Zeekoevlei - Water chemistry and phytoplankton periodicity

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Abstract

The paper provides a two-year record of Zeekoevlei's water chemistry and phytoplankton periodicity between April 1989 and March 1991. Zeekoevlei is a large (256 ha), shallow (mean depth 1,9 m) and well-mixed freshwater hyper-eutrophic lake situated in the winter-rainfall climatic region of South Africa. Water temperatures ranged from 10°C to 24°C. Due to the presence of dense cyanophyte phytoplankton populations, water transparencies ranged from 0,1 to 0,6 m with a mean of 0,28 m. Zeekoevlei experienced year-round, non-limiting nutrient concentrations. Accumulated algal sediments occupied 20% of the volume of the lake. Typical mean annual total nitrogen and phosphorus concentrations were 3,6 and 0,55 mg·ℓ^{-1}, respectively, reaching maxima during the winter. Chlorophyll *a* concentrations typically averaged 0,2 mg·ℓ^{-1}, reaching maxima of up to 0,8 mg·ℓ^{-1}.

The phytoplankton population had a low generic diversity and an atypical seasonal periodicity dominated by *Microcystis* spp., which completely muted the seasonal periodicity of other phytoplankton taxa present. Zeekoevlei is an example of a poorly-flushed, nutrient-rich "reactor" which perpetuates dominance by cyanophyte algae.

Introduction

South Africa has a number of shallow, natural lakes which lie adjacent to the coastline. These coastal lakes are found in the Southern and South-Western Cape, and in Northern Natal, from where they extend into the wetland and floodplain systems of Mozambique (Noble and Hemens, 1978). Most of these systems are estuarine in character, with 196 estuaries listed for the South African coastline (Noble and Hemens, 1978.). Others such as Swartvlei (Howard-Williams and Allanson, 1981) and Zandvlei (Morant and Grindley, 1982 ; Begg, 1976), in the Southern and Western Cape respectively, are seasonally estuarine in character, whilst Lake Sibaya in Natal (Hart and Hart, 1977) and Zeekoevlei (this study) are isolated from the coast and are now entirely freshwater systems.

Certain South African coastal lakes (e.g. Lake Sibaya and Swartvlei), have been the focus of intensive studies, the results of which are reviewed in Allanson et al. (1990). There is, however, a paucity of available information for the lakes of the South-western Cape with its Mediterranean climate (Mepham, 1987).

The principal lakes of the Cape Peninsula are Zeekoevlei, Zandvlei, Princess Vlei, Rondevlei and Little Princess Vlei (see Fig. 1). Of these, comprehensive details only of Zandvlei have been published, and this largely due to the establishment of a marina on its eastern shoreline (e.g. Begg, 1976; Howard-Williams, 1976; Morant and Grindley, 1982; Stewart and Davies, 1985; Byren and Davies, 1986). The phytoplankton diversity, assemblages and periodicity of Zeekoevlei (this study), and of Princess Vlei (Harding, 1992) and Zandvlei (Harding, unpub. data) have been studied since March 1989, while the water chemistries of all three lakes have been monitored by the Cape Town City Council for the past nine (Zeekoevlei) to thirteen (Zandvlei) years. The accumulated ecological data for Zeekoevlei and Princess Vlei have been summarised by Harding (1991).

Phytoplankton periodicity studies in South Africa have chiefly formed part of investigations undertaken on large impoundments such as Rietvlei Dam (Ashton, 1979 and 1981), Hartbeespoort Dam (NIWR, 1985; Zohary and Robarts, 1989; Zohary and Breen, 1989), Roodeplaat Dam (Pieterse and Rohrbeck, 1990), Rhenosterkop Dam (Heath et al., 1988; Robarts et al., in press), Lake Midmar (Breen, 1983), Lake Le Roux (Allanson and Jackson, 1983) and on two large coastal lakes, Lake Sibaya (Hart and Hart, 1977) and Swartvlei (Robarts, 1973; Howard-Williams and Allanson, 1981). In addition, Pieterse et al. (1986), Pieterse (1987), Pieterse and Roos (1987a;b) and Pieterse and Van Zyl (1988) have reported on aspects of the phytoplankton ecology of the Vaal River. With the exception of Swartvlei, these water bodies are all situated in the summer rainfall region of South Africa, and all have typical phytoplankton periodicities (Ashton, 1985).

This paper reports on a two-year record of Zeekoevlei's phytoplankton assemblage and periodicity in relation to the prevailing physical and chemical regimen of the lake. The aims of the study were to determine the dominant phytoplankton genera in the open waters of the lake and to follow their seasonal dynamics. The analysis provides a synthesis of the conditions prevailing in a shallow, well-mixed, hyper-eutrophic water body.

Study area

Zeekoevlei is a large (256 ha), shallow (mean depth 1,9 m) freshwater coastal lake situated on the Cape Flats of the Cape Peninsula (Fig. 1). Aspects of its limnology have been reviewed by Bickerton (1982) in a synopsis of the Zeekoevlei estuary. Early work was conducted by Stephens (1929) and Hutchinson et al. (1932). More recently, various short-term investigations have been carried out by Harrison (1962), Van Wyk (1970), King (1973), Curtin et al. (1975), Howard-Williams (1976), Hamman et al. (1977), Brummer (1981), Davies (1983), Rudnick (1986), Hall (1990), CCC (1990) and Harding (1990a-d), many of which are only available in the form of unpublished reports. In addition, the results of the routine monitoring carried out by the Cape Town City Council (CCC) are summarised annually in the reports of the City Engineer.

