Arch. Hydrobiol. 136 1 105–126 Stuttgart, March 1996

Interannual phytoplankton dynamics of a hypertrophic African lake

Tamar Zohary[1], Arcangela M. Pais-Madeira[2], Richard Robarts[3] and K. David Hambright[1]

With 9 figures and 1 table in the text

Abstract: Phytoplankton species composition and abundance were recorded weekly or biweekly for nearly 7 years in a hypertrophic lake (Hartbeespoort Dam, South Africa), together with a range of physical and chemical parameters. A total of 73 species were recorded, of which only 20 were occasionally abundant, and only 5 became dominant (>50% of total biomass) at least once (*Microcystis aeruginosa, Oocystis lacustris, Aulacoseira* (= *Melosira*) *granulata, Cyclotella meneghiniana, Carteria cordiformis*).

The earlier years of the study (1982–1986) were drought years characterized by low water levels (10–15 m below the level at full supply), excess supply of nutrients at all times of the year, and overwhelming dominance of *Microcystis aeruginosa*. This *K*-selected species proved to be well adapted to withstand the range of environmental conditions throughout summer, fall and winter but it declined in spring each year when a fast successional episode followed. Several small-celled chlorophytes, diatoms and cryptophytes appeared and disappeared until *Oocystis lacustris* became dominant for a few weeks, to be replaced by *M. aeruginosa* early in the summer. During the following rainy years (late 1986 to 1988), the lake re-filled. Major washout losses, concomitant with a considerable decline in surface water phosphorus concentrations and elevated TN/TP ratios, apparently led to the reduction in the abundance of *M. aeruginosa*. Its bloom extended over a smaller portion of the year in 1986 and 1987, and disappeared in May 1988, permitting the development of a more diverse phytoplankton community subject to control by zooplankton grazing.

This long-term phytoplankton record from Hartbeespoort Dam demonstrates the key role of a dominant species in controlling community composition and diversity in hypertrophic lakes. Stable environments lead to low-diversity and high-biomass phytoplankton assemblages dominated by *K*-strategists, while disruptions of suitable strength and frequency allow for the development and maintenance of higher species diversity.

[1] **Authors' addresses:** Israel Oceanographic and Limnological Research. The Yigal Kinneret Limnological Laboratory, P.O. Box 345, Tiberias 14102, Israel.

[2] Division of Water Technology, CSIR, P.O. Box 395, Pretoria 0001, South Africa.

[3] National Hydrology Research Institute, Environment Canada, 11 Innovation Blvd., Saskatoon, Canada.

0003-9136/96/0136-0105 $ 5.50

Introduction

Our present knowledge of phytoplankton periodicity and temporal dynamics in lakes is largely based on work carried out in the north temperate zone (REYNOLDS 1984 a, ASHTON 1985), while the understanding of phytoplankton dynamics and succession in African lakes is still in its infancy (TALLING 1986). This is mostly due to the relative scarcity of data from African lakes, especially of intensive, long-term phytoplankton studies.

Here we record the changes in phytoplankton abundance and species composition over a 7-year period in a hypertrophic African lake. Concurrently collected data on the chemical and physical characteristics of the lake are used to describe the conditions associated with changes observed. Finally, we compare the emerging patterns and associations with those described for other African and hypertrophic lakes.

The lake

Hartbeespoort Dam is a warm monomictic man-made lake, situated 50 km north of Johannesburg (25° 43′ S; 27° 51′ E) in a semi-arid, summer rain-fall (October–March) zone. It stratifies in August or September (spring), with the hypolimnion becoming anaerobic, and turns over in March or April (autumn). It is fed by several inflows, which contribute to its dendritic morphometry. When full, the impoundment has a surface area of 20 km^2, a capacity of 195×10^6 m^3, a mean depth of 9.6 m and a maximum depth of 32.5 m. Average water retention time is 0.9 years (NIWR 1985).

Initially Hartbeespoort Dam was oligotrophic (HUTCHINSON et al. 1932) and its phytoplankton were dominated by the dinoflagellate *Peridinium cinctum* (MULLER) EHR. (HUBER-PESTALOZZI 1929). Over the years the lake turned hypertrophic due to high inputs of nutrient-rich effluents from northern Johannesburg. The hypertrophic condition was manifested by extensive growth of the macrophyte *Eichhornia crassipes* (MART.) SOLMS in the late 1970s (SCOTT et al. 1980). After this exotic plant was eradicated with herbicides, persistent blooms of the cyanobacterium *Microcystis aeruginosa* KÜTZ. emend. ELENKIN developed, with annual production exceeding 1.5 kg C m^{-2} (ZOHARY 1989, ROBARTS & ZOHARY 1992).

Zooplankton in Hartbeespoort Dam include cladocerans, copepods, rotifers and midge larvae, with the herbivorous cladocerans *Daphnia pulex, Daphnia longispina* and *Ceriodaphnia reticulata* constituting the bulk of the standing stock (JARVIS 1986). *Oreochromis mossambicus, Clarias gariepinus* and *Cyprinus carpio* constitute over 90 % of the fish biomass (COCHRANE 1987). Of these, *O. mossambicus* feeds primarily on *Microcystis* and detritus (DE MOOR et al. 1986).

Methods

Hydrological and meteorological data

Daily water level data were supplied by the Directorate of Water Affairs, Pretoria. Lake volumes and percent full supply were calculated from a hypsographic curve. The Directorate also supplied total irradiance and wind speed data, which were continuously recorded on the reservoir shore with a Moll-Gorczynski solarimeter (Kipp and Zonen, Delft, Holland) and a Theis model 4.3900.10 mechanical wind recorder.

Physical measurements

Water temperature was measured at about midday with a Cole-Palmer 8502-20 thermistor at 1-m depth intervals. The attenuation of photosynthetically available radiation (PAR; 400–700 nm) was measured with a quantum sensor (Lambda Instruments, LI-185; sensor, LI-125; precision ± 0.01 $\mu E\, m^{-2} s^{-1}$). Readings were taken from just below the surface and at 25–50 cm intervals to the bottom of the euphotic zone (z_{eu}), defined as the depth of 1 % of the subsurface value.

Sampling

Water samples were collected at weekly intervals from January 1982 (chemistry samples) or from May 1982 (phytoplankton samples) until December 1986, and then at biweekly intervals to December 1988, between 10.00 and 12.00 h at a permanent station (depth: 20.3–32.5 m, depending on the water level) in the lake's main basin. A 6-L capacity opaque Van Dorn sampler was used to collect water samples from the surface and 0.5, 1, 2, 3, 4, 5, 6, 8 and 10 m, from two or three additional depths at the thermocline when it existed, and at 5-m intervals to the bottom. Surface samples were collected with the sampler held horizontally (internal diameter 110 mm) because of frequent steep algal biomass gradients near the surface. The remaining samples were collected with the sampler held vertically (length 56 cm). Dissolved oxygen and chlorophyll-a concentrations were determined on all samples. Equal volume aliquots of each of the surface to 8-m samples were combined to give an integrated phytoplankton sample. Half of the phytoplankton sample was immediately fixed with Lugol's iodine for cell enumeration and the rest was kept fresh for species identification and measurement of cell linear dimensions the following day. A 65-mm (i.d.) hosepipe was used to collect depth-integrated (0–4 m) water samples for nutrient analyses, of which filtered (GF/C) and non-filtered samples were preserved with mercuric chloride and kept refrigerated until analyzed, within a few days.

Chemical analyses

Dissolved oxygen was measured by the azid modification of the Winkler technique and determined spectrophotometrically (ASHTON & TWINCH 1985). Ammonium-N, nitrate-N, nitrite-N, soluble reactive phosphorus (SRP) and silicate in the filtered water samples were determined on a Technicon Autoanalyser II system. Total phosphorus

(TP) and Kjeldahl-N were determined as reported in ROBARTS et al. (1982). Dissolved inorganic-N (DIN) was computed as the sum of ammonia-N, nitrite-N and nitrate-N, and total nitrogen (TN) as the sum of Kjeldahl-N, nitrite-N and nitrate-N.

