

**EWUDFW**

**DNZLBORRPRWKERBJBODW** *Ceratium hirundinella*, discovered in Albert Falls Dam in October 2006, exposed DV LJQLFDQWHRORJLFDQFKDQJHQGLFDWLYRIUBXFFHWHTXDOLWLQWKLVKLVWRULFDQOPMRWURSKLFUMHYRLU7KMSDW distribution of the bloom was examined synoptically in October 2006 and January 2007; these surveys revealed generally KLJKHGLQRBJBODWHEVWLWMLQLQVKRUHBFKMRWKHDNBQGMSHLDOOLQWKHLVFKDUJHBOXPRIWKHQKZQJQJL River. *Ceratium* totally dominated the phytoplankton assemblage, accounting almost completely for coincident chlorophyll OMHVLFKJQHDOOLQFUBVHZWKGBWKWRJQHHDWHEuGFKORURSKQOPDLXP9HWLFDORJHSURQMGXULQJWKH EORRPLIHHVXEVDQWLDQOOIURPFRUUMSRQLQJ SURQMGXULQJQRQEORRPFQGLWLRQVKLVWRULFDQOOWSLFDOLQWKH Direct count data and ordination analysis using non-metric multidimensional scaling exposed marked changes in zooplankton community structure compared to seasonally congruent non-bloom conditions in other years. Changes included the effective replacement of *Moina* by *Bosmina*, substantial reductions in *Daphnia* and *Ceriodaphnia* DQPDOOHEWHEQWH increases in abundance especially of calanoid copepods, as well as cyclopoid copepods and of *Chaoborus*, although not all of these differences were apparent in both survey months. These compositional changes are attributable to intrinsic differences in feeding biology among taxa and their associated susceptibility to the altered food environment, which was commensurate with *Ceratium*'s emergence. In addition, chydorid cladocerans appeared as a new (but spatially restricted) eutrophic bio-indicator component of the zooplankton, and the species diversity of cyclopoid copepods was enriched.

The historical incidence of *Ceratium* in the lake since 1995 coincided with low NO<sub>3</sub>-N:TP values (used here as an N:P UDWLRSURSDUWLFXODUORILQRJWHVDQGWKEURDGOFRQLQFLGHWYDOXMLQWKMSEHODNE present but sparse in 1995, at average N:P ratios around 5.5. It disappeared in 1996 when the ratio increased radically to >10, and UBSSBUHLQDIWHDQHUDWLFHOLQRWIKHDWLRWRLQWKHDNTKHHOLQHQ13UDWLRRILQRJWHVVLQFH ZVFOBUODVVRFLDWHEZWKDFRQVLVWQWLVHQ73OMHVVLQQLQZPRVWSODXVLEODWUWLEXWDEOWRLQSWXWRI+RZFN WLRQVLQPEQDQXDO3FRQFHWUDWLRQVLQQLQZTURP95 to 120 Pg/l in 2007 (broadly mirrored in annual TP ORDGLQJVXJWWLQJWKDWLPSURYHRSHDWLRQDOIFLQDFDQGFSDFLWRIWKH7SODQWRIIHVDSODXVLEOHSURVSHWIRU mitigation and reversal.

**Keywords:**

An expansive literature (not reviewed here) attests that blooms of *Ceratium* and *Peridinium* species) have become widespread and prominent in many lentic freshwaters, while coastal marine environments have experienced similar blooms ('red tides') especially in the past 3 decades (e.g. Reynolds, 2006). The incidence, severity and prominence of bloom events in standing freshwater ecosystems appear to be growing exponentially, although the causes of such outbreaks remain ambiguous and/or contradictory. The relatively sudden onset of blooms of *Ceratium hirundinella* Bergh in lakes and reservoirs is especially noteworthy. In South Africa, blooms appeared suddenly in 7 reservoirs in the 1990s (Van Ginkel and Silberbauer, 2006) – most prominently in +DUWEMSRRUWDPLQ9DQ\*LQNHWDQ3DUDOOH

appearances were recorded in several reservoirs in Argentina in 1990, with northwards expansion to reach the neo-tropical 5R7HFHR5MHYRLUDOVRLQDFRQDJKWDQO Its appearance in the Paso de las Piedras Reservoir (Buenos Aires) in 1997 (Parodi et al., 2007) represents a broadly common SRQLQJWPSRUDOSURQDFRQDJKWDQOVXJ - gest that its occurrence in the neo-tropics 'could be a regional phenomenon associated with some dispersal mechanisms and favourable local conditions for its proliferation', implying that this nuisance alga (see below) may become more widespread. The analysis of factor(s) underlying or stimulating its emergence becomes correspondingly important.

Reviewing the literature, Whittington et al. (2000) describe *Ceratium hirundinella* DVDELTXWRXHODWLHODJHDQ slow-growing species characteristically found during late summer, in water bodies with a warm stable epilimnion and low nutrient concentrations. Under these low-turbulence conditions WLRQVLWVDELOLWWRXQGHWDNMLJQLFDQWGLHYHWLFDQPL WLRQV9DSSDUHQWQDEONLWVRSWLPDQSORLWDWLRQRI light and nutrients – 2 essential resources whose availability FRQWUDVWVGLUHWOLQWKHWWLFDQGLPQLVLRQGXULQJWUD +BQHQBQG)XUQDVV-DPMMDO

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Whittington et al., 2000). Seasonal periodicity of the species LVKRMHYDULDEOBUUDUWtQHOG6iQFKNDVWLOOR (2001) reported clear winter maxima for an array of Span-LVKUMHYRLUVEXWVXEVHXQWOIXUWKHKLJKOLJKW6= XOX1DWDO6RXWK6ULFDVHYMDVDFUXFLDOZWHVVRXFH the variability of its occurrence reported in the literature. Notwithstanding its putative advantage at low nutrient levels (Whittington et al., 2000), *Ceratium* occurs in eutrophic lakes HUPSRQJDQGVVW5LGE5QROGV)LJLQ Reynolds, 1996) as a component of late-summer phytoplankton associations in oligotrophic, mesotrophic and eutrophic (but not hypertrophic) temperate waters. In South Africa, *Ceratium* blooms have been recorded in 17 of 57 reservoirs, and were perceived as being 'serious' in 9 (Van Ginkel and Silberbauer, 2006). Among these reservoirs, blooms occurred in all seasons and across the trophic status range. Although most common in mesotrophic waters with total chlorophyll levels below 15 Pg/l, *Ceratium* blooms occurred in several waters of very high nutrient status, most prominently in the KSHHWURSKLF+DUWEMSRRUWDP+MHCeratium was UHRUGHIRUWKHVWVWLPHQDQVDVXGGGRQVWEORRP that generated average chlorophyll levels of up to 600 Pg/l in WKSSHWRPVWUDWXP9DQ\*LQNHWDHXLVD - lent to cell densities of around 13 500 cells/ml (see below). SXEVHXQWUXOHDVHPRGHGMORSHE9DQ\*LQNHW al. (2007) to predict *Ceratium* abundance in various hypertrophic reservoirs in South Africa relies on prevailing nutrient concentrations (either TN and TP or SRP) as input drivers, further inferring nutrient enrichment as a causal/contributory factor underlying bloom occurrence, in contrast to a previous perception of *Ceratium* as an 'indicator' species of 'clean' ZWHHBDGLViN%XFNDQG=XUN

*Ceratium* is recognised as a problem alga on 2 counts; it imparts tastes and odours to potable water, and clogs water SXULFDWLRQQWHV7KMXGGGRQVWRIEORRPVUHRUGHLQ 7 reservoirs (Van Ginkel and Silberbauer, 2006), and described LQGWDLOIRU+DUWEMSRRUWDP9DQ\*LQNHWDOLV DFFRUGLQJOYHVLJQLFDQWLQWHPVRIZWHTXDOLWPDQZHQZHQZHXMWRQV the lake. But it is also commensurately intriguing from a purely ecological perspective. Ecosystems often respond abruptly to gradual changes in forcing variables, and can exhibit unexpected discontinuous shifts to an alternative state as the ecosystem exceeds a threshold in one or more of its key variables or SURFMVM8QGHOLQJHRORJLFDOWKUMKROGVGHRQGLWLRQV the lake. ENQKGLFKDQDEUXSWFKDQJHQDTXDOLWSURSHWRUSKH :DVWKLVLVHLQJQXQSUHQHQHQRYHEORRPRFFXUUQFH UHWDHWRWRLPSOHQWDWLRQRIRWKORRLOJQLLQWHEHDLQ ZWHWUDQVIVHVKHHQVXUYRILGPDUDP was undertaken immediately after the bloom was encountered in Albert Falls in October, to determine conditions DQWKLVSXSVWUBPIHHUMHYRLUWKURXJKKLFKWKORRL 5LYHWUDQVIVHVLQWRWVKHQLVWVWHLJ ‡ :DVWKHEQKLVWRULFDOSUHQHQWWRWKHORRPLQ (SEHW)DOOV8PJQL:DWHDUFKLYDOZWHTXDOLWUHRUGV were accessed and examined for relevant evidence. ‡ :KDWXQGHOLQJFDXVDQDFWRUVRUGULYHVFRXOGDFFRXQWV WKHORRPLQ(SEHW)DOOV+LVWRULFDQZWHTXDOLWYDUL DEOMHPLQHDVVRXWOLQHIRUWK6UMLRXVTXMMWRQ 7KLVTXMMWRQLVMSHLDOOSHVLWQHJWJLYHQKHHQWDQG or sudden appearance of *Ceratium* blooms during the past decade in other South African reservoirs (Van Ginkel and Silberbauer, 2006; Van Ginkel et al., 2001; 2007) and elsewhere abroad. ‡ :KDWGLUHWorder impacts did the bloom exert on structural and functional attributes of the Albert Falls HRVWVH7KWDQJLEOHQDQGLGDMIRUHPQLQDWLRQHH