Zeekoevlei has for many years been characterised by its "pea-soup" green colour, this feature being reported as far back as the 1920s (Stephens, 1929). Between 1920 and 1948, alternating dominance of the water body by the alga *Microcystis* spp. and the rooted macrophyte *Potamogeton pectinatus* (L.) appeared to be controlled by drying phases of the system, or hydraulic flushing

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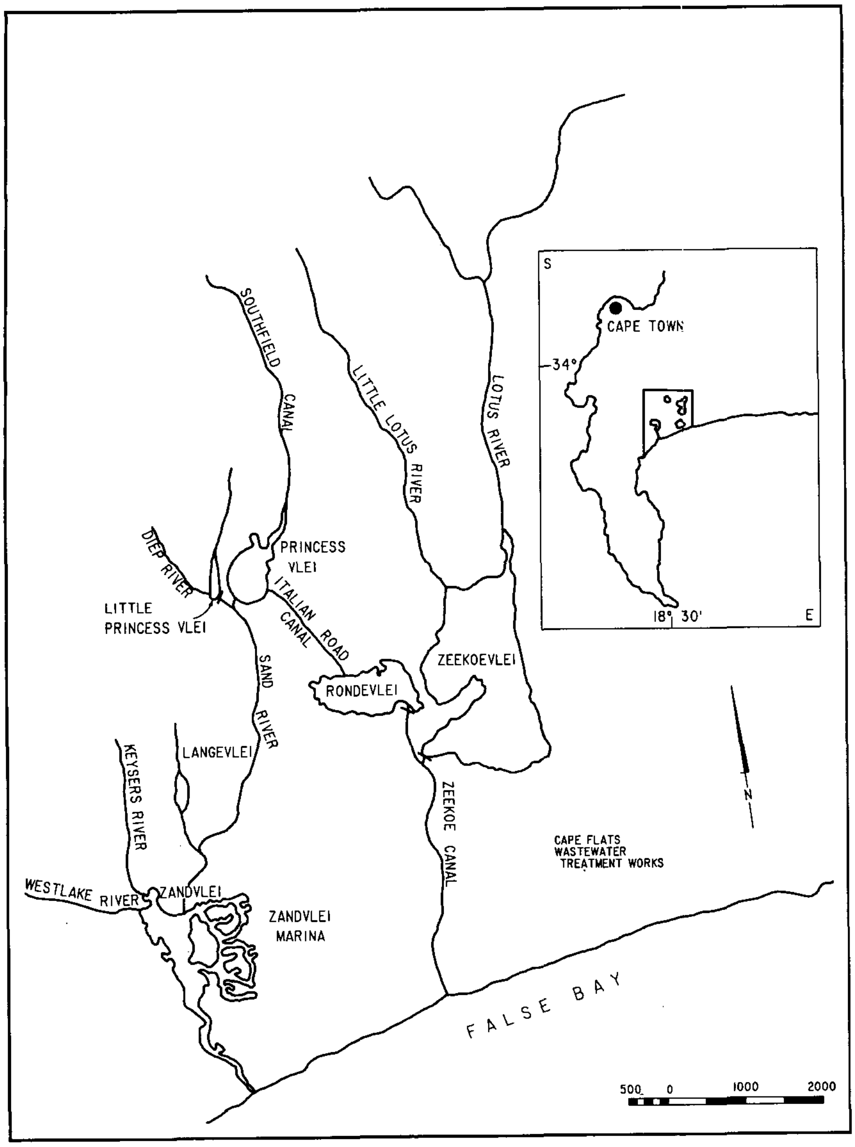

Figure 1
Map showing the position of Zeekoevlei in relation to the Cape Peninsula (insert) and to the other south-western Cape coastal lakes referred to in the text. Scale in meters

during heavy rains (Harrison, 1962). This natural cycling between macro- and microphyte dominance was precluded by the construction of an outlet weir in 1948. Subsequently, chemical removal of *Potamogeton* by spraying with sodium arsenite in 1951 (CCC, 1951), and the concomitant decay of the plant material in the lake, was followed by a massive cyanophyte-algal bloom and heralded the onset of *Microcystis* dominance of the system (Dick, 1990).

At weir crest, 5,18 m AMSL, Zeekoevlei has a volume of 5 million m^3. It is fed by two rivers (see Fig. 1) which drain a catchment of approximately 8 000 ha. Typical annual outflows average 20 000 $M\ell.a^{-1}$, with more than 80% of the inflow to Zeekoevlei coming from the Lotus River (I. Morrison, CCC, unpub. data). Land use in the Lotus River catchment is chiefly horticultural (Harding and Quick, unpublished data). Zeekoevlei overflows during the winter months into the Zeekoe Canal leading to False Bay (Fig. 1). Lake levels fluctuate by approximately 0,5 m between winter and summer as a result of evaporation.

Zeekoevlei's bathymetry comprises two large basins (Fig. 2) which have become filled with organically rich algal sediments, so that the total accumulated sediment volume in 1990 was 1 100 000 m^3, with sediment accumulation estimated to be increasing at approximately 35 000 $m^3.a^{-1}$ (Harding, 1990a). These sediments reach depths of up to 3 m. A limited dredging operation was undertaken during 1983 in the northern bay (Fig. 2) (Hill, Kaplan and Scott, 1980; Civil Engineering Contractor, 1982 and CCC, 1983).

Zeekoevlei's sediments have nutrient concentrations virtually identical to those reported for the hyper-eutrophic reservoir Hartbeespoort Dam (Dick, 1990). Mean nitrogen and phosphorus concentrations of dried samples were found to be of the order of 16 000 and 1 300 $mg\cdot kg^{-1}$, respectively (Harding, 1990b). The contribution of these sediments to the overall nutrient dynamics of Zeekoevlei is presently under investigation (I. Morrison; R. Dick, CCC, pers. comm.).