Phytoplankton abundance, species composition and diversity

Cell numbers were enumerated with an inverted microscope at 500× magnification after sedimenting (for 24 h) 1–10 ml subsample of the preserved sample, or a known dilution thereof, in glass sedimentation chambers (LUND et al. 1958). For the enumeration of *M. aeruginosa,* subsamples were subjected to a 10–30 s treatment in a high speed (20,000 rpm) Ultra-Turrax blender prior to sedimentation. This treatment caused disintegration of colonies yielding cell counts not significantly different from counts obtained using the heating method of HUMPHRIES & WIDJAJA (1979) to disrupt the colonies (ZOHARY & PAIS-MADEIRA 1987).

From May 1982 till October 1983, five fields of vision and a total of at least 400 cells per sample were counted, giving precision of 10–20 % for the dominant species (LUND et al. 1958). In order to increase reliability of counts of less common species the counting method was modified according to LEWIS (1978) from November 1983 onwards. One hundred cells of each species or 100 fields of vision, whichever came first, were counted. After each field, counting was discontinued for species whose counts exceeded 100 cells thus focusing on increasingly rare species as the count proceeded, to a limit of 100 fields. The entire chamber was examined for presence of additional rare species, which were recorded but not counted. Cell volumes were computed from the linear dimensions of cells in fresh samples using geometric equivalents. At least 20 individuals of each species were measured in each sample. The median cell volume for each species was used for conversion of cell numbers to volumes, as recommended by ROTT (1981), and then to wet weight biomass, assuming a specific gravity of 1 g cm^{-3}.

Shannon's H′ diversity index was calculated from the biomass data according to the formula given by SOMMER (1993):

$$H' = -\sum_{i=1}^{s} p_i \cdot \log_2 p_i$$

where p_i = biomass of species i/total biomass, s = no. of species. Since this index is strongly influenced by the number of species occurring, the data prior to November 1983 were excluded.

Results and discussion

The physical environment

The year-to-year variations in the seasonal patterns and ranges of solar radiation, wind speed and upper layer (0–8 m) water temperature were small (Fig. 1). Solar radiation was generally high (range: 12–30 MJ m^{-2} d^{-1}), as expected for a location at a subtropical latitude, high altitude (1162 m), with highlands climate. Winter days were usually cloudless, with solar radiation levels com-

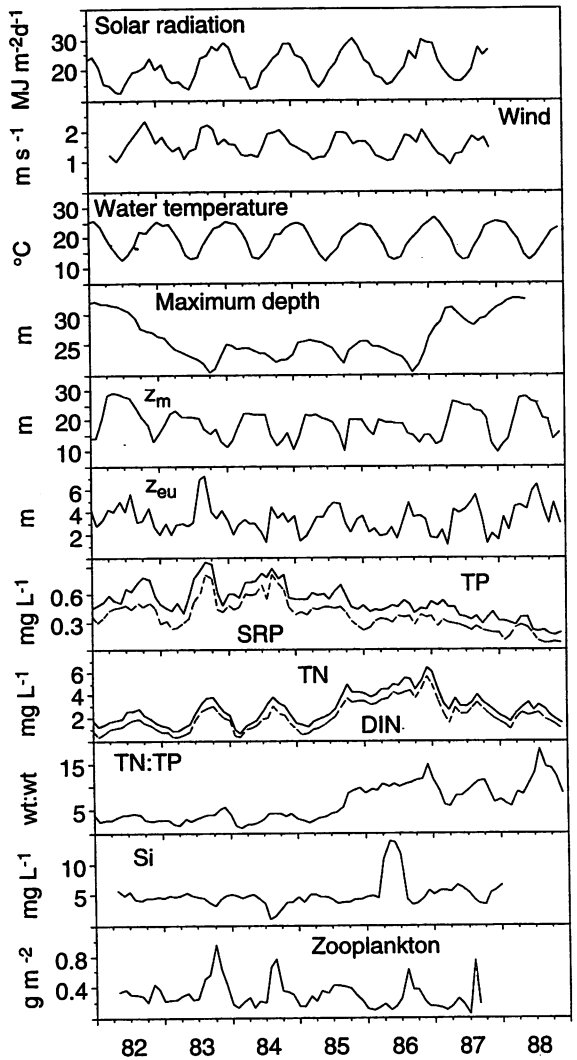

Fig. 1. Interannual changes in a range of physical, chemical and biological parameters throughout the study period in Hartbeespoort Dam, South Africa. Data shown are monthly means based on weekly (1982–1986) or biweekly (1987–1988) measurements, except for solar radiation and wind speeds which are based on continuous records. Water temperatures are means for the upper 0–8 m layer. Mixed layer depth (z_m) was the depth at which oxygen concentration declined below 1 mg l^{-1} and euphotic zone depth (z_{eu}) was the depth to which 1 % of subsurface light penetrated.

parable with mid-summer levels in the north temperate zone. Surface water temperatures ranged between summer maxima of 26–27 °C and winter minima of 11–12 °C. Wind speeds were low, with 50 % of the monthly mean values ranging between 1.2–1.8 $m\,s^{-1}$.

A severe drought starting in 1982 led to a 12.5 m drop in water level, from a maximum depth of 32.5 m (100 % capacity) in January 1982 to 20 m by September 1983, when the lake was only 21 % full. The drought continued throughout 1986, during which lake volume fluctuated seasonally but did not exceed 50 % of full capacity. The lake filled and spilled over the dam wall in the summer of 1987–88.

The depth of the seasonally mixed layer (z_m) was taken as the depth at which the oxygen concentration declined below 1 $mg\,L^{-1}$ and ranged between 8 and 28 m. The euphotic zone depth, z_{eu}, ranged between 0.45 and 8.0 m, with a multiannual mean of 3.3 m. The volume of the euphotic zone, vol_{eu} and the volume of the seasonally mixed layer, vol_m, were calculated from the hypsographic curve as the volumes above z_{eu} and z_m, respectively. The hypolimnion (the difference between total lake volume and vol_m) constituted only a small proportion of lake volume (mean: 4.2 %, range: 0–33 %) and was distinctly smaller in years of low water levels compared with high water levels (Fig. 2). The euphotic zone constituted on average 36 % (range: 5–77 %) of lake volume. The underwater light climate phytoplankton were subjected to was quantified as the ratio vol_{eu}/vol_m (Reynolds & Reynolds 1985). At all

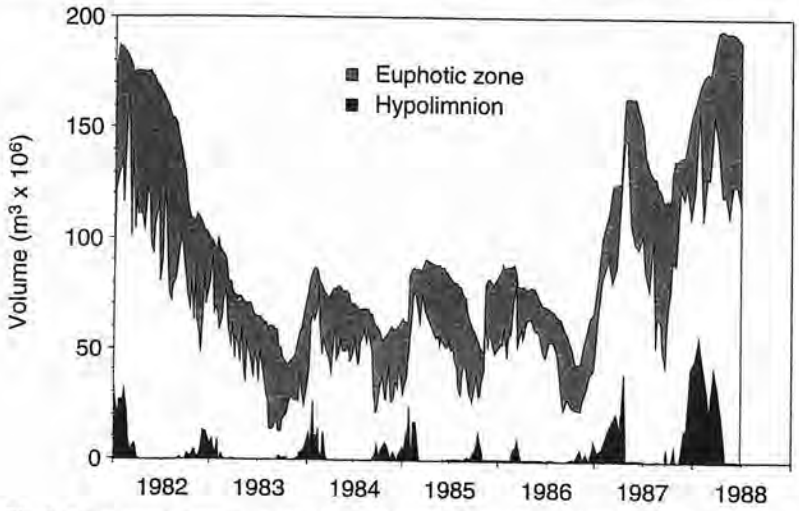

Fig. 2. Interannual changes in lake volume and in the volumes of the hypolimnion and of the euphotic zone. Volumes were derived from depths using the following relationship: ln (Volume) = −5.894 + 3.205 ln (Depth).

times, vol_{eu} was considerably smaller than vol_m, with resulting vol_{eu}/vol_m values usually below 0.4. As with the other physical variables, interannual variations of vol_{eu}/vol_m were small (not shown).

