rates in 1995 ranged from 3.08 (December) to 5.41 g O_2 m^{-2} d^{-1} (October) with a mean of 3.84 g O_2 m^{-2} d^{-1} (Figure 6). In terms of carbon assimilation, this computes to a range 0.93 to 1.69 g C m^{-2} d^{-1} and mean of 1.2 g C m^{-2} d^{-1}. The rates of primary production in 1994 was observed to be positively correlated to dissolved oxygen ($r = 0.74$ $P < 0.02$), nitrate nitrogen ($r = 0.62$, $P < 0.02$), total nitrogen ($r = 0.93$, $P < 0.001$), chlorophyll*a* ($r = 0.93$, $P < 0.001$), and total biomass ($r = 0.83$, $P < 0.001$). A positive correlation to chlorophyll*a* ($r = 0.93$, $P < 0.01$) was noted in 1995.

Discussion

Chlorophyll a

Because of its close correlation to phytoplankton fresh weight, chlorophyll *a* is widely accepted as an indirect measure of phytoplankton biomass (Voros & Padisak, 1991). Chlorophyll *a* is also the most abundant pigment in living materials (Vollenweider, 1974). The ratio between chlorophyll *a* and total biomass is, however, not constant as chlorophyll *a* has been shown to decline with a reduction in nutrient levels (Hunter and Laws, 1981), an increase in the available light (Desortova, 1981; Hunter & Laws, 1981) and an increase in algal size (Malone, 1980) and age (Messer & Ben-Shaul, 1972). This therefore means that the actual concentration of chlorophyll *a* in an aquatic system is a function of a complex of physical chemical and biotic factors with an infinite range of variability in space and time. A potential variability in chlorophyll *a* concentration for the same biomass requires that measurements of chlorophyll *a* should be supplemented by other indices of biomass. A lack of a significant difference in the spatial distribution of chlorophyll *a* at Turkwel Gorge Reservoir underscores the importance of seasonal changes in influencing the biomass distribution at the reservoir. Hence temporal changes are a more importance source of variability in the reservoir than the spatial changes.