Zeekoevlei is fringed by dense growths of emergent aquatic macrophytes, principally *Typha capensis* and *Scirpus littoralis.* These reed beds are a cause for complaint by shoreline property owners and recreational users of the lake such as anglers (Hall, 1990), as well as creating sheltered areas where dense scums of *Microcystis* accumulate according to the prevailing wind direction. Indiscriminate reed removal is discouraged by the CCC in order to offset bank erosion by wave action. Dense, isolated growths of water hyacinth, *Eichhornia crassipes* (Mart.) Solms, occur in the reed beds to the south-east of the lake, and are manually removed at regular intervals by the CCC.

Methods

Meteorology

Details of sunshine ($h \cdot d^{-1}$), incident solar radiation ($MJ \cdot m^{-2} h^{-1}$), mean hourly wind speed ($m \cdot s^{-1}$) and hourly mean wind direction (degrees) for the Cape Peninsula were obtained from instruments operated by the SA Meteorological Bureau at DF Malan Airport near Cape Town. Wind speeds were recorded at the lake surface at the time of sampling using a hand-held anemometer. Rainfall data ($mm \cdot d^{-1}$) were obtained from daily readings taken at three gauges, one situated 1 km south of Zeekoevlei, one on the northern shore of Princess Vlei (Fig. 1) and one at DF Malan Airport.

Physical, chemical and biological variables

One fixed sampling station per river, situated approximately 1 km north of the lake (Fig. 1), and four fixed lake sampling stations were routinely monitored (see Fig. 2). River samples were collected from the bank, while the lake stations were sampled from a motorboat. Samples were invariably collected between 09:00 and 12:00.

Measurements of lake and river water temperature, pH, electrical conductivity, dissolved oxygen and water transparency (not rivers) were performed weekly *in situ* at all stations (see Table 1 for procedures), together with collection of samples for determinations of chlorophyll *a* and phytoplankton composition, which were carried out in the laboratory. Phytoplankton and pigment analyses did not form part of the influent river monitoring programme.

Samples of river water for subsequent chemical analyses were collected using a 5-ℓ bucket lowered into the water using a rope. The sample was then transferred to a twice-rinsed (with sample) 2-ℓ high density polyethylene (HDPE) bottle and stored in an insulated container for transport to the laboratory. Sample bottles were machine washed without detergent in the laboratory prior to sample collection. On the lake, samples for chemical analysis, chlorophyll *a* and phytoplankton composition were collected as integrated columns using a 2 x 0,04 m perspex tube sampler fitted with an airtight valve. The tube was lowered vertically into the water to a depth just above the vlei bottom, the valve was closed and the contents transferred to 2-ℓ HDPE bottles.

Determinations of nitrogen (total Kjeldahl, nitrate and nitrite and ammonia), phosphorus (total, total filterable and soluble reactive), reactive silicon, total alkalinity and suspended solids (see Table 1 for the analytical methods employed) were carried out monthly on water samples collected from all stations concurrently with one of the fortnightly visits (see above).

Phytoplankton composition was determined using the inverted microscope methods of Utermohl (1958) and Lund et al., (1958). Preserved material was examined after sedimention using Lugols iodine containing acetic acid (Vollenweider, 1974). Identification and counting were performed in pre-calibrated transects of 2,5 mℓ *Zeiss* plankton chambers fitted with 0,17 mm-thickness bottom coverslips. The samples were examined using a *Zeiss* phase contrast Invertoscope-D inverted microscope over a range of magnifications from 200 to 1 000x. Cell numbers were expressed per mℓ of lake water.

Colonial species such as *Microcystis* were disrupted using a *Polytron* blender according to the method described by Zohary and Pais Madeira (1987), and counted in plankton chambers at 1 000x magnification using a 20x20 eyepiece (*Whipple*) grid.

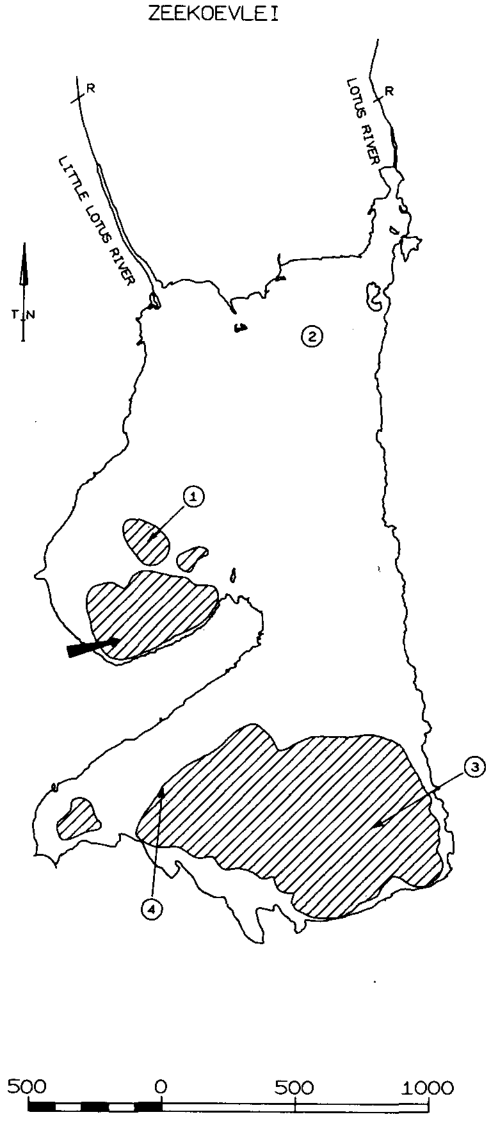

Figure 2
Map showing the location of the sampling points (rivers = R and lake 1-4, circled) in Zeekoevlei, the position of the sediment basins (shaded) and the site of the dredging operation conducted during 1983 (bold arrow). Scale in metres

Diatom frustules were cleaned prior to identification by heating equal volumes of (harvested) sample and concentrated sulphuric acid until the mixture became dark brown. Concentrated nitric acid was then added dropwise until the solution became yellow or straw-coloured. The acid was then removed from the residue by repeated washing with water and centrifugation in conical glass centrifuge tubes.