Nutrients

Phosphorus- and nitrogen-chemistry in Hartbeespoort Dam has been described previously (Chutter 1989, Thornton & Ashton 1989, Chutter & Rossouw 1992). Here we present monthly mean concentrations of the key nutrients for the upper 4 m (Fig. 1). During 1982–1985, surface water SRP concentrations were high at all times of the year, with annual means in excess of 0.4 $mg\,L^{-1}$. Exceptions were a few sampling occasions in 1983 when SRP concentrations dropped below 0.2 $mg\,L^{-1}$. A general pattern of lower concentrations in summer and increasing concentrations following overturn was evident, with exceptionally high summer concentrations (>0.5 $mg\,L^{-1}$) in 1983 and 1984. With SRP usually constituting ca. 60 % of TP, the pattern for TP was similar (Fig. 1).

From 1984 onwards, SRP concentrations gradually declined, as indicated by annual means of 0.60 $mg\,L^{-1}$ for 1984, 0.32 $mg\,L^{-1}$ for 1986, 0.26 $mg\,L^{-1}$ for 1987, and a considerably lower value of 0.14 $mg\,L^{-1}$ for 1988. The annual mean value for 1988 was lower than any value recorded between 1982 and 1987. This decline was associated with reduction in external phosphorus loading and increasing water levels (Chutter & Rossouw 1992). During the hydrological years 1982–83 to 1986–87, the external phosphorus load to Hartbeespoort Dam ranged from 17 to 37 $g\,m^{-2}\,yr^{-1}$. In 1985, legislation restricting the concentration of phosphorus in industrial effluents to 1 $mg\,L^{-1}$ came into effect. Full compliance with the standard was attained only in 1988, resulting with the 1988–89 phosphorus load being 9 $g\,m^{-2}\,yr^{-1}$ (Chutter & Rossouw 1992). Chutter & Rossouw (1992) also proposed that the drastic increase in water level in 1986/87 which resulted in a >3-fold increase in lake sediment surface area, may have increased adsorption of phosphorus by the newly inundated sediments, leading to its removal from the water column. Indeed, surface water TP concentrations tended to decline as water levels increased (Fig. 1).

Surface water DIN concentrations usually exceeded 1 $mg\,L^{-1}$ and constituted the bulk of TN. DIN was generally lowest in February or March and highest in September or October each year (details in Chutter 1989). DIN and TN increased considerably in 1985 and peaked in 1986, but then declined with the filling of the lake. TN : TP (by weight) was low in 1982–1984, with annual means below 3.5 (Fig. 1). In the following years higher nitrate concentrations coupled with declining phosphorus concentrations led to increased ratios, with an annual mean ratio of 10.8 in 1986, 9.0 in 1987 and 10.1 in 1988. A similar pattern was revealed when the ratio was calculated for the dissolved nutrients, DIN : SRP (not shown).

Table 1. A list of the phytoplankton taxa from Hartbeespoort Dam, South Africa, 1982–1988. D = dominant, S = seasonally abundant, I = infrequently abundant, + = present at times.

Cyanobacteria	
Order:	Chroococcales
S	*Aphanothece* sp.
+	*Chroococcus* sp.
+	*Gloeocapsa* sp.
S	*Merismopedia* sp.
D	*Microcystis aeruginosa* KÜTZ. emend. ELENKIN
Order:	Nostocales
I	*Anabaena circinalis* RABENH.
+	*Anabaena* sp.
Order:	Oscillatoriales
+	*Oscillatoria* sp.
S	*Pseudanabaena* sp.
+	*Spirulina* sp.
I	Unidentified cyanobacterium
Chlorophyta	
Order:	Chlorococcales
+	*Actinastrum* sp.
S	*Ankistrodesmus* spp.
+	*Ankyra* sp.
+	*Chlorella* sp.
S	*Coelastrum microporum* NAEG.
+	*Coelastrum reticulatum* (DANG.) SENN
+	*Crucigenia mucronata* (SMITH) KOM.
+	*Crucigenia tetrapedia* (KIRCHN.) WEST & WEST
+	*Crucigeniella* sp.
+	*Dictyosphaerium pulchellum* WOOD
+	*Kirchneriella* sp.
+	*Micractinium* sp.
D	*Oocystis lacustris* CHOD.
+	*Oocystis parva* WEST & WEST
+	*Oocystis solitaria* WITTROCK
S	*Pediastrum boryanum* (TURP.) MENEGH. var. *boryanum*
+	*Pediastrum boryanum* var. *brevicorne* A. BR.
S	*Pediastrum boryanum* var. *cornutum* (RACIB.) SULEK
+	*Pediastrum boryanum* var. *longicorne* REINSCH
+	*Pediastrum duplex* MEYEN var. *duplex*
+	*Pediastrum simplex* MEYEN var. *simplex*
+	*Pediastrum simplex* var. *sturmii* (REINSCH) WOLLE
I	*Scenedesmus acuminatus* (LAGERH.) CHOD. var. *acuminatus*
+	*Scenedesmus balatonicus* HORTOB.
I	*Scenedesmus disciformis* (CHOD.) FOTT & KOM.
+	*Scenedesmus eupectinatus* DEDUS.
I	*Scenedesmus linearis* KOM.
S	*Scenedesmus* spp.
S	*Schroederia* sp.

Table 1. Continued.

Order:	Tetrasporales
+	*Golenkinia* sp.
Order:	Volvocales
I	*Carteria cordiformis* (CARTER) DIESING
I	*Chlamydomonas* sp.
+	*Eudorina* sp.
S	*Pandorina* sp.
Order:	Zygnematales
+	*Closterium aciculare* var. *subpronum* WEST & WEST
I	*Cosmarium laeve* RABENH.
+	*Micrasterias* spp.
I	*Staurastrum* spp.
Cryptophyta	
S	*Chroomonas* sp.
S	*Cryptomonas* sp.
Euglenophyta	
Order:	Euglenales
+	*Euglena* sp.
+	*Phacus* sp.
+	*Trachelomonas* spp.
Order:	Eutreptiales
+	*Eutreptia* sp.
Bacillariophyta	
Order:	Biddulphiales
S	*Cyclotella meneghiniana* KÜTZ.
+	*Cyclotella* sp.
S	*Melosira granulata* var. *angustissima* MÜLLER
S	*Melosira granulata* (EHR.) RALFS (= Aulacoseira granulata (EHR.) SIMONSEN
S	*Melosira varians* AGARDH.
+	*Stephanodiscus* sp.
Order:	Bacillariales
+	*Achnanthes* sp.
+	*Caloneis* sp.
+	*Cocconeis* sp.
+	*Cymatopleura* sp.
+	*Diatoma vulgare* BORY
+	*Eunotia* sp.
+	*Gomphonema* sp.
S	*Navicula* spp.
S	*Nitzschia* spp.

Phytoplankton species composition, abundance, and diversity

A total of 73 phytoplankton species were observed in the epilimnion of the main basin of Hartbeespoort Dam over the years 1982–1988 (Table 1). Of these, only 41 occurred in sufficient numbers to be counted at least once; 20 were seasonally abundant. The richest division in number of species was

Chlorophyta (40 species), followed by Bacillariophyta (17), Cyanobacteria (11), Euglenophyta (3) and Cryptophyta (2). Pyrrophyta (dinoflagellates) were never observed.