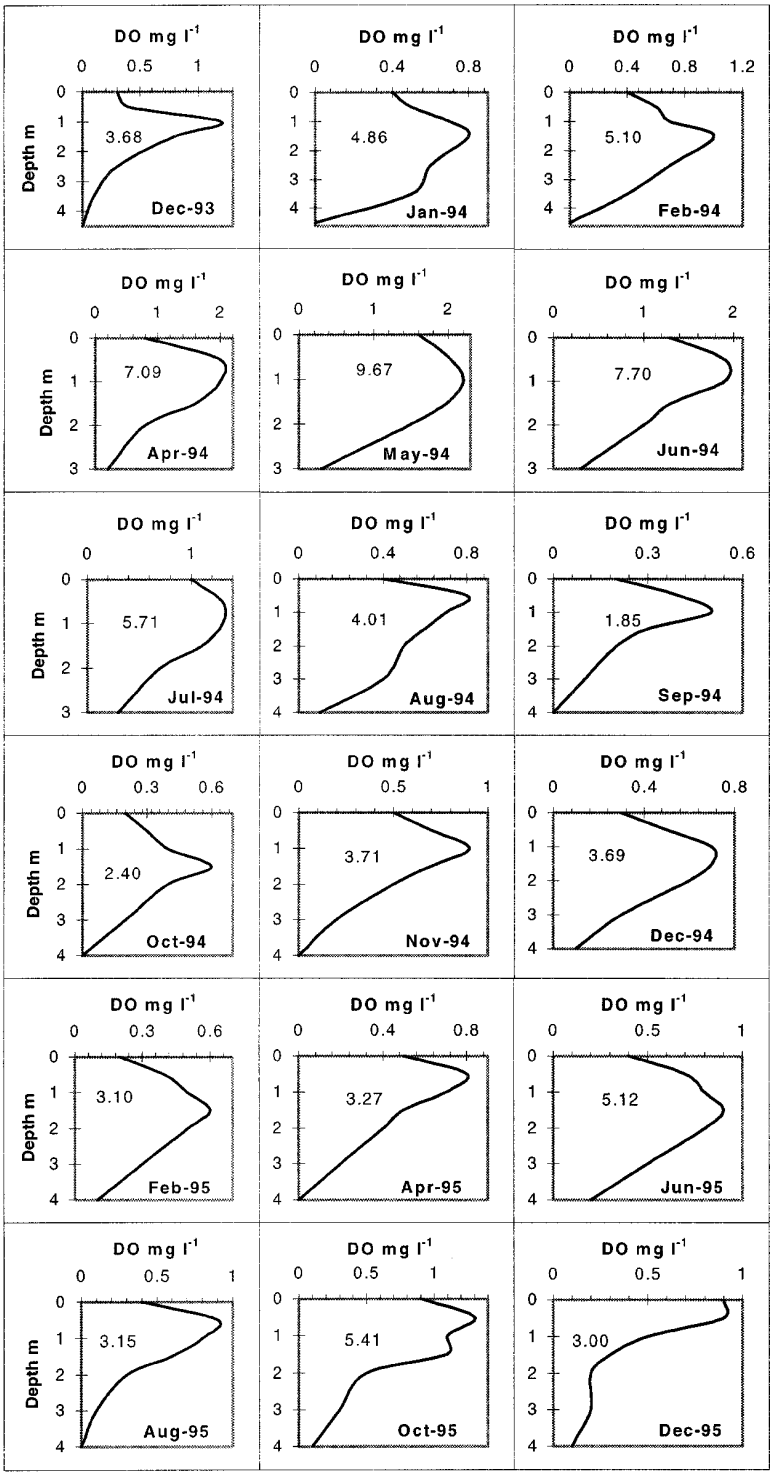

Figure 6. Primary production profiles as obtained at different dates of the months indicated during the period from Dec. 1993 to Dec. 1995. The value given in each profile is the areal rate of primary production (in g m^{-2} d^{-1}) as obtained by the interpolation of the linear rate depth plot using the Simpson's formula (Vollenweider, 1974).

A difference in the CVs of the two years of investigation show that seasonal changes do not necessarily reflect a repeatable annual pattern. A CV of 42.49% based on the 1994 results places the reservoir into a group of tropical lakes that exhibit pronounced seasonal fluctuation in biomass (Pattern A according to Melack, 1979). However, a CV of 7.6% obtained in 1995 corresponds to Melack's second group (Pattern B) which describes lakes with a little coupling of their fluctuations to seasonality of weather. The difference between the two years can be inferred from the positive correlation between inflow volume and chlorophyll *a*. Higher inflows result in higher levels of chlorophyll *a*. Comparatively, a higher inflow was received in 1994 than in 1995 (458.65 and 306.20 million cubic meters respectively). The result was a greater range of chlorophyll *a* measurements (hence a higher CV) and a higher mean chlorophyll *a*. Given that the inflowing river has an annual inflow volume of 568 million cubic meters, it is expected that the reservoir is capable of a higher variability and even higher levels of chlorophyll *a*. However, the impact of short intense flooding episodes as compared to a greater volume of annual inflow that is uniformly spread over a longer period of time needs to be further investigated.