The extensive re-structuring of plankton communities (both autotroph and zooplankton components) associated with emergent blooms of *Ceratium* can be broadly likened to a change of state, which, while perhaps 'unstable', is otherwise loosely analogous to switches between hydrophyte- and algal-GRPLQDWHVKDOORZDNMHRVV+HMMFULEH the sudden appearance of *Ceratium* at bloom densities in (SEHW)DOOVDPQDQVLEOUHVLWQJWKWUDQVVFHQGRIDQ ecological threshold) and attempt to evaluate the likely causal-LWDQGHVWVWPHFRQVHXQFMRIWKLVMQZLPLQVLRQLQDQDQ ‡ 'old' (mature) reservoir of paramount strategic importance in a water-scarce nation.

6WXGDUBFRQWMDQGTXMWLRQV

7KHQLFDWFKPQWFRYHLQJURXJKONP 2 of central IRUWKHUBWHXUEDQDQGG3LWHPDULWEXUJOWURSRQLDWQ areas. Roughly 45% of the province's population occupies this region, which accounts for some 20% of South Africa's gross national product (Keinze et al., 1997). With such concentrated economic activity, an assured supply of potable water and the PDLQWHDQFRIJRRGZWHTXDOLWU6UMQWPDRIUFDQOQJUM :DWHTXDOLWPRQLWRULQJUHDLQVSDUDPRXQWWRLGHVWLDLQ PDQLMWDWLRQRIGHOLQLQJZWHTXDOLWDKHGRIREMMWLYH ORJLFDQVFXWLQDQDQGFULWLFDOMDOXDWLRQRIFDXVMFRQVHXQ prognoses, and prospective mitigation interventions.

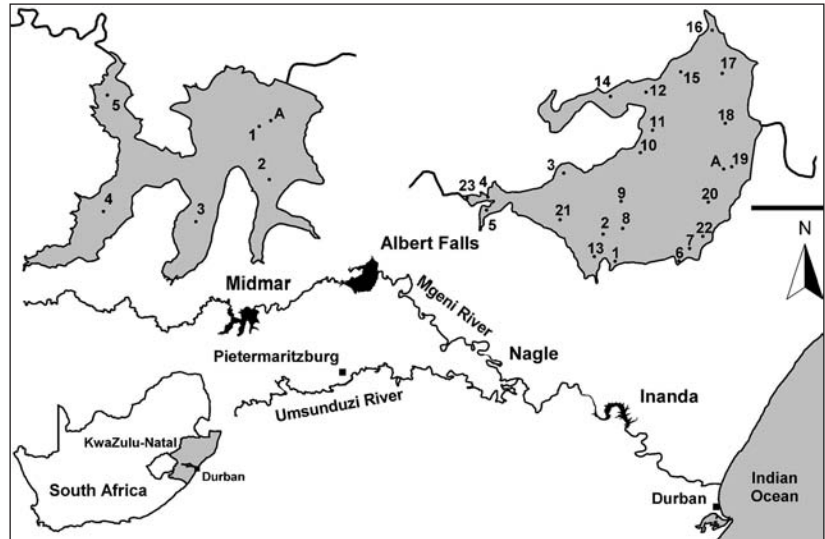
:DWHTXDOLWQDWXUDOODQGLQMLWDEOGHOLQMSURJUM VLYHGRZVWUBPDORQJWKHQL5LYHUMHYRLUFDVFDGH )LJ+RMMHDWOH6VWVKSSHUMHYRLUV+0LGPDUWQD Albert Falls Dams – remained mesotrophic (or better), with QRREYLXVGVWHLRUDWLRQLQZWHTXDOLW6IRUHXHD contemporary phase of zooplankton and associated limnology-FDOUMHUFKUNZVWVHPLQDW6+DUW8S WRWKLVLWLPQRVLJQLFDQWDOJDOEORRPVKDQDQGLMHWBLQWKMM UMHYRLUV+DUWLQNHQLQJZWKWKHRZSROOXWLRQ potential modelled for their respective local catchments (Kein- QWDOIRDGYHVFKDQJMLQZWHTXDOLWVWDWVX VHXEOLFOUSRUW6IURPWKQJRLQJURXWLQZWHTXDO ity monitoring of key chemical and algal variables by Umgeni Water, the parastatal authority with dedicated responsibility for management of water resources and associated infrastructures LQWKHQLFDWFKPQW

SDLQVWVKHERYHDFNJURXQGWK6HFWHLRQRIDPDRU GLQRZHQDWHORRPGXULQJDPXOWLVLW6QRSWLFVXUYRIL Albert Falls, fortuitously undertaken as a student-training exercise, in October 2006 was entirely unexpected, and stimulated the more comprehensive investigation and analysis reported herein. We sought answers to and/or explanations for the following QZHQZHXMWRQV ‡ :RXOGWKHORRPSHVLVWVWLQWLP6HQGVSDWLDOWH6W\$ repeat synoptic survey of Albert Falls was undertaken in KLJKVXPPH-DQXDU7KHQLQJVRIRWKLVOHLQ WXUQWRQMFDOMSDWLDOLQYMWLJDWLRQRIGLQRZHQDWH GLVWULEXWLRQLQWKHLYHLQZDQGGGLVFKDUJ6OXPHLRQV the lake.

:DVWKLVLVHLQJQXQSUHQHQHQRYHEORRPRFFXUUQFH UHWDHWRWRLPSOHQWDWLRQRIRWKORRLOJQLLQWHEHDLQ ZWHWUDQVIVHVKHHQVXUYRILGPDUDP was undertaken immediately after the bloom was encountered in Albert Falls in October, to determine conditions DQWKLVSXSVWUBPIHHUMHYRLUWKURXJKKLFKWKORRL 5LYHWUDQVIVHVLQWRWVKHQLVWVWHLJ ‡ :DVWKHEQKLVWRULFDOSUHQHQWWRWKHORRPLQ (SEHW)DOOV8PJQL:DWHDUFKLYDOZWHTXDOLWUHRUGV were accessed and examined for relevant evidence. ‡ :KDWXQGHOLQJFDXVDQDFWRUVRUGULYHVFRXOGDFFRXQWV WKHORRPLQ(SEHW)DOOV+LVWRULFDQZWHTXDOLWYDUL DEOMHPLQHDVVRXWOLQHIRUWK6UMLRXVTXMMWRQ 7KLVTXMMWRQLVMSHLDOOSHVLWQHJWJLYHQKHHQWDQG or sudden appearance of *Ceratium* blooms during the past decade in other South African reservoirs (Van Ginkel and Silberbauer, 2006; Van Ginkel et al., 2001; 2007) and elsewhere abroad.

:KDWGLUHWorder impacts did the bloom exert on structural and functional attributes of the Albert Falls HRVWVH7KWDQJLEOHQDQGLGDMIRUHPQLQDWLRQHH

**Figure 1**  
Map of the Mgeni River reservoir cascade, showing its location in South Africa (lower left), with enlarged outlines (upper) of its upstream reservoirs, marked to show synoptic survey sites on Albert Falls and Midmar used during this study. Points labelled A indicate approximate position of historical reference sampling sites. Scale bar represents 2 km on the enlarged reservoir outlines, which are at the same scale.



immediately obvious. First; changes in vertical oxygen  
SURQUMXOWLQJIURPWKPIWDEROLFDFWLYLWRIOLYLQJ  
DOJDBHQGSURVSHWVRIVXEVHXQVWVMMHRIQDWLWRO  
following collapse and decomposition of the bloom, with  
associated rapid and vertically extensive hypolimnetic  
GRHQDWLRQDQGSRVVLEOMKNLOOVVZSODXVLEOH  
Second; by virtue of its large size and 'armouring' horns,  
*Ceratium* is effectively immune to grazing by microphagous  
zooplankton. Changes in zooplankton composition  
IROORZQJWKBOJDOVKLIWWRWKLVLQGLEOHQRBJ  
accordingly investigated by reference to historical records  
+DUWDQGXQSXEOLVKHUHRUGV  
‡ &DQDQVIVWRWKEXMFWLRQUHDUGLQJXQGHOLQJFDXVPR  
IDFWRUVSURYLGRUDQREMLWLYKWXUXURJQRVLVD  
KDSVLGQWLIHRORJLFDODSSURSULDWHLWLJLDWLR

**Methods**

Sampling sites for the synoptic survey (see Fig. 1), undertaken on 7 to 8 and 14 to 15 October 2006, were chosen to provide UMSUMQWDWLYHRYHJDJIRSRQDWHDFNDWHDQGLQAZ reaches of the reservoir, as well as a range of site distances from the nearest shoreline. Following discovery of the bloom reported here, the synoptic survey was repeated on 22 Janu-DUQBGLQLQWUXUQRWDVSDWLDQOQHVFDOMXUYRNIWVHYHLQWKQKGGZWKIRUPDOLQ3ULRUWRQXPHDWLRQVDPSON 0JL5LYHLQADQGGGLVFKDUJUSOXPRQ-DQXDU\ 6LWHRUGLQDWMZHWHPHQZWKD\*DUPLQORGEH portable GPS.