The temporal changes in the phytoplankton of Hartbeespoort Dam are shown as variations in the absolute and relative abundances of the major phytoplankton groups (Fig. 3). Striking features were: (1) the overwhelming dominance of cyanobacteria; (2) the high standing crops encountered at times; (3) the irregular occurrence of the biomass peaks over the annual cycle; (4) the wide range of biomass values, spanning 3 orders of magnitude (0.37–303 $g\,m^{-3}$) and (5) the relatively simple phytoplankton assemblage (typically only 7–8 species).

Cyanobacteria dominated the phytoplankton assemblage 6 to 10 months each year, except in 1988, when their dominance did not extend beyond May. Chlorophytes dominated for 2–3 months between August and October. Diatoms (Bacillariophyta) and cryptophytes were occasionally abundant with no distinct pattern to their occurrence. Euglenophytes occurred occasionally but never in large enough numbers to be counted.

Microcystis aeruginosa was by far the most abundant phytoplankton species, accounting for the dominance of cyanobacteria. It appeared in two forms: the net-shaped colonies of *M. aeruginosa* forma *aeruginosa* and the spherical or lens-shaped colonies of *M. aeruginosa* forma *flos aquae* (REYNOLDS et al. 1981).

Due to large week-to-week fluctuations in *Microcystis* abundance caused by horizontal transport of surface scums, the biomass data are presented in Fig. 4 as running means for 5 consecutive weeks, from which two peak abundance points attributed to scum formation were excluded. Presented this way, a characteristic annual pattern of growth and decline emerges, although the precise timing, the rate of increase, and the eventual standing crop varied from one year to another. Lowest concentrations of *Microcystis* were recorded in August and September (spring) each year. By October or November the population was rapidly increasing, reaching maximal standing crops around January or February (mid-summer). The large standing crops and dominance of *Microcystis* were maintained all autumn, and in the earlier years of the series they persisted most of the winter, until an abrupt decline in August. In 1985, the population gradually declined from April to August. In 1987 a substantial proportion of the population was artificially removed from the lake in May by flushing downstream thick scums that formed at the dam wall. In 1988 *Microcystis* was repeatedly flushed over the dam wall in April–May and a new population did not develop. CHUTTER & ROSSOUW (1992) reported that *Microcystis* did not bloom again in 1989 or 1990.

The filamentous cyanobacterium *Pseudanabaena* sp. (identified according to RIPPKA et al. 1979) usually infested the mucilaginous sheath of *Microcystis*

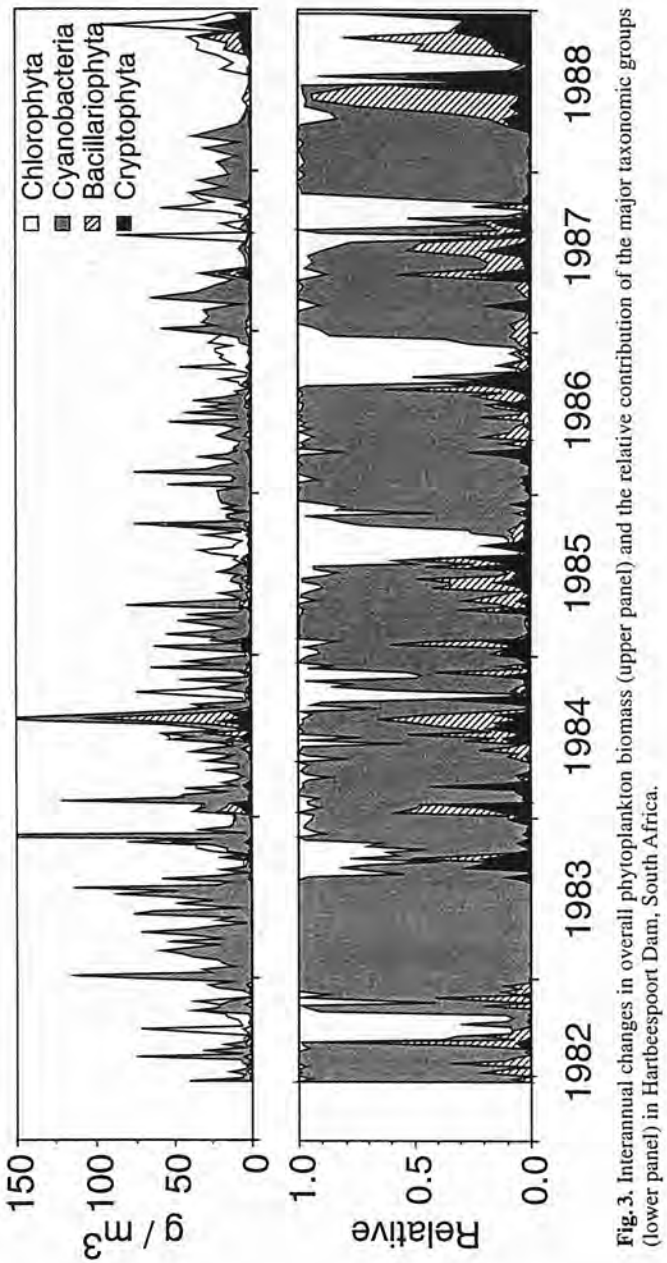

Fig. 3. Interannual changes in overall phytoplankton biomass (upper panel) and the relative contribution of the major taxonomic groups (lower panel) in Hartbeespoort Dam, South Africa.

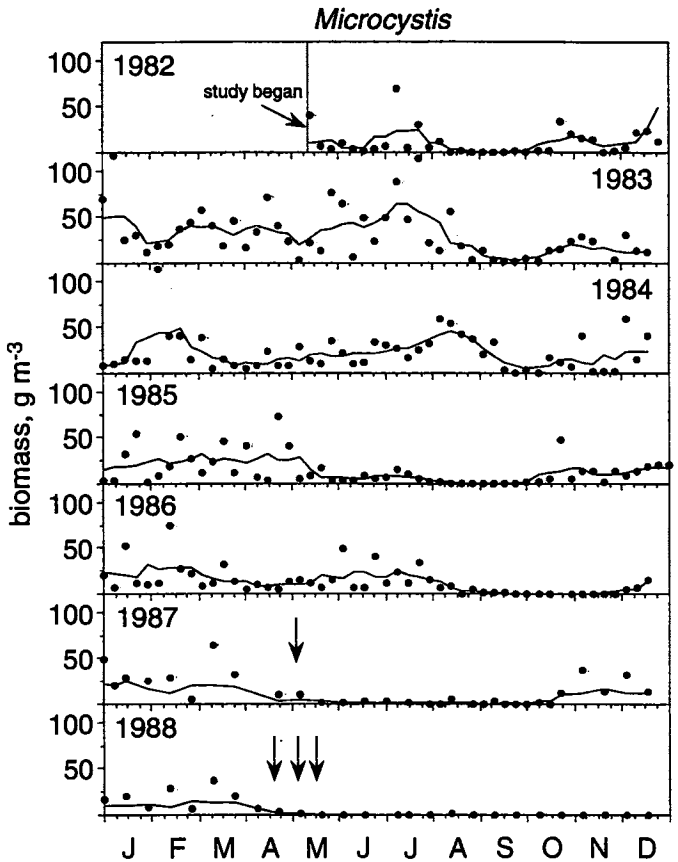

Fig. 4. Interannual variations in the abundance of *Microcystis aeruginosa* in Hartbeespoort Dam, South Africa. Points are actual data; line shows the running mean for 5 consecutive sampling dates. Arrows indicate times when *Microcystis* scums were spilled over the dam wall.

colonies. These small filaments (usually 3 to 5 cells of 1 µm diameter by 7 µm length) were found on both forms of *Microcystis*, but were more often associated with the net-shaped colony structure. *Pseudanabaena* was usually most abundant in late spring and again in late summer. While this small cyanobacterium was nearly always present in water samples, its contribution to the total phytoplankton biomass was minor. Other cyanobacteria (*Aphanothece* sp., *Merismopedia* sp. *Anabaena circinalis, Oscillatoria* sp. and *Spirulina* sp.) were seasonally abundant but rarely contributed significantly to total phytoplankton biomass.