The limited impact of abiogenic turbidity on chlorophyll *a* concentration observed at the reservoir has also been reported for some South African reservoirs (Hart, 1996). Through a monitoring of density changes, this condition has been shown to be the result of an increase in the relative density of ruderal species (Hart, 1996). A decline in chlorophyll *a* concentration at R1 in May when the Secchi depth was extremely low (0.1 m), however, suggests that this condition operates within some turbidity limits. A significant negative correlation between chlorophyll *a* and Secchi depth has been documented for other tropical reservoirs (e.g. Branco & Senna, 1996) and is possibly the result of nutrient rich turbid inflows bringing about a reduction in Secchi depth while promoting biomass accumulation. According to Goldman & Horne (1983: Figure 20-1), in the absence of abiogenic turbidity, a reduction in Secchi depth with an increase in algal concentration follows a hyperbolic tangent whose lowest Secchi depth is about 0.8 m. A chlorophyll *a* concentration above this value does not produce any further reduction in Secchi depth. Based on the relations described by Goldman & Horne (1983), a depth of 0.8 m corresponds to a chlorophyll *a* concentration of approximately 25 μg l^{-1}. A Secchi depth of about 0.1 m obtained in May 1994 for a chlorophyll *a* concentration of 25.33 μg l^{-1} can only be the result of abiogenic turbidity.

A positive correlation between chlorophyll *a* and total phosphorus, total nitrogen and NO_3-N in 1994 raises the possibility of both phosphorus and nitrogen limiting phytoplankton biomass accumulation (Ryding & Rast, 1989). However, an absence of a repeat of the same in 1995 raises the possibility a constant change in the limiting nutrient. A closer correlation to total nitrogen, one that was observed in both 1994 and 1995 suggests that nitrogen may be a frequent limiting nutrient.

Phytoplankton density

Density changes provide a better picture of phytoplankton successional patterns. However, taxonomic uncertainty, a more serious problem in the tropics (Hart, 1996), limits the full understanding of successional changes; especially as it relates to morphologically similar taxa. An irregularity in density changes of most taxa studied is possibly a combined effect of a contagious distribution (Fogg & Thake, 1987) and succession interruption, a feature common to tropical phytoplankton succession and results from changes in the depth of the mixed layer (Lewis, 1996). According to Reynolds (1993), in an uninterrupted phytoplankton succession sequence, one species requires 12 to 16 generations (covering 35 to 60 d) to reach ecological climax. A difference in the peak periods of the different species is possibly explicable by a variation in their growth strategies.

The growth strategy of *Achnanthes* can easily be related to reservoir hydrodynamics. Optimum growth conditions for this alga are provided by the environmental conditions of the wet season. This season is characterized by episodes of high inflow, slightly lower ambient temperatures (resulting from lower cloud cover) and greater water movement (the result of episodes of high volumes of river inflow). In 1994, such conditions were well developed and resulted in the prolonged dominance by *Achnanthes* at the reservoir and the outflowing river. An abrupt decline in the density of this species which started in the middle of the wet season possibly resulted from silica limitation. The failure of *Achnanthes* to reach an equally high density levels in 1995 can be attributed to the relatively drier conditions and lower inflows received.

The wax and wane pattern that was observed in most species can be linked to an irregular creation of suitable growth conditions, the creation of "gaps" as

would be the case in a terrestrial succession sequence. The smaller peaks may be the result of interrupted succession or suboptimal growth conditions. The more dynamic pattern observed during the dry season is possibly the result of short term surface water stability changes. Surface water stability has been linked to changes in the mixed layer (e.g. Reynolds et al., 1987; Capblancq & Catalan, 1994; Lewis, 1996). It must however be emphasized that the rise and fall pattern that was very distinct with some taxa may well have been the result of peak periods of the different species included in the group. For example, the irregular variation of the centric diatoms may be a function of distinct density peaks of the different species.

In temperate latitudes, brief peak appearance of cryptomonads is common following the onset of mixing (e.g. Scharf, 1997). However, the cause of the brief peak appearance at Turkwel Gorge Reservoir is not clear but is possibly a combination of grazing pressure, daily migration and the opportunistic growth habit of *Cryptomonas* (Klaveness, 1991). The continued presence of a species like *Tetraedron* even in the face of distinct environmental changes is possibly because their limiting conditions are not related to these changes. It can therefore be concluded that species density changes at the Turkwel Gorge Reservoir is a function of reservoir hydrodynamics which in turn are regulated by weather changes particularly at the catchment area.