9HWLFDOSURQLQJRIWPSHDWXUBHQGLLVROYEHRHQ (DO) was undertaken at 1 m intervals from the lake surface WRWKERWWRPRIWKZWHFROXPQ\*PZWKDQHHWURQLF WRELRPDVVXVLQJFRHFLQWVSHLQLO7DEOPKIKH <6.0RGH7PSHDWXUBPWH In situSRQLQIWRWDO chlorophyll, and its relative partitioning between greens, blue-JUHFVUSWRSKWMQDQGGLDWRPVAium – see below) was undertaken at 1 m intervals from 0 m to 5 m depth, using a bbe OROGDQIKEXEPHVLEOJXRURSURESHWURXRURPWVH6XE surface samples (50 ml) of water were collected concurrently ZWKPRVWVXEVXUIDFNRURSUREHEHGLQJVDQGSUMHYEHRQ andl, 1998). Further analytical protocols are detailed else-VLWZWKXJROYLRGLQIRUVXEVVHXQWODERUDWRUQXPXKHHDUW WLRQRIGLQRBJHODWHEHVLWLM6HFKLGSVWKWUDQVSDUQEQZV measured in shade (where possible) with a 22.5 cm diameter white disk.

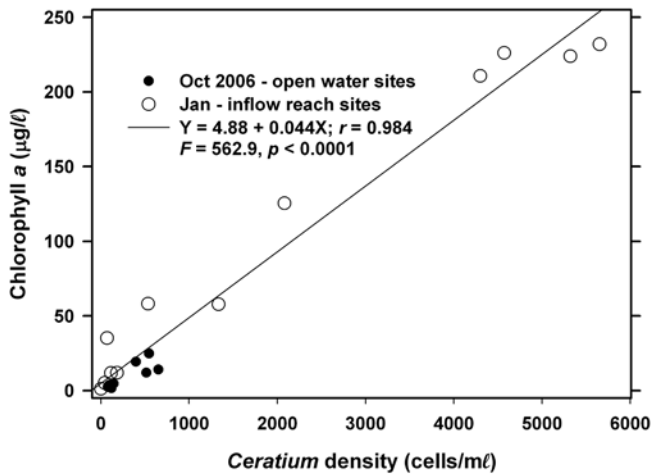
=RRSODQNWRQZVVFROOHWHLQYHWFDOQMWKDXOVVIRA roughly 1 m above bottom to the surface, using a conical

**TABLE 1**

	W	PJ
<i>Daphnia</i> (large)		10
<i>Daphnia</i> (small-medium)		4
<i>Ceriodaphnia</i>		3
<i>Diaphanosoma</i>		2
<i>Bosmina</i>		1
Calanoid copepods (adults)		7
Calanoid copepods (copepodites)		2
Copepod nauplii (all)		0.5
Cyclopoid copepods (adults & copepodites)		1
<i>Chaoborus</i> (large)		25
<i>Chaoborus</i> (small-medium)		5

Nansen-type net with a reducing cone, mouth diameter of 25 cm and mesh pore aperture of 53 µm. Samples were pre-HYHLQWKQKGGZWKIRUPDOLQ3ULRUWRQXPHDWLRQVDPSON were washed through 160 µm mesh to reduce the obscuring and smothering effects of *Ceratium*. Our analysis was thus primarily restricted to macro- and meso-zooplankton. Samples were standardised to 50 ml, generally with 4 replicate 1 ml sub-samples thereof being enumerated. Counts were converted WRELRPDVVXVLQJFRHFLQWVSHLQLO7DEOPKIKH 'bivore' biomass fraction comprised all zooplankton excluding *Chaoborus* (generally an obligate carnivore – but see Xie et DODQGSUWRIWKHFORSRLGFRSEIRGFRPSRQHW a fractional allocation based on the mixed functional role of Cyclopoid copepods as herbivores and carnivores in different VSHLMDQGRUOLIKLVWRUUVVDJMH-DQVQDQGG6DQWH (Xie et al., 1998). Further analytical protocols are detailed elsewhere. Assuming a uniform biomass (or density) per unit volume through the water column, biomass or density per unit area will obviously increase with water depth (haul length); conversely, as water depth increases. To counter these inevitable biases,





**Figure 2**

Chlorophyll a concentration in relation to *Ceratium* cell density in open water synoptic survey sites during October, in inflow and discharge plume sites in January, and the overall regression relationship.

zooplankton abundance and biomass over the lake at large (during the synoptic surveys) is reported both in areal (/m<sup>2</sup>) and volumetric (/m<sup>3</sup>) terms. Numerical abundance values are used in preference to the corresponding derived biomass estimates, wherever appropriate.

Cross-calibration of *Ceratium* probe values (Y) of ‘diatom’ chlorophyll at sites sampled on the 2<sup>nd</sup> day of the October survey provided unambiguous evidence (Y = 79.03 + 22.71X, r = 0.840, n = 9, p < 0.001); genuine diatoms were barely evident in concurrent samples. Furthermore, it is clear that ‘total’ chlorophyll values are almost completely accounted for by corresponding *Ceratium* densities across the full range of values encountered during both synoptic surveys (Fig. 2). Accordingly, as and where appropriate in the following account, chlorophyll is used as a direct proxy for *Ceratium* density.

Lake-wide patterns of chlorophyll concentration and zooplankton biomass were interpolated from the synoptic survey site values and mapped. Using ArcView 3.3, the common use practice of estimating values at each map pixel as a weighted average of the values at a subset (12 in this case) of nearest sampling stations, each station being weighted by the reciprocal of its cubed distance from that point, was employed. Peninsulas were treated as barriers, so that sampling stations their separation distance over water (around the peninsulas), not their distance over land.

Umgeni Water’s archival database of an array of chemical and at an offshore site in the Dam (DAF001 and DAF003) provide an historical record against which to examine the changes reported here.

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mean values, these records were not merely excluded, but were applied literally (as 3, 15 and 0.05). Without TN values, the N:P values reported here are surrogate ratios based on NO<sub>3</sub>-N:TP. Nutrient loads for Albert Falls were calculated as the product of monthly mean nutrient concentrations (4 recorded values per month). In a few cases where no nutrient values were available for the calendar month, an average value interpolated from the straddling months was applied.

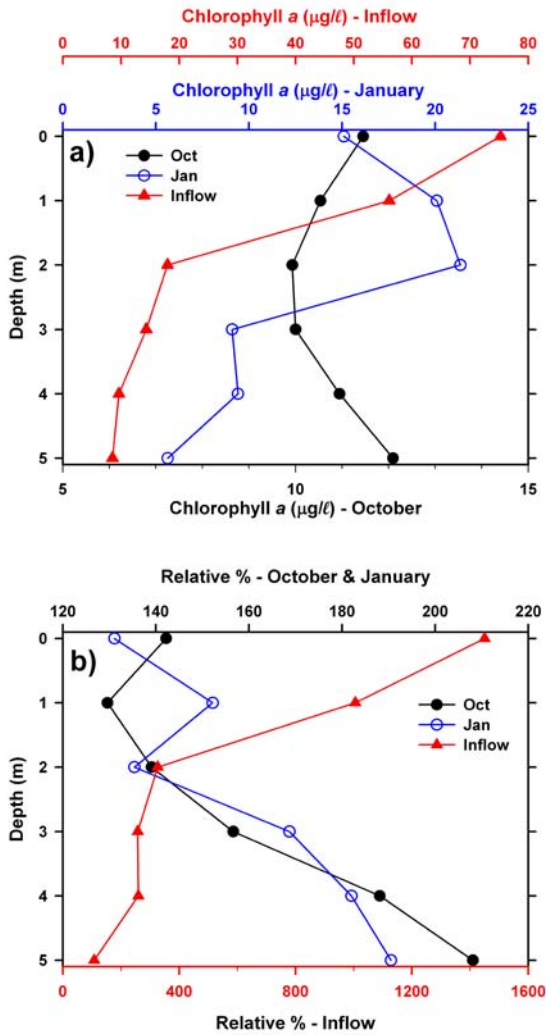
Overall statistical analysis of these data (using Statistica 98) was constrained by the limited temporal co-incidence of time series records, especially in recent years when *Ceratium* was common. For instance, correlation matrices of *Ceratium* abundance, nutrient concentrations, and estimated water column stability (based on concurrent vertical temperature profiles) were calculated. For instance, correlation matrices of *Ceratium* abundance, nutrient concentrations, and estimated water column stability (based on concurrent vertical temperature profiles) were calculated. For instance, correlation matrices of *Ceratium* abundance, nutrient concentrations, and estimated water column stability (based on concurrent vertical temperature profiles) were calculated.