A photomicrographic record of the taxa observed was compiled using a *Zeiss* Photomicroscope Model 2 with phase and Normaski differential interference contrast (DIC).

Phytoplankton identifications were made according to Smith (1950), Huber-Pestalozzi (1955), Fott (1959), Ward and Whipple (1959), Schoeman and Archibald (1976), Komarek and Fott (1983), Streble and Krauter (1985) and Truter (1987).

Statistical differences were determined using paired comparison tests based on the standard deviation of the mean (Davies, 1967). Correlation coefficients were determined using linear regression analysis.

TABLE 1

PHYSICAL AND CHEMICAL VARIABLES MONITORED / ANALYTICAL METHODS EMPLOYED (accuracy of measurement/lower limit of detection in [])

Variable	Units	Summary of procedure followed	Reference for method
Field measurements			
pH	pH	Hanna pH meter with automatic temperature compensation, calibrated against pH 7 and 10 buffers [0, 01pH units]	Standard Methods (1989)
Temperature	°C	pH meter thermistor probe calibrated against Grade A mercury in glass thermometer [0,2 K]	Standard Methods (1989)
Wind speed at lake surface at time of sampling	$m \cdot s^{-1}$	Deuta hand-held anemometer	Standard Methods (1989)
Water transparency	m	0,25 m perforated Secchi disc. [0,05 m]	Standard Methods (1989)
Dissolved oxygen	$mg \cdot \ell^{-1}$	YSI 57 DO meter with automatic temperature and air pressure compensation, calibrated in air [0,1 $mg \cdot \ell^{-1}$]	Standard Methods (1989)
Oxygen saturation	%	Directly from dissoloved oxygen meter or by using the formulae of Green and Carritt (1967)	
Conductivity	$mS \cdot m^{-1}$	WTW 196 conductivity meter with automatic temperature compensation, using 25°C as reference temperature, calibrated against 0,01N KCl [0,5% of measured value]	CRC (1971)
Laboratory analyses			
Kjeldahl -N	$mg \cdot \ell^{-1}$	Digestion and conversion to $(NH_4)_2SO_4$, followed by Nesslerization using NH_4Cl as standard [0,05 $mg \cdot \ell^{-1}$ N]	EPA 351,3 (1979)
Ammonia -N	$mg \cdot \ell^{-1}$	Distillation into boric acid using NH_4Cl standard [0,01 $mg \cdot \ell^{-1}$ N]	EPA 350,2 (1979)
Nitrate and nitrite -N	$mg \cdot \ell^{-1}$	Cadmium reduction followed by diazotising and autoanalyzer colorimetry using NO_2^- as standard [0,01 $mg \cdot \ell^{-1}$ N]	EPA 353,2 (1979)
Reactive silicon	$mg \cdot \ell^{-1}$	Molybdate reduction using a 25 $\mu g \cdot \ell^{-1}$ Si standard solution [0,001 $mg \cdot \ell^{-1}$ Si]	DOE (1972)
Total and total-dissolved -P	$mg \cdot \ell^{-1}$	Persulphate digestion followed by ascorbic acid reduction and direct colorimetry using KH_2PO_4 standard [0,001 $mg \cdot \ell^{-1}$ P]	EPA 365,2 (1979)
Ortho- (soluble reactive) -P	$mg \cdot \ell^{-1}$	Ascorbic acid method followed by direct colorimetry using KH_2PO_4 as standard [0,001 $mg \cdot \ell^{-1}$ P]	EPA 365,2 (1979)
Total alkalinity	$mg \cdot \ell^{-1}$	Titrimetric mixed indicator using 0,1N HCl as standard. [2 $mg \cdot \ell^{-1}$ $CaCO_3$]	DWA 1988 (#100602)
Suspended solids	$mg \cdot \ell^{-1}$	Gravimetric determination using Whatman 0,45µm glass fibre membrane filters, dried at 105 °C [0,01 mg]	EPA 160,2 (1979)
Chlorophyll *a*	$\mu g \cdot \ell^{-1}$	Ethanol extraction, followed by UV spectrophotometry, corrected for phaeophytins [2 $\mu g \cdot \ell^{-1}$ Chl *a*]	DWA 1988 (#2020001)

TABLE 2
ZEEKOEVLEI WATER CHEMISTRY DATA FOR THE PERIOD (APRIL 1989 - MARCH 1991)

Parameter	Mean, x	Min	Max	x - SD	x + SD	n
Temperature, °C	17,7	10,3	23,6	14,3	22,0	203
Dissolved oxygen, mg·ℓ⁻¹	9,6	7,1	16,7	8,3	11,0	191
Oxygen saturation, %	101	68	171	87	116	189
Water transparency, m	0,28	0,10	0,58	0,21	0,38	203
Suspended solids, mg·ℓ⁻¹	59	14	153	39	89	88
pH	9,5	7,9	10,6	9,0	10,0	199
Conductivity, mS·m⁻¹	131	88	202	108	161	203
Kjeldahl-N, mg·ℓ⁻¹	3,6	1,4	6,6	2,5	5,1	103
Ammonia-N, mg·ℓ⁻¹	0,10	0,00	1,26	0,04	0,27	101
Nitrate-N, mg·ℓ⁻¹ *	0,14	0,00	2,80	0,03	0,58	100
Total-P, mg·ℓ⁻¹	0,55	0,26	1,25	0,38	0,80	103
Soluble-P, mg·ℓ⁻¹ *	0,16	0,01	1,12	0,06	0,45	96
Ortho-P, mg·ℓ⁻¹	0,13	0,01	1,07	0,04	0,40	105
Reactive silicon, mg·ℓ⁻¹	0,44	0,01	3,28	0,18	1,04	80
Total alkalinity, mg·ℓ⁻¹	147	82	219	119	183	92
Chlorophyll *a*, µg·ℓ⁻¹	192	69	796	117	314	151