Biomass

Temporal changes in biomass of the main divisions is a reflection of seasonal environmental change. Although the diatom dominance of the wet season may be explained by their preference for higher nutrient and turbulent water conditions (Fogg & Thake, 1987) and their ability to tolerate lower light than other groups (Sommer, 1991), it is however clear from the changes in individual taxa that the peak diatom biomass was mainly due to *Achnanthes* as other diatom groups peaked outside the wet period. Diatom dominance of the wet season is supported by the 1995 results. However, the much lower levels of biomass in 1995 can be attributed the relatively lower inflow nutrient supply. Overall, the biomass changes show the existence of one yearly peak which coincides with the peak biomass of *Achnanthes*.

A positive correlation between river inflow volume and biomass measurements at the reservoir suggests that reservoir biomass accumulation is dependent on inflow supply of growth requirements. This also means that the inflow water is usually quickly distributed to have an immediate impact on the biomass levels of the reservoir; a feature that can be attributed to the episodic nature of the inflow regime. Reservoir studies have shown that the consequence of storm related inflows from erodible watersheds is a reduction of available light, an increase in nutrient levels, a horizontal and vertical displacement of phytoplankton (e.g. Kimmel, 1981; Goldman & Kimmel, 1978). The impact of this on phytoplankton growth and production include an initial suppression of productivity by abiogenic turbidity, followed by a stimulation of primary production and finally a reduction in productivity to previous levels following a decline in nutrient levels (Kimmel, 1981). Perhaps because of a rapid settlement of inflow silt loads, light limitation did not appear to have been important in most parts of the reservoir.

Primary production

Primary production in reservoirs is controlled by the same energy and nutrient inputs that govern other planktonic systems (Brylinsky & Mann, 1973; Schindler, 1978; Brylinsky, 1980). Whereas nutrient and light control are generally recognized as the most important limiting factors to production in natural lakes and rivers respectively, the two are usually regarded as important in reservoirs (Bruce et al., 1990). At the Turkwel Gorge Reservoir, the limited impact of the wet season low Secchi depth readings suggests that nutrient limitation is more important. The mean primary production values for each of the two years places the reservoir within the mesotropic range of tropical lakes (Robarts, 1982; cited in Ryding & Rast, 1989). However, in a growing season, the reservoir production varies from that of a eutrophic system to that of an oligotrophic system. Compared to other tropical reservoirs, primary production range at the Turkwel Gorge Reservoir has a wider annual range (0.58 to 3.02 g C m^{-2} d^{-1}) than Gebel Auliya (Talling, 1957, 1.8 to 3.2 g C m^{-2} d^{-1}) and a lower annual range to that of Nasser (Raheja, 1973, 0.8 to 5.2 g C m^{-2} d^{-1}) and Volta (Viner, 1969, 1 to 5 g C m^{-2} d^{-1}). Mean primary production rates (1.2 to 1.56 g C m^{-2} d^{-1}) are generally higher than those of Mazoe (0.6 g C m^{-2} d^{-1}) and Mwenje (0.4 g O_2 m^{-2} d^{-1}) but lower than that of McIlwaine (1.8 g O_2 m^{-2} d^{-1}), all in Zimbabwe (Mitchell & Marshall, 1974.

Diversity relations

Phytoplankton diversity and its causal factors has been the subject of debate for years. Interest in the subject can be traced to Hutchinson's (1961) observation in his 'paradox of the plankton' that more plankton species can occur in parcel of water than can be explained by the competitive exclusion principle. Subsequent efforts to explain the paradox using theoretical and experimental approaches have according to Sommer et al. (1993) not received universal acceptance. In recent years, Connell's (1978) Intermediate Disturbance Hypothesis (IDH), an idea founded on community ecology has become very popular among plankton ecologists as basis of resolving the paradox. The hypothesis attributes the maintenance of a high diversity to the intervention of factors delaying progress towards, or preventing the attainment of an equilibrium condition (Sommer et al., 1993). According to Reynolds et al., (1993), the hypothesis is a reasoned expression of the interaction between the internally driven progress towards community organization and energetic equilibrium, and the externally imposed stochasticity of environmental variability operating at a variety of temporal and spatial scales.