Community composition was summarised using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity, implemented in the R package vegan. Starting points converged on the same ordination. Before analysis, each density value was divided by the maximum density in any year for that species, and then by the maximum density of any species for that year (procedurally termed Wisconsin double standardisation) to ensure that uncommon species and years of generally low density were given the same weight as more abundant species and more productive years.

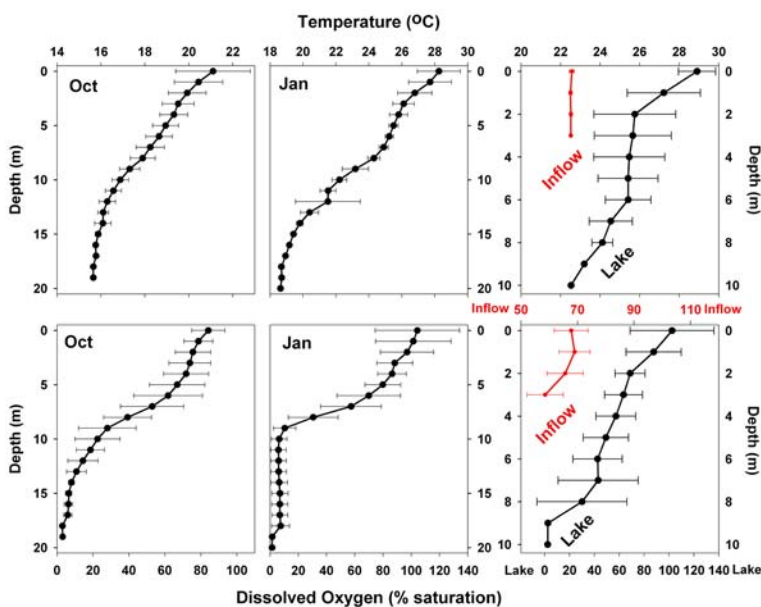
### 5.1. Spatial variation in total chlorophyll

Surveys revealed considerable spatial variation in total chlorophyll (Fig. 3a), chlorophyll showed a clear west-east gradation along the lake axis of the lake, with distinctly higher values (10 µg/l) of *Ceratium* over roughly a third of the lake area, yielding a lake-wide station average of 11.7 µg/l. While chlorophyll values were distinctly and significantly higher in the west (16.4 µg/l) than in the east (10.0 µg/l) taken shortly after this synoptic survey, revealed an astonishingly abrupt appearance of *Ceratium* in the lake, and its general





**Figure 6**  
 a) Vertical profiles of lake-wide average chlorophyll concentrations (absolute) in October and January, and in the inflow plume region in January.  
 b) Corresponding relative profiles (see text) for lake-wide surveys show deep water chlorophyll maxima. Note different axis scaling.



**Figure 7**  
 Lake-wide mean ( $\pm$  SE) vertical profiles of temperature and dissolved oxygen during October and January synoptic surveys, and corresponding January values in the river inflow and discharge plume in the lake.

distinction between temperature and light intensity as determined by *Ceratium* density (inferred from diatom chlorophyll) across all depths at offshore sites 10 m or deeper correlated negatively both with dissolved oxygen saturation levels ( $-0.32^{ns}$  in January), and with dissolved oxygen saturation levels ( $-0.395^{**}$ ). This inverse *Ceratium*-oxygen relationship indicates that vertical depletion in oxygen (Fig. 7) may be largely attributable to *Ceratium*'s potential impact on water column de-oxygenation. This inverse *Ceratium*-oxygen relationship, strongly supports this hypothesis.

Indications of diel vertical migration by *Ceratium* are observed in October (Fig. 8a). A surface accumulation of cells in the early morning declined notably during the solar azimuth, leading to a subsurface chlorophyll maximum (at 2 m). By late afternoon, peak values were again established in surface waters. These changes were essentially independent of the corresponding diurnal changes in thermal regime (Fig. 8b), and most probably related to changes in thermal regime (Fig. 8b), and most probably related to changes in thermal regime (Fig. 8b), and most probably related to changes in thermal regime (Fig. 8b).

These changes were essentially independent of the corresponding diurnal changes in thermal regime (Fig. 8b), and most probably related to changes in thermal regime (Fig. 8b), and most probably related to changes in thermal regime (Fig. 8b).

Conversely, chlorophyll values were astonishingly low, ranging between 1.45 and 1.76  $\mu\text{g/l}$  (average = 1.6  $\mu\text{g/l}$ ), with commensurate main basin water transparency levels at virtually unprecedented highs (Secchi depth range = 4.0 to 5.3 m). *Ceratium* was present but very sparse in zooplankton



virtually undetectable density in un-concentrated water samples. This effectively excludes inter-basin transfers (IBT) IURPWKORRL5LYHDVDGLUHWFDXVDODJQWRIEORRPVLQ Albert Falls. In any event, this alga was present in Albert Falls before the IBT was implemented (see below), and explanations for its development to bloom levels in Albert Falls must be sought 'closer to home'.

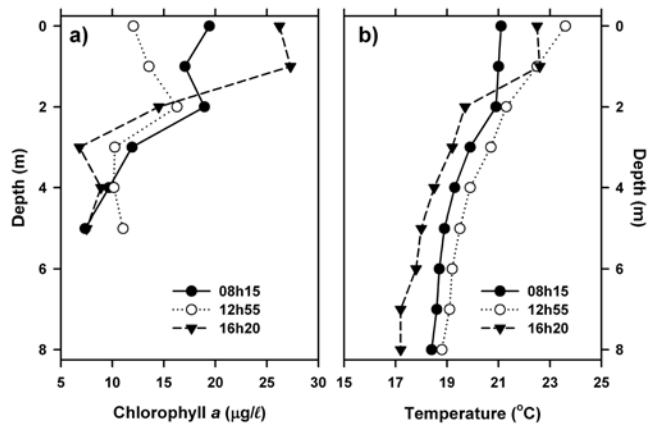
**Ceratium in**



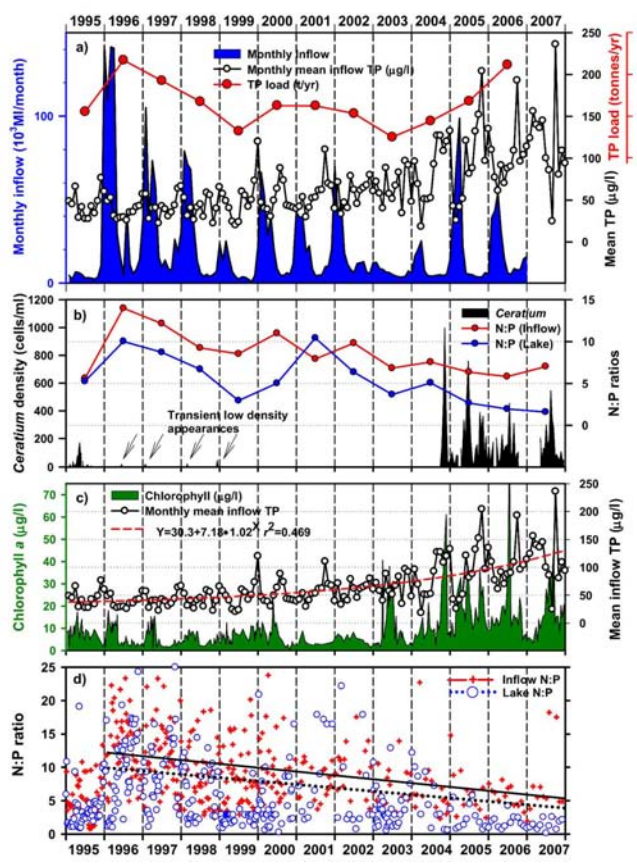
Inspection of Umgeni Water archival data (Fig. 9) revealed low-density occurrences of *Ceratium* in 1995 (Fig. 9b), and transient appearances in the following 4 years, preceding an extremely abrupt and unprecedented outburst in 2004 (Figs. 9b and 11a). Similar pre-emptive low-density occurrences in 1992 DQGZHSRURUWHE+DUW6LQFHLQRJHODWH densities at a routine main basin sampling site in Albert Falls (A on Fig. 1) were considerably greater in 2004 (Fig. 11a) than those we encountered in 2006/2007, concurrent densities in WKUHLQZHLRQLQFDQRQEPDILQKH appearance of any bloom of such severity presumably invoked concern and diagnostic attention by the responsible parastatal water authority, but received no open publicity.