SD = standard deviation, n = number of samples/readings
* Nitrate-N expressed as sum of nitrite and nitrate-N
* Soluble-P = total filterable phosphorus

TABLE 3
LOTUS RIVER WATER CHEMISTRY DATA FOR THE PERIOD APRIL 1989 - MARCH 1991

Parameter	Mean, x	Min	Max	x -SD	x + SD	n
Temperature, °C	18,6	10,9	27,8	14,2	24,3	49
Dissolved oxygen, mg·ℓ⁻¹	9,9	5,4	19,4	7,5	13,0	46
Oxygen saturation, %	106	51	233	74	151	46
Suspended solids, mg·ℓ⁻¹	15	4	105	7	35	22
pH	8,2	7,1	9,1	7,8	8,6	48
Conductivity, mS·m⁻¹	133	72	171	107	165	49
Kjeldahl-N, mg·ℓ⁻¹	2,2	1,0	7,8	1,4	3,6	24
Ammonia-N, mg·ℓ⁻¹	0,26	0,01	1,67	0,07	1,02	24
Nitrate-N, mg·ℓ⁻¹ *	2,80	0,66	9,02	1,37	5,70	23
Total-P, mg·ℓ⁻¹	0,64	0,22	1,54	0,35	1,19	24
Soluble-P, mg·ℓ⁻¹ *	0,40	0,11	1,29	0,19	0,83	24
Ortho-P, mg·ℓ⁻¹	0,34	0,09	1,21	0,16	0,75	24
Reactive silicon, mg·ℓ⁻¹	2,50	0,42	8,93	1,28	4,88	20
Total alkalinity, mg·ℓ⁻¹	221	128	270	178	274	22

SD = One standard deviation, n = number of samples/readings
* Nitrate-N expressed as sum of nitrite and nitrate-N
* Soluble-P = total filterable phosphorus

Results

Meteorological measurements

During the study the mean daily sunshine ranged between 6,0 and 11,1 h·d⁻¹, with minima during June and July and maxima during January. The wind speed, as measured at the lake surface during sampling, ranged between 0 and 35 m·s⁻¹, with a mean speed of 8,8 m·s⁻¹. Calm conditions at the lake surface, expressed as wind speeds of less than 1 m·s⁻¹, were measured on 8 out of 61 occasions. During the study period, only 69 and 78 d during 1989 and 1990, respectively, experienced more than 12 h with wind speeds <1 m.s⁻¹. There were no completely calm days (i.e. 24 h <1 m.s⁻¹) during 1989 and only four during 1990. Wind speeds were lowest during the winter and spring, concomitant with the greatest incidence of calm periods. The prevailing wind directions were, characteristically for the Western Cape, southerly during the spring and summer and north-westerly during the winter. No continuously recorded wind speed and direction data were available for the Zeekoevlei area. Zeekoevlei has been shown previously to have an almost total lack of calms and an absence of winds of less than 2 m.s⁻¹ (Fuggle, 1978).

Annual rainfall totals for the individual years of the study were 552 and 560 mm, respectively. The heaviest falls were recorded