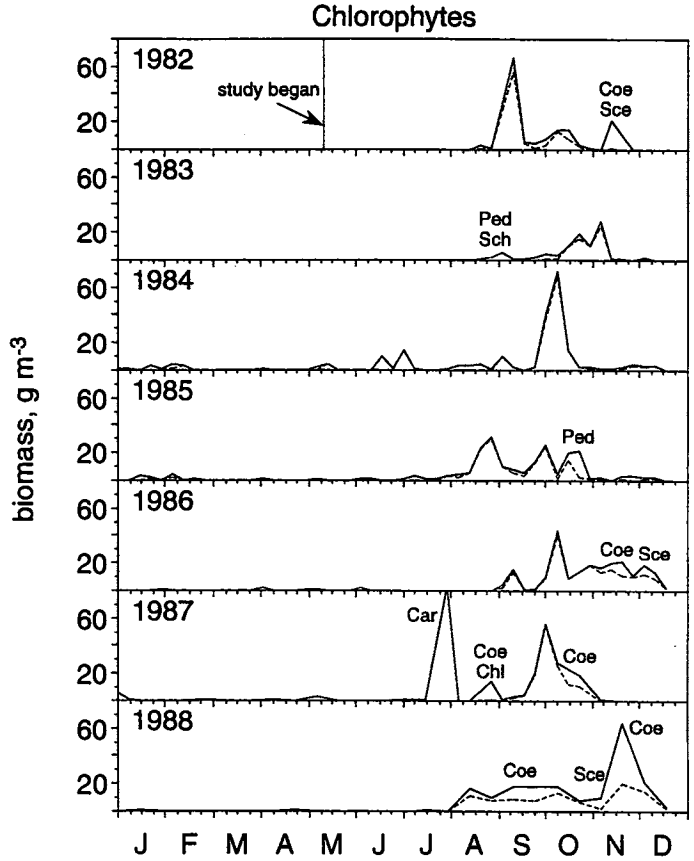

Fig. 5. Interannual variations in the abundance of *Oocystis lacustris* (dotted line) and total chlorophyte biomass (full line) in Hartbeespoort Dam, South Africa. (Car = *Carteria*, Coe = *Coelastrum*, Ooc = *Oocystis*, Ped = *Pediastrum*, Sce = *Scenedesmus*, Sch = *Schroederia*).

The chlorophyte *Oocystis lacustris* (Fig. 5) was second to *Microcystis* in overall abundance and was the only other species that dominated the phytoplankton of Hartbeespoort Dam (>50 % total biomass) for several weeks every year. Its peak abundance (in some years >50 g m^{-3}) was always in spring, during the period of lowest epilimnetic concentration of *Microcystis*. The increase of *Oocystis* coincided with increasing wind speeds and water temperatures and the onset of stratification (Zohary & Robarts 1989).

Pediastrum spp. also appeared in spring each year, more or less at the same time as *Oocystis* sp., but its biomass was considerably smaller (highest wet-

weight attained: 18.8 g m^{-3} in October 1985). Of the 8 *Pediastrum* species and varieties identified from Hartbeespoort Dam only *P. boryanum* var. *boryanum* and *P. boryanum* var. *cornutum* contributed significantly to phytoplankton biomass. Other seasonally abundant chlorophytes were *Ankistrodesmus* sp., *Scenedesmus* spp., *Coelastrum microporum* and *Schroederia* sp.

Only once throughout the study did a green alga other than *Oocystis* become overwhelmingly dominant. This occurred in winter 1987 when for about one week *Carteria cordiformis* constituted 98 % of the phytoplankton biomass. *Carteria* was not observed during the earlier years of the study and appeared for the first time on 7 July 1987. On 21 July a concentration of 258 cells ml^{-1} was recorded. By 4 August the number of *Carteria* cells had increased to 251,000 ml^{-1}, equivalent to a net increase rate of 10 doublings in 14 days. By then all other phytoplankton species were practically excluded, chlorophyll-a concentration at 0.5 m reached 250 mg m^{-3}, and the z_{eu} decreased from 4.4 m on 21 July to 2.2 m on 4 August. The *Carteria* bloom occurred at a time of lowest annual temperature (12 °C), coinciding with a distinct increase in wind speed and ambient ammonia concentrations. Its rapid disappearance could be attributed to zooplankton grazing. Zooplankton biomass increased from 59 g m^{-2} on 7 July to a peak of 1464 g m^{-2} on 4 August and then declined to 370 g m^{-2} by 11 August (JARVIS, unpublished data). A week later the bloom was gone, *Carteria* cell numbers were below detection level of our counting technique, and z_{eu} increased to 7.1 m. *Carteria* occurred again in June 1988, but in low numbers.

Of the diatoms, *Aulacoseira* (formerly *Melosira*) *granulata* and its variant *A. granulata* var. *angustissima* were the most abundant species. *Aulacoseira* appeared in most years after overturn and was present in the water column in concentrations of about 2 g m^{-3} until the onset of stratification (Fig. 6). In 1988 *Aulacoseira* was practically absent.

Another seasonally abundant centric diatom was *Cyclotella meneghiniana* (Fig. 6). While it was rarely observed in 1982 and 1983, it formed a conspicuous bloom in August 1984 when it reached a biomass of 97 g m^{-3} (39,000 cells ml^{-1}). This was the only time during the 7 years when a distinct drop in epilimnetic silica concentrations was recorded, from an ambient concentration of 4–5 mg l^{-1} to 0.35 mg l^{-1} on 28 August 1984. The peak of *Cyclotella* was followed by a distinct increase of a likely grazer, *Bosmina* sp. (JARVIS 1986), with the effect that by early September 1984 *Cyclotella* had practically disappeared. The August 1984 bloom of *Cyclotella* did not exclude a large coexisting *Microcystis* population (59 g m^{-3}; Fig. 3). During 1985, 1986 and 1987 *Cyclotella* was occasionally abundant. Another conspicuous bloom of this diatom occurred in October–November 1988, the only spring in which *Microcystis* numbers were low. *Cyclotella* reached a peak biomass of 22.7 g m^{-3} on 26 October, equivalent to 57 % of total algal biomass.