According to IDH, regular or irregular disturbance resets the succession clock in aquatic ecosystems. A disturbance of an intermediate scale promotes the contemporaneous coexistence of many species hence maintaining a high diversity. At Turkwel Gorge Reservoir, the inverse relationship between diversity and total unit count may be related to changes in nutrient levels. During the wet season, a continuous supply of nutrients provides the necessary stability for progressive succession which results in an increase in total counts and its dominance by a few species. From the relationship between H' and H' max., it is clear that low diversity can be accounted for to a greater extent by changes in relative density. A higher diversity in the intervening period is the result of short term fluctuations in environmental conditions. Changes affecting the mixed layer have been demonstrated to be important for the maintenance of diversity (Capblancq & Catalan, 1994; Reynolds et al., 1987; Lewis, 1996). According to Lewis (1996), variation in the depth of the mixed zone in the tropics is enough to reset the succession clock as it alters the physical and chemical environment through, for example, an improvement of nutrient conditions. The high diversity is possibly the result of the existence of a mix of species at different growth phase, some possibly declining and others increasing.

It can be argued from the results that stability during the wet season period is primarily the result of nutrient availability as the environmental conditions affecting the depth of the mixed layer (e.g. wind stress) where not confined to the dry season. This therefore means that under adequate nutrient supply conditions, community progress to ecological equilibrium is more resilient to small scale disturbance than under nutrient limitation. Varied community resilience to disturbance has been recognized (e.g. Sommer et al., 1993). As observed by Reynolds et al. (1993), one condition characteristic of low diversity periods, that is, the presence of a large biomass dominated by a single species, was met at Turkwel Gorge Reservoir. However, the size of the dominant species was much lower than an estimate of > 100 μm by Reynolds et al. (1993). Stability dependence on nutrient supply is clearly demonstrated by a rapid decline in the biomass of the dominant diatom species as a result of silica depletion and which was followed by a rise in species diversity. This therefore means that even in environments that are prone to a wide fluctuation in environmental conditions some stabilization (hence low diversity) can result from a constant supply of nutrients. However, in such a case, the theoretical maximum diversity does not change appreciably. Less inflows in 1995 meant a lower nutrient supply and hence a lower stability and therefore a relatively higher diversity.

From the foregoing discussion, it can be concluded that the principle environmental factor that regulates the phytoplankton ecology of Turkwel Gorge Reservoir is its hydrodynamics. Inflows regulate the timing, duration and magnitude of peak biomass levels and also the succession stages. Oligotrophy results from a prolonged dry spell with limited or no river inflow. Episodic flood inflows transforms the reservoir into a hyper-eutrophic state. Complete mixing depresses the biomass levels through deep circulation and a dissolved oxygen depletion. Because the inflow and weather cycles varies from year to year, phytoplankton characteristics do not fit into a predictable annual pattern of change. A strong dependence of biomass levels and primary production rates on reservoir hydrodynamics limits the value of trophic state classification schemes (oligotrophy to eutrophy) to the understanding of the trophic conditions of the reservoir.

Acknowledgements

This work was carried out with the support grant from the German Academic Exchange Service (DAAD) and the East African Wildlife Society. The Authors wish to thank the Management of Kerio Valley Development Authority for providing logistic support at the study site and the Institute of Freshwater and Fish Ecology, Neuglobsow for facilitating the analytical work. Special thanks are due to Prof. S.G. Njuguna and the Department of Botany Kenyatta University for providing most of the field equipment. Gratitude is also extended to the KVDA staff at Turkwel for their assistance with the field work.

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