**8QGHOJQJFDXVDOGULYHVRICeratiumblooms**

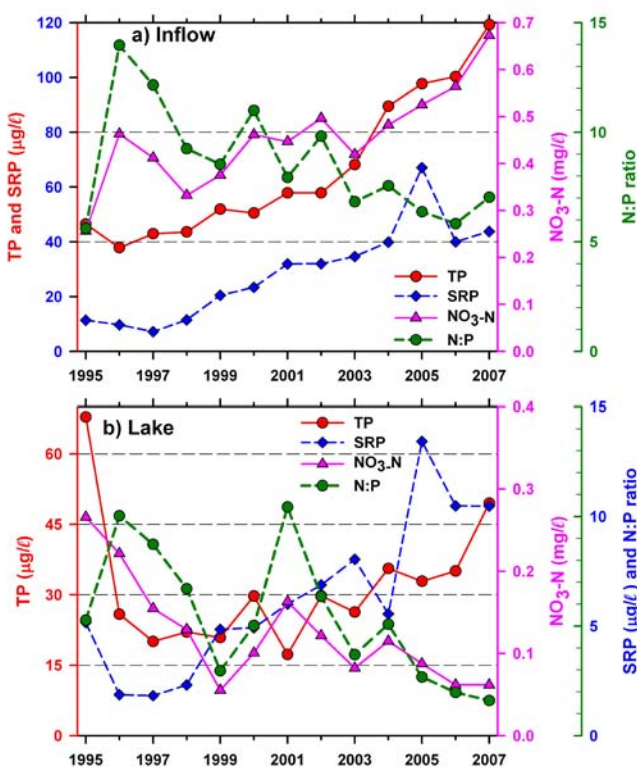
Any unprecedented and/or abrupt appearance of a species, and especially its attainment of high densities, clearly manifests some ecological change or switch, or the surpassing of some HRORJLFDOWKUMKROG+LVWRULFDQZWHTXDOLWUHRUGV)LJVA and 10) point irrefutably to progressive nutrient enrichment as a contributory or direct causal factor. Nutrient concentrations LQODNHOZWHVKDYHQFUBVHLQRUDEOIQURP )LJZWKPHQDQXQDOLQZXLWLFWRQFHWUDWLRQV (Fig. 10a) rising most strongly for SRP (3.6-fold), but also for TP (2.8-fold) and NO<sub>3</sub>-N (2.2-fold). Calculated annual P loadings have also risen (Fig. 9a), albeit less markedly. Data for total N levels are unfortunately not available. Broadly parallel increases in SRP and TP levels were evident in the lake itself DVLQLWVLQRZMSHLDOOIQURP)LJEDOWKRXJK



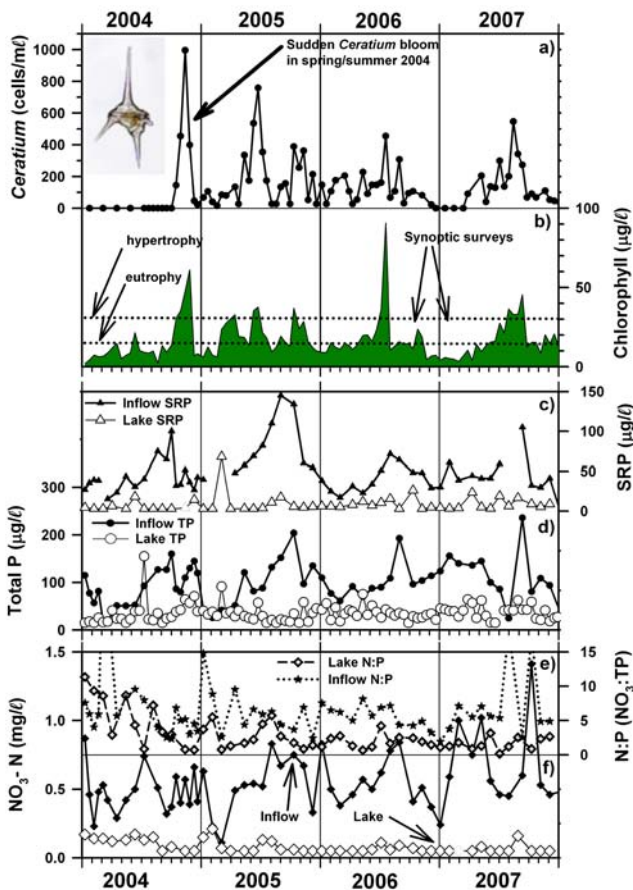
**Figure 8**  
Diurnal temporal changes in a) chlorophyll and b) temperature at an inshore station (Site 14) in Albert Falls Dam in October.



**Figure 9**  
Long-term profiles of a) Albert Falls inflow volumes, monthly and annual TP loads; b) *Ceratium* abundance in relation to mid-lake and inflow N:P ratios; c) mid-lake chlorophyll concentrations in relation to monthly mean TP values of inflow water (with fitted regression, where X is time in months since January 1995); d) comparative N:P ratios in inflow and mid-lake waters.



**Figure 10**  
Annual mean nutrient concentrations and nutrient ratios in a) inflow water and b) mid-lake region of Albert Falls.



**Figure 11**

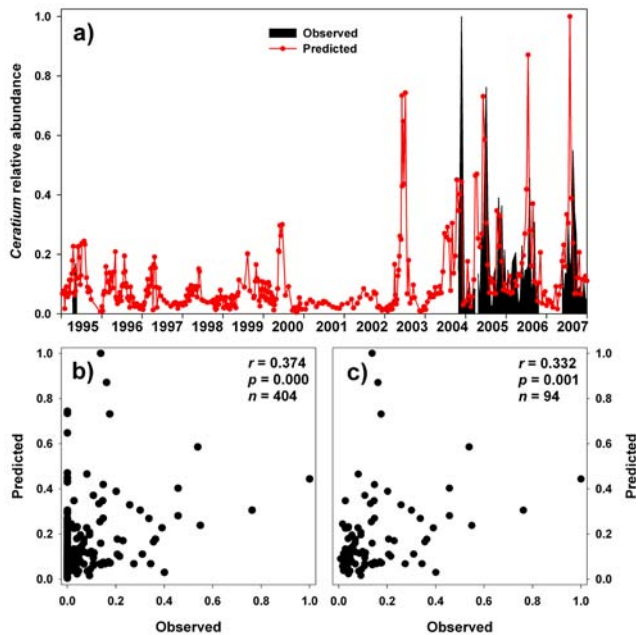
Seasonal periodicity of a) *Ceratium* and b) corresponding chlorophyll levels (showing conventional higher trophic status limits) in Albert Falls since the appearance of this dinoflagellate at bloom density levels in late 2004, in relation to concurrent inflow and in-lake levels of c) SRP; d) TP; and corresponding e) N:P ratios; and f)  $\text{NO}_3\text{-N}$  levels.

the magnitude of increase in the lake was lower, undoubtedly buffering and assimilative mechanisms.

The initial presence of *Ceratium* in 1995 coincided with the highest mean annual TP levels (nearly 70  $\mu\text{g}/\text{l}$ ) in this data set. The lake N:P values < 5 (Figs. 9b and 10b). Despite extreme variability in N:P values (perhaps exaggerated by annual variability in inflow and lake N:P values) and the lake declined progressively from 1996 (see trend lines in Fig. 10a). The P source is most plausibly attributable to the lake (Fig. 10a).

### *Ceratium*

The inconsistent and/or contradictory pattern of seasonal occurrence in *Ceratium* in Albert Falls, in its periodicity (at a single deep-water offshore site) within



**Figure 12**

Predicting *Ceratium* abundance in Albert Falls with a rule-based model. a) Observed vs. predicted time-sequence values between 1995 and 2007, with comparative observed vs. predicted scatter plots: b) for the entire time sequence, including the prolonged initial period of *Ceratium* absence; and c) for periods when *Ceratium* was actually present.

*Ceratium* in 2004 was an early summer outbreak. Although present throughout the year in 2005, suggestions of an underlying annual bimodality nonetheless exist; *Ceratium* showed a PDMUSBNLQBHOZQWHDQGDVXEVIHXQWLQFUBVHQBODWH spring/early summer. While no obvious peaks were evident in 2006, weak suggestions exist of its increase in early spring. In 2007, peak densities were reached in early spring. Collectively over these 4 years, the underlying phenology displayed by *Ceratium* is indicative of a temporal association with periods of instability or circulation. Its consistent absence or sparseness LQPLGVXPPHLVFRQJUXHFWLQWKLWUHDUG+RMHVWDWLWVLFDO evaluation of such perceived correlations was unfortunately not SRVVLEORRUUEBVRQVEODLQHLQWQWVWKRGRV% XWRYHDOOWKH general temporal trend exhibited in Albert Falls is somewhat at variance with its placement as a late-summer component in the seasonal associations described for temperate waters by Rey-QROGVWKLWUHQIRUFMVKHRQFOXVLRQESpUDUWtQH seasonal distribution of *C. hirundinella* have yet to be fully elucidated. With its sudden appearance at bloom densities, and its impact on potable water supplies, better resolution of this problem is clearly warranted. The following section explores potential advances in this respect.