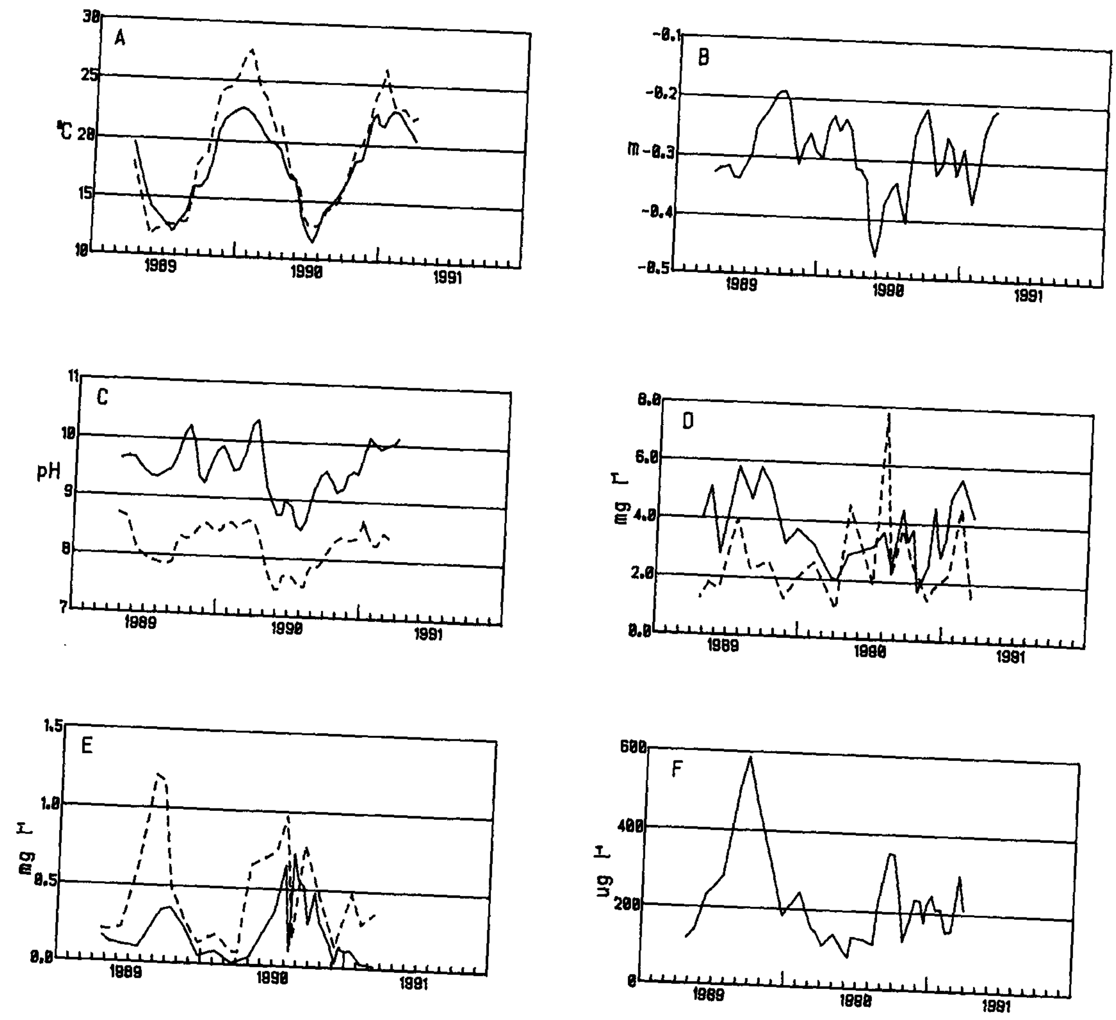

Figure 3
Trends of certain physical and chemical variables referred to in the text: (A) Water temperature; (B) Water transparency; (C) pH; (D) Total (Kjeldahl) nitrogen; (E) Total phosphorus; (F) Chlorophyll a. *Solid and broken lines represent Zeekoevlei and the Lotus River, respectively*

during August 1989 (106 mm) and April 1990 (141 mm), with lowest falls (<2 mm) during December of both years. Hydraulic flows were much higher during 1990 compared with 1989. The 1990 outflow was calculated as 27 300 Mℓ, compared with 19 000 Mℓ for 1989 (I. Morrison, CCC, pers. comm.).

Physical and chemical measurements

The physical and chemical data for Zeekoevlei and the Lotus River during the study period are summarised in Tables 2 and 3. Because it delivers more than 80% of the annual inflow to Zeekoevlei, only data for the Lotus River are presented.

Zeekoevlei was well mixed, both vertically and horizontally, with no evidence of thermal or chemical stratification. No spatial inter-station variation could be found for any of the measured parameters ($p < 0{,}001$).

The water temperature of Zeekoevlei ranged between winter minima of 10°C in June and July to summer maxima of 24°C during February. No thermal stratification was recorded. Oxygen saturation was generally high, ranging between 68 and 171% and averaging 101%. Water temperatures, oxygen saturation and electrical conductivity were similar in both the rivers and the lake, but suspended solids and pH levels were highest in the lake water (Tables 2 and 3). Water transparencies displayed a narrow range of 0,1 to 0,6 m, with a mean transparency of 0,28 m. Water transparencies and pH levels were lower during the second year (see Fig. 3).

Nutrient concentrations demonstrated a marked seasonal pattern in both the rivers and the lake, with nitrogen and phosphorus levels reaching maxima towards the end of the rainfall period during August and September (Fig. 3). Summer minimum concentrations of N and P in the lake did not fall below 1,0 and 0,22 mg·ℓ$^{-1}$, respectively. Inorganic N:P ratios ranged between <1 and 12 throughout the study. Silicon concentrations ranged between 0,01 and 3,28 mg·ℓ$^{-1}$ in the lake, reaching maximum concentrations in the lake and both rivers during June-July of both years.

No data were available concerning the internal nutrient loading of the lake from the accumulated sediments. Preliminary investigations have shown that the sediments contain very high levels of nitrogen and phosphorus which are comparable to those found in the hyper-eutrophic reservoir Hartbeespoort Dam (Dick, 1990; Harding, 1990b).

Phytoplankton assemblage

Phytoplankton diversity in Zeekoevlei was low, with a range of 11 to 24 genera and a mean of 17 per sampling occasion. The phytoplankton assemblage was dominated by representatives of three Divisions:- Cyanophyta, Chlorophyta and Bacillariophyta (diatoms, Division Chrysophyta). Of these the Cyanophyta, and in particular *Microcystis* spp., predominated both numerically and in terms of contribution to the total (calculated, results not shown) phytoplankton cell volume. *Microcystis* consistently comprised >95% of the total cyanophyte numbers. The Chlorophyta and Bacillariophyta were never dominant, but were occasionally co-dominant. Total counts of cyanophyte genera ranged between 4 000 and 7 000 000 cells·mℓ$^{-1}$, those of the Chlorophyta, with *Scenedesmus* spp. being the major component, from 3 000 to 20 000 cells·mℓ$^{-1}$, and the Bacillariophyta from 100 to 120 000 cells·mℓ$^{-1}$. Overall, total counts for all three divisions were lower during 1990 than was the case during 1989. The generic composition of the three principal divisions is presented in Table 4.

Small numbers (<3 000 cells·mℓ$^{-1}$) of *Cryptomonas* spp. were recorded during the winter of both years, whilst *Euglena* spp. (<100 cells·mℓ$^{-1}$) were observed on two occasions. Some unidentified species of dinoflagellates (Division Pyrrophyta) were observed on six occasions.