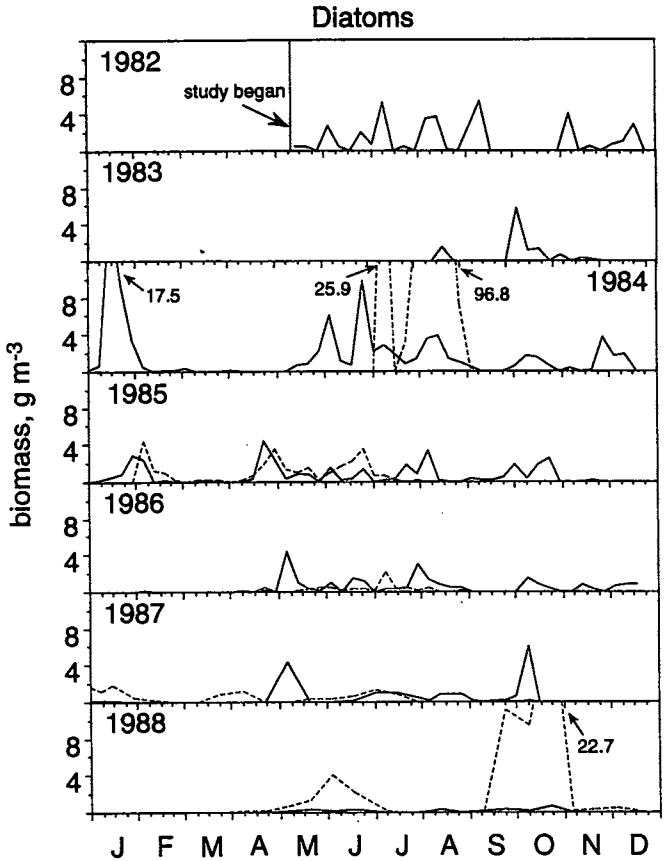

Fig. 6. Interannual variations in the abundance of *Aulacoseira granulata* (full line) and *Cyclotella* spp. (dotted line) in Hartbeespoort Dam, South Africa.

Pennate diatoms, especially *Navicula* spp. and *Nitzschia* spp. often occurred, but never contributed significantly to phytoplankton biomass.

Cryptophytes, mainly *Cryptomonas* sp. and *Chroomonas* sp. (Fig. 7), constituted another common component of the Hartbeespoort Dam phytoplankton, but never attained dominance. Cryptophytes increased substantially in January 1984 and again in July–August 1984. Their absolute and relative abundances were largest late in 1988, when *Microcystis* was absent (Fig. 3).

In general, species diversity was low; Shanon's diversity index rarely exceeded 1.5 (Fig. 8). Diversity was typically lowest in summer (Jan–Mar), and highest between May and October, depending on the year. A trend of increase

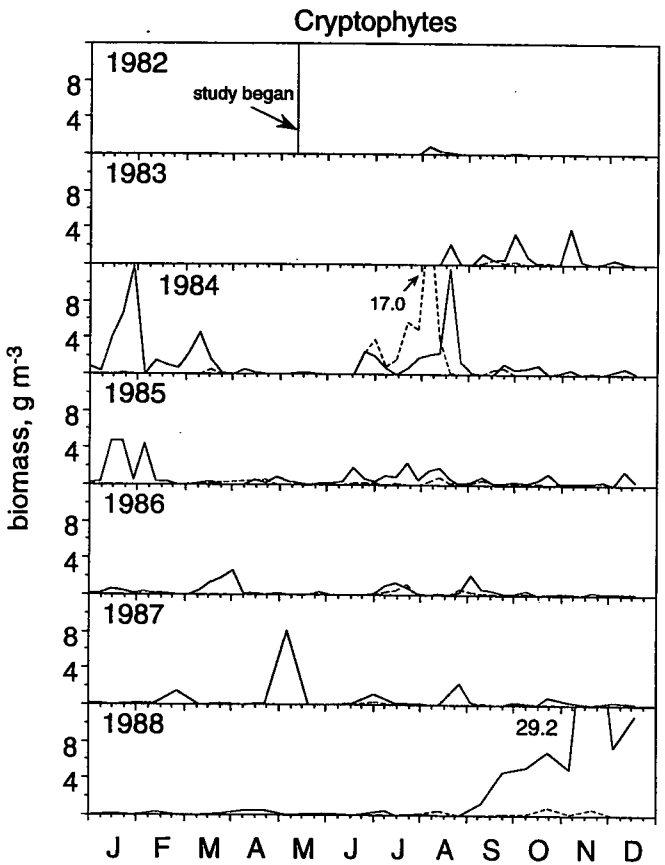

Fig. 7. Interannual variations in the abundance of *Cryptomonas* spp. (full line) and *Chroomonas* spp. (dotted line) in Hartbeespoort Dam, South Africa.

in diversity during the May to October period was evident during 1986–1988, as *Microcystis* dominance declined.

Successional patterns

The earlier years of the study were characterized by an overabundance of nutrients at all times and minor year-to-year variations of environmental parameters. It is therefore not surprising that during these years *Microcystis*, an extreme *K*-strategist (REYNOLDS 1984b, 1988), dominated the phytoplankton for 8–9 months each year (Fig. 3). Its resistance to grazing (JARVIS 1986, JARVIS et al. 1987) and its ability to regulate its position in the water column made it possible for *Microcystis* to maintain the high standing stocks attained in summer throughout autumn and winter, despite suboptimal temperatures and low growth rates, while controlling the underwater light climate to the practical exclusion of other species (ROBARTS & ZOHARY 1984, ZOHARY & ROBARTS 1989). This high-biomass, single-species community structure is probably the ultimate manifestation of hypertrophy.

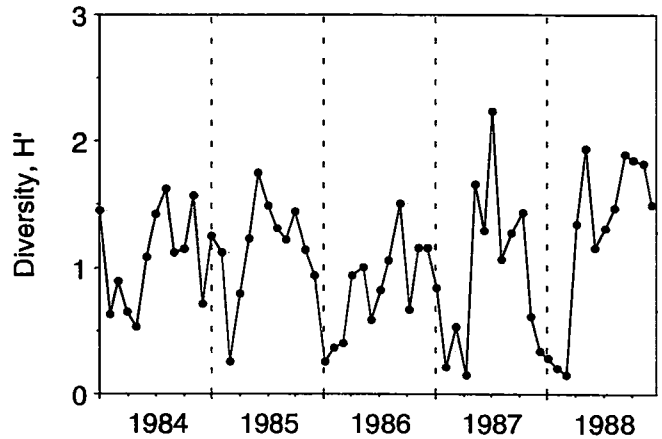

Fig. 8. Temporal variation in Shannon's H' diversity index. Values shown are monthly means calculated from weekly or bi-weekly phytoplankton biomass data.

For a short period in spring each year, following the *Microcystis* decline, the euphotic zone doubled in size, "making room" for other species. Hence, a successional episode was initiated in July or August each year, in which fast-growing *r*-selected species developed sequentially until the establishment of *Oocystis lacustris* (e.g. in 1983: *Chroomonas* → *Cryptomonas/Chlamydomonas* → *Schroederia* → *Pediastrum* spp. → *Oocystis lacustris*, or in 1984: *Cyclotella meneghiniana/Chroomonas* → *Cryptomonas* → *Oocystis lacustris*), which was the only species to attain dominance. The abundance of non-cyanobacterial phytoplankton stimulated the growth of zooplankton, which peaked between August and October each year (Fig. 1). Indeed, high zooplankton grazing pressure was shown by JARVIS (1986) to be a main factor controlling spring phytoplankton.

During the later years of the study (1986–1988) the prevailing year-to-year stability in Hartbeespoort Dam was disrupted by repeated natural and human-induced perturbations. Examples were reduced external phosphorus loading and declining ambient SRP concentrations, a ca. 8-m increase in water level within one rainy season between November 1986 and April 1987 and another

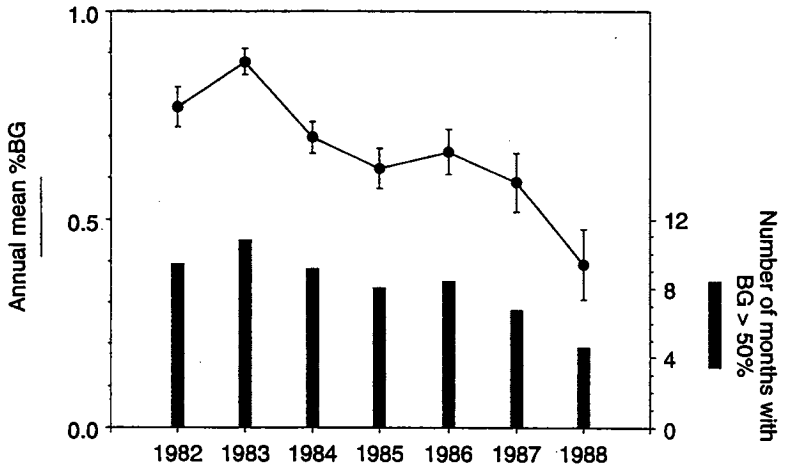

Fig. 9. The annual mean (± SE) relative abundance of cyanobacteria (% BG; circles), and the number of months each year in which cyanobacteria represented >50 % of total phytoplankton biomass (grey bars) in Hartbeespoort Dam, 1982–1988. *Microcystis aeruginosa* usually comprised 95–100 % of total cyanobacterial biomass.