A rule-based 'hybrid evolutionary algorithm' model to predict *Ceratium* abundance (as biomass volume) in hyper-eutrophic reservoirs was developed by Van Ginkel et al. (2007). While PRGHVRIWKLWVSHHXLUHWUDLQQLJRUORFDOFRQLWLRQVWR yield effective predictions, we casually tested the model's transferability to the vastly different nutrient arena of Albert Falls



Dam without appropriate ‘training’. For Albert Falls, where chlorophyll levels (Chl a) remain below 190 Pg/ℓ, the ELSE rule RIWKHRGH9DQ\*LQNHWDOSUHLFWVGLQRRLJHODWH biomass (DinoBiomass – cm<sup>3</sup>/m<sup>3</sup>) as:

$$\text{DinoBiomass} = ((\text{Chl a} / ((T_{\text{surf}} * 0.662) - 5.829)) / \ln(|\text{DIP}|))$$

where:

$T_{\text{surf}}$  is surface temperature  
 DIP is dissolved inorganic P (Pg/ℓ)

As the units and corresponding ranges of observed and predicted values were fundamentally different (observed range of 0 to 996 cells/ml vs. predicted range of 0 to 9.02cm<sup>3</sup>/m<sup>3</sup>), we normalised both data sets relative to their respective maxima for comparative purposes. The resulting observed and predicted values show broad temporal concordance when *Ceratium* was present in the lake, indicating the model’s potential, although the model incorrectly predicts a continuing presence of the alga (Fig. 12a). Nonetheless, observed and predicted YDOXMMMLJQLFDQWOFRUUHDWERYHDOO)LJEDVHO as when the analysis was restricted to periods when *Ceratium* was actually present in the lake (Fig. 12c). The model’s erroneous prediction of sustained *Ceratium* presence (Fig. 12a) is attributable to its underlying structure which, EDVHRQLWVWUDLQLQJGDWDXVMFKORURSKOOERW input driver (effectively a proxy for *Ceratium* abundance which Van Ginkel et al. (2007) did not measure directly), and again as an implicit outcome response variable. Accordingly, where *Ceratium* is absent and does not contribute to input level chlorophyll values, the model continues to predict *Ceratium*’s existence, as it does not and indeed cannot distinguish the taxonomic origin of the chlorophyll level input driver. Its usefulness will accordingly be limited where *Ceratium* is not an ongoing component of the phytoplankton.

6RPHLUHWLPSDFWVRQWK6EHW)DOOVDP  
 HRV\WVPDVRFLDWBZWK **Ceratium blooms**

**De-oxygenation**

**2006/07**

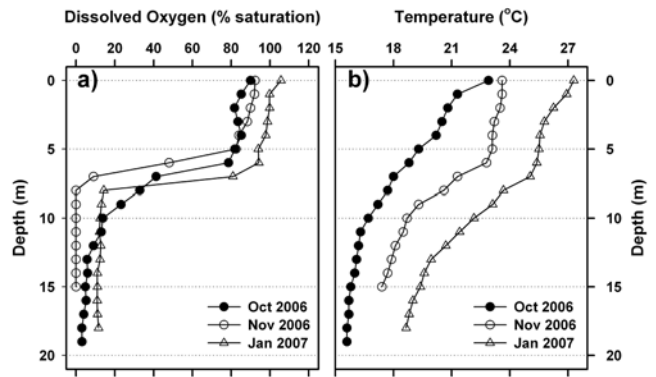
(Station 19) in 3 successive months during 2006/2007 are shown in Fig. 13a. During the *Ceratium* bloom in October, severe and rapid de-oxygenation was evident below 5 m, leading to complete anoxia below 8 m by early November. Some recovery (re-oxygenation) of deep-water was evident in late 1RYPEHSURQHRWVKRQLQJXUZWKIXUWKHUHYH\ E\DXDU)LJD:KLOWKRIQSURQHQ2FWREH0V SRRUOFRQFRUGDQWZWKWKHRQFXUUHWKHPDOSURQKLFK ODFNHDQVKDUSYHWLFDOWUDQVLWLRQVXEV\XQWR\QSRU QMPPRUHURDGOFRQFRUGDQWZWKWKHPDOFRQGLWLRQV (Fig. 13b).

While confounded by inter- and intra-annual variability, a relatively shallow onset and severity of dissolved oxygen depletion with depth was evident in October 2006 – relative to FRPSDUDEOEFWREHSURQMLQRWKHEUV)LJD6LQFR HXLYDOQWOZGHLVSDULWHVWVLQWKHRUUMSRQGLQSRWPHQLVUAWHLQELRPDVP SURQMLJEWKRIQGSOWLRQREVHYHLQLV most plausibly related to metabolic activity associated with the *Ceratium* bloom.

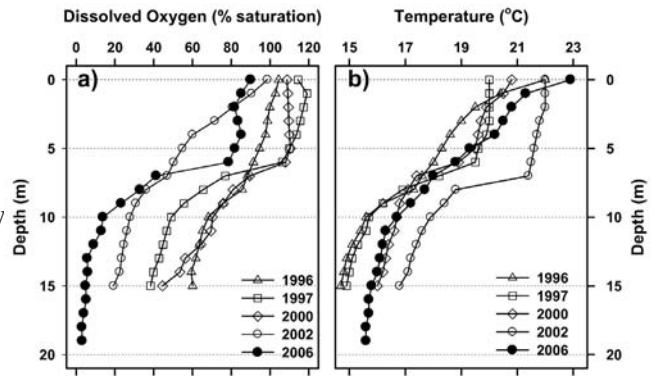
**Zooplankton abundance and community structure**

**2006/07**

palpable differences in zooplankton abundance and composi-



**Figure 13**  
 Temporal changes in vertical profiles of a) dissolved oxygen and b) temperature at Site 19 during the bloom event reported here.



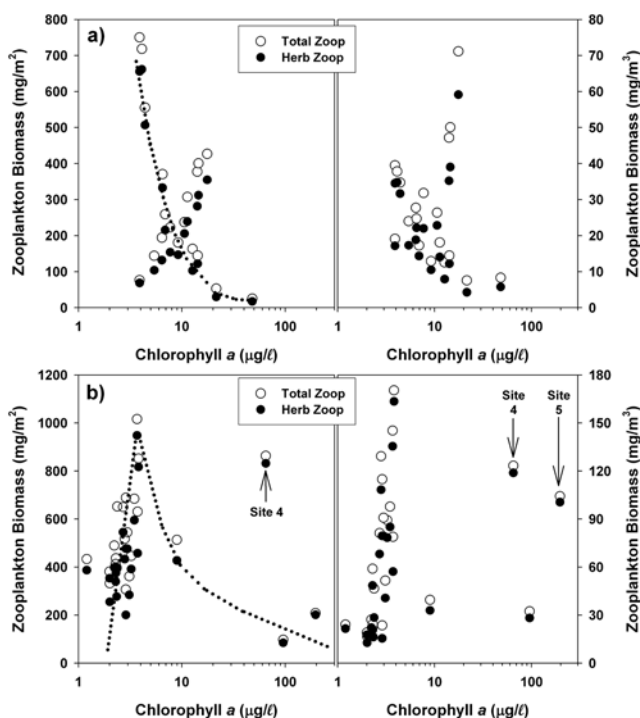
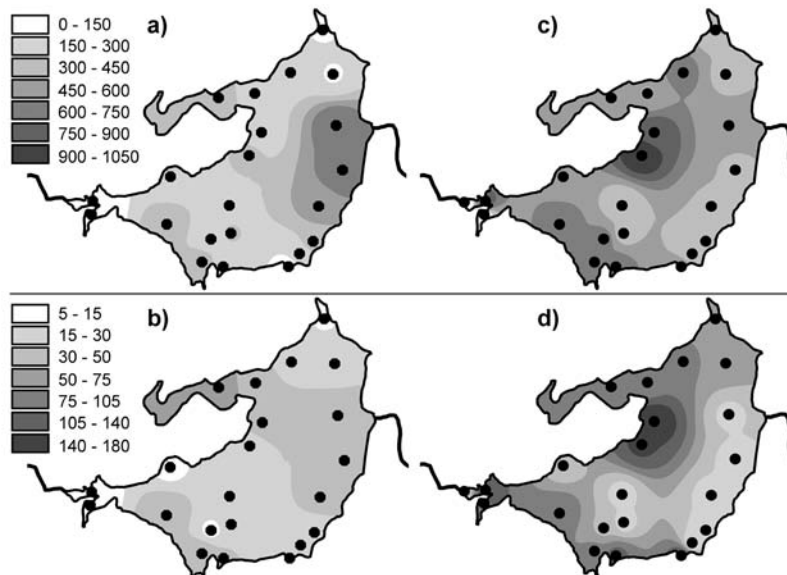
**Figure 14**  
 Comparative vertical profiles of dissolved oxygen saturation levels (a) and temperature (b) in October of various years at the same or comparable open-water site in Albert Falls Dam. The severity of oxygen depletion during the bloom in 2006 is largely unrelated to annual differences in thermal profiles – notably so in 1997 and 2002. Previous profiles recorded by Hart (2001; 2004; 2006) and unpublished.

tion were evident between the present synoptic surveys and FRQLQXRXVWQGHVWXGLMEWZDQG+DUW 2000; 2001; 2004). We start with an overview of whole-lake zooplankton biomass distribution patterns during the synoptic VXUYMKLKFQRQWVXDOODVVLVWVWKMXEVHXQWGMFULSWL and evaluations of inter-annual differences.