Phytoplankton periodicity

Cyanophyte periodicity showed early spring maxima during both years of the study, reaching an average maximum of 4 x 10^6 cells .mℓ$^{-1}$ during the spring (September/October) of 1989 and 1,6 x 10^6 cells.mℓ$^{-1}$ during the same period in 1990 (see Fig. 4). During both years, collapse of the *Microcystis* peak was followed by an increase in numbers of *Anabaena circinalis* (Kutz) Rab. of up to 2 500 cells.mℓ$^{-1}$. Increased numbers of *Aphanocapsa* were recorded during January of both years. Cyanophyte cell numbers correlated significantly with the concentrations of nitrogen and phosphorus in the vlei (respectively, $r = 0,376$ and 0,336; $n = 51$, $p < 0,05$).

Seasonal periodicity of diatoms was limited to short duration mid-winter maxima of a small centric diatom, *Thalassiosira nana* (Fig. 4). Apart from the contribution made by this species, combined total counts of the diatoms were usually less than 1 000 cells.mℓ$^{-1}$.

Winter-summer fluctuations within the Chlorophyta varied by less than a single order of magnitude. Maximum counts were reached during the summer, with lowest numbers recorded at the onset of spring (see Fig. 4). Chlorophyte numbers correlated significantly with temperature ($r = 0,364$; $n = 46$).

Chlorophyll *a* concentrations were high, averaging 200 μg.ℓ$^{-1}$ and increasing to an average level of 600 μg.ℓ$^{-1}$ during the 1989 period of peak *Microcystis* growth. Peak chlorophyll *a* concentrations were considerably lower during 1990 than was the case during 1989 (Fig. 3).

Discussion

Comparison of Zeekoevlei's water transparency and in-lake nitrogen, phosphorus and chlorophyll *a* concentrations with models of lake trophic state (e.g. OECD, 1982; Vollenweider and Kerekes, 1980; Carlson, 1979) highlighted the hyper-eutrophic condition of this lake. The dominance of the lake by cyanobacterial species is characteristic of a water body which has non-limiting nutrient concentrations, high pH levels, N:P ratios consistently less than 10:1, regular mixing of the water column and a shallow euphotic zone.

The phytoplankton assemblage present in Zeekoevlei from April 1989 to March 1991 was typically representative of a eutrophic water body (Hutchinson, 1967) and similar to the

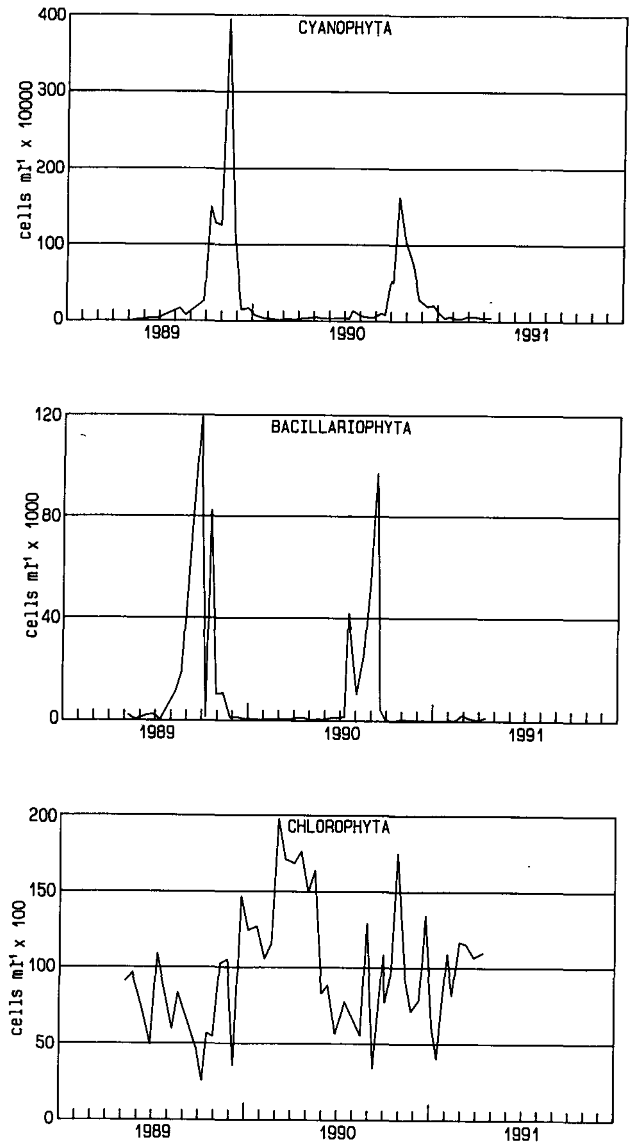

Figure 4
Periodicity of the dominant phytoplankton divisions present in Zeekoevlei. Note scale differences on y-axes

TABLE 4
GENERIC COMPOSITION OF THE PRINCIPAL PHYTOPLANKTON DIVISIONS REPRESENTED IN ZEEKOEVLEI

Cyanophyta	Chlorophyta	Bacillariophyta
Anabaena	*Actinastrum*	*Chaetoceros*
Anabaenopsis	*Ankistrodesmus*	*Cyclotella*
Aphanocapsa	*Carteria*	*Melosira*
Chroococcus	*Chlamydomonas*	*Navicula*
Microcystis	*Chlorella*	*Nitzschia*
Merismopedia	*Coelastrum*	*Thalassiosira*
Pseudanabaena	*Crucigenia*	
Raphidiopsis	*Golenkinia*	
Spirulina	*Kirchnierella*	
	Micractinium	
	Oocystis	
	Pedias trum	
	Phacotus	
	Scenedesmus	
	Selenastrum	
	Tetraedron	

assemblages recorded in the eutrophic, *Microcystis*-dominated Lake George (Burgis et al., 1973). In addition, the low generic diversity of the phytoplankton is typical of a lake having elevated nutrient concentrations.