3 m the following year (Fig. 1), and extensive export of *Microcystis* by repeated flushing of thick scums through the dam's sluice gates in 1987 and 1988 (Fig. 4). These led to the gradual reduced dominance of cyanobacteria, both in terms of its standing stock and the proportion of the year it dominated the phytoplankton (Fig. 9), and to its eventual elimination in 1989 and 1990 as reported by CHUTTER & ROSSOUW (1992).

As *Microcystis* declined other species took over. *Oocystis* dominated over longer periods than in the earlier years (Figs. 3, 5). *Cyclotella meneghiniana* became a more common component of the phytoplankton (Fig. 6). Genera that were never observed in the earlier years (e.g. *Crucigenia, Ankyra, Golenkinia, Kirchneriella*) appeared for the first time, others that were rarely seen occurred more frequently. An extreme example was that of the July 1987 bloom of *Carteria,* which was rarely observed previously. *Carteria* behaved as a classical small-celled (diameter: 15–20 µm), fast-growing opportunistic *r*-strategist.

Comparison with other African lakes

Many African freshwater lakes and reservoirs are dominated by cyanobacteria over extended parts of the year, possibly due to the "endless summer" conditions typical of Africa (KILHAM & KILHAM 1990). Blooms of N_2-fixing cyanobacteria are common (e.g. Rietvlei Dam, ASHTON 1985; le Roux and Wuras

Dams, ALLANSON et al. 1990; Lake Malawi, PATTERSON & KACHINJIKA 1993; and Lake Victoria, HECKY 1993). However, the non-N_2-fixing *Microcystis aeruginosa* is by far the most common bloom-forming cyanobacterium in Africa. It dominated the nutrient-rich reservoirs of the Transvaal highlands (e.g. Roodeplaat Dam, PIETERSE & ROHRBECK 1990; Rietvlei Dam, ASHTON 1985; Brakpan, T. ZOHARY, unpublished; and Bon-Accord Dam, W. E. SCOTT, personal communication), as well as oligotrophic Midmar Dam, Natal (ALLANSON et al. 1990), and mesotrophic Lakes Kariba (HANCOCK 1979) and McIlwaine, Zimbabwe (ROBARTS 1979). *Microcystis* blooms also occur in some of the large African lakes, e.g. Lake George, Uganda (GANF 1974) and Lake Turkana, Kenya (LITI et al. 1991). This ubiquitous dominance of *Microcystis* in African freshwaters is unmatched in North temperate lakes, where any one of several cyanobacterial genera may dominate (usually *Anabaena, Aphanizomenon, Oscillatoria* or *Microcystis;* REYNOLDS 1987).

In African lakes diatoms (often *Aulacoseira granulata*) tend to alternate dominance with cyanobacteria (usually *Microcystis*) either seasonally or annually (TALLING 1986). Examples are Lake McIlwaine (TALLING 1986), L. Kariba (RAMBERG 1987), Lake Malawi (PATTERSON & KACHINJIKA 1993) and Lake Victoria (HECKY 1993). In Hartbeespoort Dam these two species were conspicuous components of the phytoplankton, but TALLING's dominance alternation pattern was more typical of *Microcystis* and *Oocystis,* whereas *Aulacoseira* often co-existed with *Microcystis* (Fig. 3). Moreover, when *Microcystis* disappeared in 1988, *Aulacoseira* did as well while *Oocystis* remained.

The absence of dinoflagellates from the phytoplankton assemblage of hypertrophic Hartbeespoort Dam is conspicuous, especially that this group dominated the lake's phytoplankton during its earlier oligotrophic state (HUBER-PESTALOZZI 1929). Dinoflagellates tend to dominate the less-enriched African waterbodies, such as the newly constructed Rhenosterkop Dam (ROBARTS et al. 1992). They are distinctly missing or quantitatively minor components of Lake Victoria (TALLING 1987) and most lakes of the African Rift Valley (HECKY & KLING 1987).

Conclusions

The long-term phytoplankton record from Hartbeespoort Dam demonstrates the key role of a dominant species in controlling community composition and diversity in hypertrophic lakes. When *Microcystis* was abundant, other species were usually excluded; when *Microcystis* was absent, species diversity increased. The potential for a bloom of another species probably existed but it did not occur until *Microcystis* disappeared, as happened with the 1987 *Carteria* bloom. Interestingly, *Microcystis* did not become dominant in Hartbees-

poort Dam until the water hyacinth *Eichhornia crassipes* was eliminated with herbicide spraying and manual removal of seedlings (SCOTT et al. 1980). The data from Hartbeespoort Dam also demonstrate how stable environments lead to a low-diversity and high-biomass phytoplankton assemblage dominated by *K*-strategists, while disruptions of suitable strength and frequency allow for the development and maintenance of higher species diversity.

Acknowledgements

This is a contribution to the Hartbeespoort Dam Ecosystem Programme, initiated and coordinated by F. M. CHUTTER. We thank the South African Directorate for Water Affairs for supplying raw meteorological and hydrological data, the analytical chemistry unit of the Division of Water Technology (DWT), CSIR for carrying out the chemical analyses, P. J. ASHTON for providing lake volume data, W. E. SCOTT and U. POLLINGHER for assistance with species identifications, A. JARVIS for unpublished zooplankton data and U. POLLINGHER for comments on an early draft. The study was funded by the South African Water Research Commission and by DWT, CSIR. The field work was carried out while the first 3 authors were employed by CSIR.

References

ALLANSON, B. R., HART, R. C., O'KEEFFE, J. H. & ROBARTS, R. D. (1990): Inland waters of southern Africa: An ecological perspective. – Kluwer Academic Publishers, Dordrecht.

ASHTON, P. J. (1985): Seasonality in Southern Hemisphere freshwater phytoplankton assemblages. – Hydrobiologia **125:** 179–190.

ASHTON, P. J. & TWINCH, A. J. (1985): An assessment of a rapid and convenient spectrophotometric adaptation of the Winkler procedure for the determination of dissolved oxygen in fresh waters. – J. Limnol. Soc. sth. Afr. **11:** 62–65.

CHUTTER, F. M. (1989): Evaluation of the impact of the 1 mg l^{-1} phosphate-P standard on the water quality and trophic state of Hartbeespoort Dam. – Contract Report to the Water Research Commission, WRC 181/1/89, Pretoria.

CHUTTER, F. M. & ROSSOUW, J. N. (1992): The management of phosphate concentrations and algae in Hartbeespoort Dam. – WCR Rep. 289/1/92. Water Research Commission South Africa, 37 p.

COCHRANE, K. L. (1987): The biomass and yield of the dominant fish species in Hartbeespoort Dam, South Africa. – Hydrobiologia **146:** 89–96.

DE MOOR, F. C., WILKINSON, R. C. & HERBST, H. M. (1986): Food and feeding habits of *Oreochromis mossambicus* (PETERS) in hypertrophic Hartbeespoort Dam, South Africa. – S. Afr. J. Zool. **21:** 170–176.