6SDWLDOYDULDWLRQLQELRPDVP

zooplankton biomass varied considerably over the lake during the synoptic surveys in October and January (Fig. 15), with up to 10-fold spatial variation evident in terms of biomass per unit area (Figs. 15a and c) and per unit volume (Figs. 15b and d). In October, biomass/m<sup>2</sup> (Fig. 15a) increased generally from west to east, in contrast to the converse decline in chlorophyll (Fig. 3a) and *Ceratium* abundance. A broadly similar pattern from values elevated by shallow water depth on the south-western shore, and in the north-western embayment (Fig. 15b). In January, zooplankton abundance (as mg/m<sup>2</sup> and mg/m<sup>3</sup>) generally increased from east to west, with highest values occurring off the north-western peninsula-like intrusion into the lake (Figs. 15c and d), and ZWKJUBWQWMDWBYDOXMLQWKQHLQLQZQFRQWUDVWWR (October), broadly in line with elevated chlorophyll levels there

**Figure 15**  
Lake-wide distribution of total zooplankton biomass in Albert Falls Dam in October 2006 (a, b) and January 2007 (c, d). Biomass as  $\text{mg}/\text{m}^2$  in panels a) and c), and as  $\text{mg}/\text{m}^3$  in panels b) and d). Sampling points correspond with those numbered in Fig. 1.



**Figure 16**

Lake-wide zooplankton-chlorophyll relationships in Albert Falls a) in October and b) in January, in biomass per unit area (left) and per unit volume (right). Dotted lines (fitted by eye) show general patterns for herbivores. Arrows identify apparently deviant or anomalous data at Sites 4 and 5 in January (see text).

(Fig. 3b).

The overall relationships between zooplankton abundance and chlorophyll are more transparent in simple scatter plots of total and herbivorous zooplankton biomass above chlorophyll levels of around 3 to 4  $\mu\text{g}/\text{l}$ , which we ascribe to a depressive or inhibitory effect of *Ceratium* on zooplankton (see below). Two apparently anomalous cases of elevated biomass at high chlorophyll levels are evident (and arrowed) in Fig. 16b. The

of its species composition. Abundance here was bolstered by *Bosmina*, *Diaphanosoma* and calanoid copepodites, taxa that are relatively immune to feeding disruption by large particles, and which were present here at respective densities of 5.3, 2.8 and 3.0 times the concurrent lake average. Site 5 lies in an embayment within a distinct sub-catchment somewhat isolated from the main hydraulic axis of the dam, and accordingly biomass (as  $\text{mg}/\text{m}^3$ ) is here exaggerated by very shallow water depth (2 m); densities of most taxa were barely 10 to 20% of the lake average, only *Diaphanosoma* being marginally higher than average.

synoptic surveys was lower on average than the multiyear average values determined (at Site A) in corresponding months between 1989 and 1998 (Table 2). Conversely, however, a fairer comparison using only DOWS values suggests that zooplankton was comparably or more abundant in October 2006 and less abundant in January 2007 than the corresponding long-term averages. The (marginally) elevated zooplankton biomass values in October 2006 must be seen in the context of low density suggested above.

Exclusion of drought years of high mineral turbidity, which is well-known to constrain daphniid zooplankton especially

**TABLE 2**

	<i>Ceratium</i> blooms	
	2006	2007
9 yr average (Site A)	566	749
7 yr average (Site A, excluding drought years)	623	768
Synoptic survey – DOWS	675	453
Synoptic survey – all sites	287	518

**TABLE 3**

	LWUJ		26	All sites	28	
22%	U	U			DR	
<i>Daphnia</i>	35 568 ± 46	40 474 ± 36	51 758 ± 17	16 526 ± 97	1.28	+
<i>Ceriodaphnia</i>	0	0	0	0		a
<i>Bosmina</i>	45 ± 300	58 ± 265	1 188 ± 65	1 948 ± 102	20.48	+++
<i>Diaphanosoma</i>	23 ± 300	0	0	0		a
<i>Moina</i>	258 ± 300	0	0	0		a
Calanoids	6 585 ± 70	6 375 ± 77	6 448 ± 36	6 915 ± 71	1.01	a
Cyclopoids	79 268 ± 52	87 760 ± 47	131 685 ± 20	95 312 ± 53	1.50	+
<i>Chaoborus</i>	1 106 ± 83	1 245 ± 76	1 867 ± 16	1 782 ± 89	1.51	+
Total/m <sup>2</sup>	122 853 ± 46	135 912 ± 42	192 945 ± 18	122 483 ± 50	1.42	+
-\$85<						
<i>Daphnia</i>	16 780 ± 97	18 656 ± 93	85 ± 173	69 ± 257	0.005	a/RVW
<i>Ceriodaphnia</i>	23 780 ± 199	30 537 ± 172	15 782 ± 17	14 463 ± 122	0.52	--
<i>Bosmina</i>	0	0	7 297 ± 30	9 164 ± 117	'	New
<i>Diaphanosoma</i>	40 435 ± 136	23 715 ± 69	35 042 ± 16	45 934 ± 56	1.48	+
<i>Moina</i>	6 851 ± 240	1 079 ± 122	0	0	0.00	Lost
Calanoid copepods	10 813 ± 60	11 872 ± 55	34 279 ± 10	40 068 ± 90	2.89	++
Cyclopoid copepods	125 458 ± 62	133 059 ± 60	102 158 ± 7	134 111 ± 53	0.77	-
<i>Chaoborus</i>	1 439 ± 54	1 419 ± 42	2 036 ± 76	3 031 ± 94	1.43	+
Total/m <sup>2</sup>	225 557 ± 54	220 338 ± 48	196 679 ± 3	246 840 ± 38	0.89	-

9-year average values in Table 2. For the 7-year averages, values for 1993 and 1995 with corresponding Secchi depths of 30 and 15 cm, were excluded from the October calculations; for January, values for 1993 and 1994 (Secchi depths of 75 and 40 cm), were excluded. Congruent Secchi depth values in other years ranged from 100 to 280 cm.

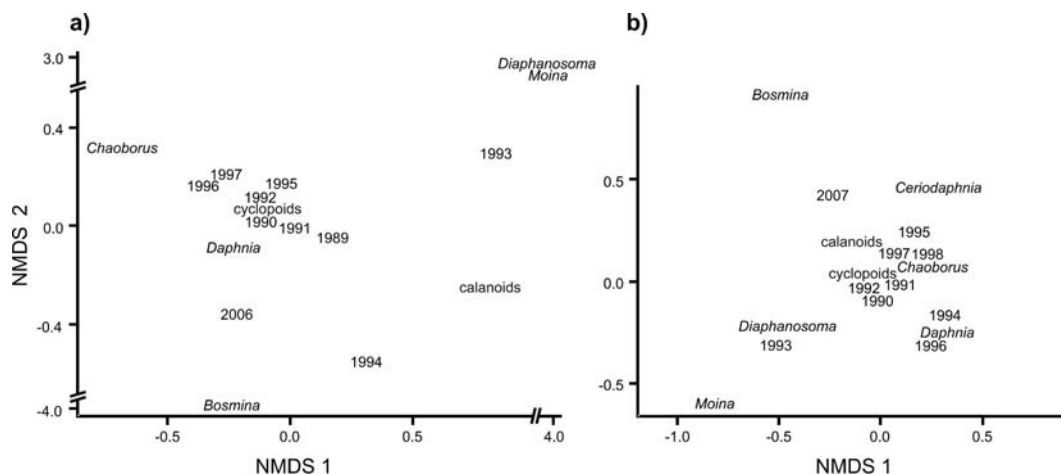
,QWHDQXDOYDULDWLRQLQRSODQNWRQFRPPXQLWFRPSRVLWLRQ

Table 3 summarises comparative data on zooplankton abundance and composition during the synoptic surveys (for the entire lake as well as for DOWS), with temporally congruent

historical records at Site A. The DOWS subset is compared ZWKKLWVRULFDOGDWDIRU6LWHLQ106RUGLQDWLRQV)LJ the low stress values of which (0.05 and 0.03 for Figs. 17a and 17b, respectively) indicate that most of the year-to-year variation is accounted for. Table 3 and Fig. 17 should be considered together.

The relative distance between years in the ordinations UHWVVLPLODULWLQFRPPXQLWFRPSRVLWLRQ%RWKLQ2FWREH (Fig. 17a) and in January (Fig. 17b), the community in 2006/07 was highly distinct from the communities of previous years; only during the January 1993 to January 1994 drought (and inexplicably in the post-drought January 1996, when a Secchi depth of 110 cm still indicated relatively high turbidity) was the community as distinct as the 2006/07 community was from

**Figure 17**  
Non-metric multi-dimensional scaling representations of year-to-year variation in Albert Falls zooplankton community composition in October (a) and January (b) at DOWS (2006/2007) and Site A (1989-1998), based on numbers/m<sup>2</sup> of each taxon.