The phytoplankton periodicity in Zeekoevlei was atypical, presenting as reversed when compared with the more traditional seasonal paradigm of periodicity (e.g. Fogg, 1975; Reynolds, 1983 and 1984). Classically, the onset of spring is accompanied by increased development of diatoms. Diatoms are best suited to survival during the cold winter months, and this characteristic imparts a selective advantage in terms of cell numbers present in the water at the onset of spring. Diatom development is usually terminated by depletion of silicon, and gives way to chlorophyte species which predominate during the summer. The slower growing cyanobacterial genera such as *Microcystis* become dominant during the summer to late summer period. This sequence may be modified by prevailing environmental forcing factors.

In Zeekoevlei, *Microcystis* was dominant throughout the year and there was no clearly defined seasonal progression from one dominant division to another. The features of the green and diatom algal periodicities were evident as muted, sub-dominant progressions beneath the canopy of *Microcystis* cells. The periodicity is atypical in that spring rather than summer maxima of *Microcystis* were recorded. The observed winter build-up of a single genus of diatoms was not sustained into the spring, and the subsequent decline in cell numbers appeared to be linked to a fall in reactive silicon concentrations. The possibility that allelopathic effects of cyanobacterial origin restrict the development of diatoms and green algae in Zeekoevlei cannot be ruled out.

Although cell numbers for the three principal phytoplankton divisions in the vlei were lower during the second year of the study, when increased hydraulic throughput was recorded, washout does not appear to have been causal because:

- Daily outflows from Zeekoevlei only attained or exceeded the 10% of the vlei volume necessary to bring about significant cell losses (Welch, 1984) on 10 non-consecutive days during 1990 (I. Morrison, CCC, pers. comm).
- All three divisions were not equally affected, with the Chlorophyta showing a nett increase in numbers coincident with the lower cyanobacterial peak.
- At the time of the 1990 spring maximum of *Microcystis* rainfall and outflow had already ceased.
- The size of the *Microcystis* inoculum present in the vlei at the onset of spring 1990 was of the same order of magnitude as that at the same period during 1989.

Similarly, nutrient limitation does not appear to be implicated as the ratios of NO_3-N and ortho-P to chlorophyll *a* prevailing at the time of the 1990 peak *Microcystis* development were 6:1 and 1.1, respectively. These ratios indicate that there was reserve nitrogen and phosphorus available for further cell development (Bailey-Watts, 1987). It is surmised that the wind regime prevailing during the late winter and early spring plays a significant role in the degree of spring development of *Microcystis* in Zeekoevlei (see below).

Model of *Microcystis* dominance in Zeekoevlei

The perennial dominance of Zeekoevlei by *Microcystis* may best be described by the following hypothetical model, which considers the lake as a chemostat or continuous-fermentor growth system for this alga. Several aspects of this model remain to be proven by investigation.

In this non-nutrient-limited model, high growth rates of *Microcystis* during the summer would be sustained by internal nutrient fuelling from the sediments, and high ambient water temperatures and light availability. Sustained wind-induced mixing of the algal cells throughout the water column would offset nutrient stratification. The extremely shallow nature of the lake, high mean insolation, and regular mixing ensure that the algal cells spend long periods in the light-rich zone. By the same token, the high summer wind speeds would serve to prevent dense populations and blooms of *Microcystis* from developing. The growth of buoyant cyanobacterial species and their ability to form blooms is known to be negatively affected by wind speeds in excess of 3,7 $m \cdot s^{-1}$ (Scott et al., 1969). The dense reed beds around the lake would act as sheltered nurseries for the development of dense scums of *Microcystis* cells.

During winter, water column temperatures fall only briefly below the 12 to 15°C temperature level at which *Microcystis* growth becomes negatively inhibited and cell losses through death and sedimentation become significant (Zohary and Robarts, 1989). In addition, the lower wind speeds prevailing during the winter would allow the buoyant *Microcystis* cells to spend longer periods near the lake surface, thus making optimal use of the reduced light available due to the shortened daylength. Complete mixing of the water column would still take place on a daily basis. This combination of factors would result in a large inoculum of *Microcystis* cells being present in the lake at the onset of spring, imparting a selective advantage to this slow-growing alga. The model assumes that cell losses due to hydraulic flushing are insignificant.

With the onset of spring, cell numbers of *Microcystis* would increase along with increasing hours of sunlight and water temperature. Concentrations of nitrogen and phosphorus would be maximal at this point in the annual cycle, just after the winter rains. Wind speeds would be relatively low, but wind-induced mixing would still be diurnal. This combination of physical and nutrient factors would support the development of a dense population of *Microcystis* cells with chlorophyll *a* concentrations reaching peaks in excess of 500 $\mu g \cdot \ell^{-1}$. The nature of the wind regime immediately prior to and during this phase of the model would determine the size of the resultant *Microcystis* population. Too much wind will negatively affect the degree of growth and result in a smaller maximum.

Conclusions

Validation of the model proposed for *Microcystis* dominance of Zeekoevlei requires investigation of the underwater light climate, wind patterns and the role of the nutrients deposited in the sediments and macrophytes in the internal nutrient cycling of the lake. Zeekoevlei is an ideal lake in which to study the effects of various forcing physical forcing-factors on phytoplankton dynamics under non-nutrient-limited conditions.

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