GANF, G. G. (1974): Diurnal mixing and the vertical distribution of phytoplankton in a shallow equatorial lake (Lake George, Uganda). – J. Ecol. **62:** 611–629.

HANCOCK, F. D. (1979): Diatoms associations and succession in Lake Kariba, South Central Africa. – Hydrobiologia **67:** 33–50.

HECKY, R. E. (1993): The eutrophication of Lake Victoria. – Verh. Int. Verein. Limnol. **25:** 39–48.

HECKY, R. E. & KLING, H. J. (1987): Phytoplankton of the great lakes in the rift valleys of Central Africa. – Arch. Hydrobiol., Ergebn. Limnol. **25:** 197–228.

HUBER-PESTALOZZI, G. (1929): Das Plankton natürlicher und künstlicher Seebecken Südafrikas. – Verh. Int. Verein. Limnol. **4:** 343–390.

HUTCHINSON G. E., PICKFORD, G. E. & SCHUURMAN, J. F. M. (1932): A contribution to the hydrobiology of pans and other inland waters of South Africa. – Arch. Hydrobiol. **24:** 1–154.

HUMPHRIES, S. E. & WIDJAJA, F. (1979): A simple method for separating cells of *Microcystis aeruginosa* for counting. – Br. Phycol. J. **14:** 313–316.

JARVIS, A. C. (1986): Zooplankton community grazing in a hypertrophic lake (Hartbeespoort Dam, South Africa). – J. Plankton Res. **8:** 1065–1078.

JARVIS, A. C., HART, R. C. & COMBRINK, S. (1987): Zooplankton feeding on size-fractionated *Microcystis* colonies and *Chlorella* in a hypertrophic lake (Hartbeespoort Dam, South Africa): implications to resource utilization and zooplankton succession. – J. Plankton Res. **9:** 1231–1249.

KILHAM, P. & KILHAM, S. S. (1990): Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. – Freshwat. Biol. **23:** 379–389.

LEWIS, W. M. Jr. (1978): A compositional, phytogeographical and elementary structural analysis of the phytoplankton in a tropical lake: Lake Lanao, Philippines. – J. Ecol. **66:** 213–226.

LITI, D., KALLQVIST, T. & LEIF, L. (1991): Limnological aspects of Lake Turkana, Kenya. – Verh. Int. Verein. Limnol. **24:** 1108–1111.

LUND, J. W. G., KIPLING, C. & LE CREN, E. D. (1958): The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. – Hydrobiologia **11:** 143–170.

National Institute for Water Research (NIWR) (1985): The limnology of Hartbeespoort Dam. – South African National Scientific Programmes Report no. 110.

PATTERSON, G. & KACHINJIKA, O. (1993): Effect of wind-induced mixing on the vertical distribution of nutrients and phytoplankton in Lake Malawi. – Verh. Int. Verein. Limnol. **25:** 872–876.

PIETERSE, A. J. H. & ROHRBECK, M. A. (1990): Dominant phytoplankters and environmental variables in Roodeplaat Dam, Pretoria, South Africa. – Water SA **16:** 211–218.

RAMBERG, L. (1987): Phytoplankton succession in the Sanyati basin, Lake Kariba. – Hydrobiologia **153:** 193–202.

REYNOLDS, C. S. (1984 a): The ecology of freshwater phytoplankton. – Cambridge University, Cambridge.

– (1984 b): Phytoplankton periodicity: the interactions of form function and environmental variability. – Freshwat. Biol. **14:** 111–142.

– (1987): Cyanobacterial waterblooms. – Adv. Bot. Res. **13:** 67–143.

– (1988): The concept of biological succession applied to seasonal periodicity of phytoplankton. – Verh. Int. Verein. Limnol. **23:** 683–691.

REYNOLDS, C. S., JAWORSKI, G. H. M., CMIECH, H. A. & LEEDALE, G. F. (1981): On the annual cycle of the blue-green alga *Microcystis aeruginosa* KÜTZ. emend. ELENKIN. – Phil. Trans. R. Soc. Lon. B **293:** 419–477.

REYNOLDS, C. S. & REYNOLDS, J. B. (1985): The atypical seasonality of phytoplankton in Cross Mere, 1972: an independent test of the hypothesis that variability in the physical environment regulates community dynamics and structure. – Br. Phycol. J. **20:** 227–242.

RIPPKA, R., DERUELLES, J., WATERBURY, J. B., HERDMAN, M. & STANIER, R. Y. (1979): Generic assignments, strain histories and propertied of pure cultures of Cyanobacteria. – J. Gen. Microbiol. **111:** 1–61.

ROBARTS, R. D. (1979): Underwater light penetration, chlorophyll a and primary production in a tropical African lake (Lake McIlwaine, Rhodesia). – Arch. Hydrobiol. **86:** 423–444.

ROBARTS, R. D., ASHTON, P. J., THORNTON, J. A., TAUSSIG, H. J. & SEPHTON, L. M. (1982): Overturn in a hypertrophic, warm, monomictic impoundment (Hartbeespoort Dam, South Africa). – Hydrobiologia **97:** 209–224.

ROBARTS, R. D. & ZOHARY, T. (1984): *Microcystis aeruginosa* and underwater light attenuation in a hypertrophic lake (Hartbeespoort Dam, South Africa). – J. Ecol. **72:** 1001–1007.

– – (1992): The influence of temperature and light on the upper limit of *Microcystis aeruginosa* production in a hypertrophic reservoir. – J. Plankton Res. **14:** 235–247.

ROBARTS, R. D., ZOHARY, T., JARVIS, A. C., PAIS-MADEIRA, A. M., SEPHTON, L. M. & COMBRINK, S. (1992): Phytoplankton and zooplankton population dynamics and production of a recently formed African reservoir. – Hydrobiologia **237:** 47–60.

ROTT, E. (1981): Some results from phytoplankton counting inter-calibrations. – Schweiz. Z. Hydrol. **43:** 34–62.

SCOTT, W. E., ASHTON, P. J., WALMSLEY, R. D. & SEAMAN, M. T. (1980): Hartbeespoort Dam: a case study of a hypertrophic, warm, monomictic impoundment. – In: BARICA, J. & MUR, L. R. (eds.): Hypertrophic ecosystems. – Developments in Hydrobiology, 2, W. Junk, The Hague, pp. 317–322.

SOMMER, U. (1993): Disturbance-diversity relationships in two lakes of similar nutrient chemistry but contrasting disturbance regimes. – Hydrobiologia **249:** 59–65.

TALLING, J. F. (1986): The seasonality of phytoplankton in African lakes. – Hydrobiologia **138:** 139–160.

– (1987): The phytoplankton of Lake Victoria (East Africa). – Arch. Hydrobiol., Ergebn. Limnol. **25:** 229–256.

THORNTON, J. A. & ASHTON, P. J. (1989): Aspects of the phosphorus cycle in Hartbeespoort Dam (South Africa) Phosphorus loading and seasonal distribution of phosphorus in the reservoir. – Hydrobiologia **183:** 73–85.

ZOHARY, T. (1989): Cyanobacterial hyperscums of hypertrophic water bodies. – In: COHEN, Y. & ROSENBERG, E. (eds.): Microbial mats: physiological ecology of benthic microbial communities. – Amer. Soc. Microbiol. Washington, DC., pp. 52–63.

ZOHARY, T. & PAIS-MADEIRA, A. M. (1987): Counting natural populations of *Microcystis aeruginosa:* A simple method for colony disruption into single cells and its effect on cell counts of other species. – J. Limnol. Soc. sth. Afr. **13:** 75–77.

ZOHARY, T. & ROBARTS, R. D. (1989): Diurnal mixed layers and the long-term dominance of *Microcystis aeruginosa*. – J. Plankton Res. **11:** 25–48.

Submitted: 21 February 1995; accepted: 5 July 1995.