The emergence of *Ceratium* at bloom densities results in a YDULWRIXQGMUDEOHRQVHXQFMUDQJLQJIURPLWVQNHKLGHWRXQGHWDNWKHQLWLDQHGVDPSOLQJLQ2FWREHVDQFMDOXHQFORJLQJWHSXULFDWLRQQWHVVKURMHIKVERPVED the existence of a *Ceratium*EORRP-XWLQDWYDULRXVLPDFWVRQDIIFWHDTXDWLFRVWVHV:LWKSHEUIn the January 2007 lake survey. Umgeni Water, the to the latter, the observed re-structuring of zooplankton composition accompanying or associated with its appearance provided access to and permission to use their historical UHRUGVRIDWHTXDOLWQXWULQWVDQGDQJMSHLDOWKDNVU6WMPHUIRUUMROYLQJYDULRXVTXHLMUHDUGLQJWKMMH the reduction or loss of large-bodied *Daphnia* in particular raw data, and for supplying GIS base layers. The chlorophyll-UHFXMQDWXUDQWUDWLRQUDWMRWKHPDQWHPHSURQLQJXRURSUREMSHWURXRURPWHDVNLQGOORDQHE\ some natural controls on algal proliferation. It also reduces 3URISQR3HLVVLQRWWR8.=1XUEDQDFPSXV IRRGUMRXUFMIRUMYQLOMKWKDWLQWXUQVHYHVIRRGIRU

10DQDJHQWSURVSHWVIRUPLWLJDWLRQ

%DVHRQWKBERYHGWLFDWLRQRIVKDUSOULVLQJ73FRQ and decline of water blooms. *Acta Hydrobiol.* **34** 139-155.

(based on NO<sub>3</sub>-N:TP values) as contributory or causal factors plankton food limitation across gradients of depth and productivity FHWUDWLRQVLQLQADWHVZWKDVVRFLDWHRH13UDWIMV DE EYTO E (2001) *Chydorus sphaericus* as a biological indicator of DWHTXDOLWLQODNM. *Int. Ver. Limnol.* **27** 3358-3362. inference that this change in nutrient stoichiometry arises from increasing P loading from the local WWT plant, it seems certain that bloom formation can be reduced, if not avoided, by WHQVIRUWKSDQNRWQLFLQRHODWHLHirundinella in a LPSURYHFRPSOLDQFZWK.:7HXQWVWDQGDUGVDQGDVVRFI eutrophic lake. *Freshwater Biol.* **14** 401-421. DWHUBHVHDQDJHQW2SHDWLRQDQGLQFLMLQ.:7 SODQWPDQDJHQWQGTXDOLWFRQWUROKDYHJZGHSXEORBORBÉLY G (2003) Deep chlorophyll maximum by *Ceratium* FRUUHWLYHVVXUMWRPDLQWDLQVSHLHXQWVWDQGDUGQ evaluation of contributory factors. *Verh. Int. Ver. Limnol.* **27** 1933-1939. cised as an increasing national problem in recent press articles and an extensive 'grey literature'. The following excerpt from DQXURUWEQXQLNSDUDSKUDVMWKHUREOH updated record and evaluation of occurrence and periodicity of *Tropodiatomus spectabilis* and *Metadiatomus meridianus* (Cope- 'Since 2004 a spate of surveys and technical papers have noted that up to 70 percent of municipal waste-treatment works face collapse for lack of proper maintenance and extension, while around a third require "immediate intervention" and another third intervention "within the short to medium term".' Apart from routine operational problems, WWT facilities also face increasing loads, commonly exceeding their design capacity. 7KXVMQKHSUMFULEHIXQWVWDQGDUGVIPJ l resources on the development, survival and reproduction of the two P) are upheld by WWT plants, consideration of total discharge volumes is also necessary, given the explosive increase in residential units connected to individual sewerage reticula- WLRQQWZUNV.PSOHQWDWLRQRIDQGDGKHQFWRVSHLH5.5 & RPSDUDWLYHQRJWHPSHLRGLFLWRI Diaphano- WRWDOQXWULQWORDGLQJOLPLVVLVFOBUOUHXLUHLQDQGLWLRQDQDFHYDPPDWHLPSRPHQVZWBQ turbid reservoir. *Freshwater Biol.* **19** 123-139. FRUUHWLYHVVXUMWRPDLQWDLQVSHLHXQWVWDQGDUGQ evaluation of contributory factors. *Verh. Int. Ver. Limnol.* **27** 1933-1939. such standards need also to be upgraded to more stringent levels. These various corrective measures need urgent attention if the rampant pollution spiral is to be halted, and preferably reversed, in Albert Falls as in other strategically crucial reser- +\$75&7ZFDODQRLGVWZKODNMDQGDGHDGRUWZQ updated record and evaluation of occurrence and periodicity of *Tropodiatomus spectabilis* and *Metadiatomus meridianus* (Cope- voirs. Our observations lend unambiguous support to the need DOVRIRUDMGLFLRXVDSURDFKWRKXPDQSRXSODWLRQSPQXVDBQRQHDQSHLRGLFLWSDWWHQVLQUBDWLRQWR selected environmental factors in two cascading warm-water reser- WKOLGPDUFDFWFKPWLQFOXGLQJSURSRSVHKRXVLQJGMORS voirs over a decade. *Hydrobiol.* **526** 99-117. PHWVXFKFDV.KDHLVKD+ROO;RRG

FNQRZHEJPQWV

7KLVLYQMWLJDWLRQDQVWVLPXODWHEHGFHXUMMURQYHJ 2 weekends for students enrolled in the Ecosystem Ecol- RJDQGDQDJHQWFRXUVHFRORJDWWKBLQYHVLW\ RI.D=XOXIDWDO8.=1LQ6DUDK%DWVHIDWDVVM %XVKQMMWHDQLWJHDOG7HUFHLYHVDJH Thembeke Nxele, Tracy Odendaal, Gail Potgieter, Wade

Shrives, Jade Tegg, Kate Watts, Amy Wilson and Peter Wragg

U6WMPHUIRUUMROYLQJYDULRXVTXHLMUHDUGLQJWKMMH raw data, and for supplying GIS base layers. The chlorophyll-3URISQR3HLVVLQRWWR8.=1XUEDQDFPSXV

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ER C (2004) Living with Constraints – Food Quality Effects on =RRSODQNWRQ3KLVVHWDWLRQ8QLYHVLWRLH\*HPDQ\ 115 pp. %5\$)=HLQJVWUDWHLMRISODQNWRQLFFORSRLGVLQ lacustrine ecosystems. *J. Mar. Syst.* **15** 87-95. %8&.+DQG=85(.57URSKLFBHDWLRQVEWZSKWRDQG RRSODQNWRQLQDQGHHLPLQWLRQWKHVVSHWRIWKHURPDWLRQ and decline of water blooms. *Acta Hydrobiol.* **34** 139-155. plankton food limitation across gradients of depth and productivity LQVPPDOOVWUDWHLHODNMLimnol. *Ocea* **49** 1408-1416. DE EYTO E (2001) *Chydorus sphaericus* as a biological indicator of DWHTXDOLWLQODNM. *Int. Ver. Limnol.* **27** 3358-3362. )5(0321\*(SVVRQDOVHXQFFRIGLHGLVWULEXWLRQSDW - WHQVIRUWKSDQNRWQLFLQRHODWHLHirundinella in a eutrophic lake. *Freshwater Biol.* **14** 401-421. \*5,\*256=,.<.356%25.&6\*6&+,7&+(1&DQG BORBÉLY G (2003) Deep chlorophyll maximum by *Ceratium* hirundinella2000HHLKQVBOORRERZD U *Hydrobiol.* **506-509** 209-212. \* 52)0\$30 , BARON JS, BLETT T, GOLD AJ, \* 220\$, \* 81(5621/+ , / (9,1621%0 ,380(50\$ ,385+; PETERSON GD, LEROY POFF N, REJESKI DW, REYNOLDS JF, 7851(50\* , : (\$+(56.& and WIENS J (2006) Ecologi- cal thresholds: The key to successful environmental management RUDQLPSRUWDQWFRQFBSWZWKQRSUDFWLFDKODSSOLFWDWLRQ" 1-13. +\$6(10DQG6\$7(5%7KHQXQFRIIRRG resources on the development, survival and reproduction of the two cyclopoid copepods: *Cyclops vicinus* and *Mesocyclops leuckarti*. *J. Plankton Res.* **17** 631-646. +\$75&=RRSODQNWRQIHLLQJUDWMLQUHDWLRQWRVXVSHQGH VBLPQWFRQWQWSRWQWLDOLQXQFMQRFRPPXQLWVWUXFWXUHQ turbid reservoir. *Freshwater Biol.* **19** 123-139. +\$75&RPSDUDWLYHQRJWHPSHLRGLFLWRI Diaphano- DQGLWLRQDQDFHYDPPDWHLPSRPHQVZWBQ evaluation of contributory factors. *Verh. Int. Ver. Limnol.* **27** 1933-1939. +\$75&7ZFDODQRLGVWZKODNMDQGDGHDGRUWZQ updated record and evaluation of occurrence and periodicity of *Tropodiatomus spectabilis* and *Metadiatomus meridianus* (Cope- poda: Calanoida), and alternative stable states in two cascading impoundments. *Hydrobiol.* **453** 269-283. +\$75&3KWRSDQNRWQGDPLFVDQGSHLRGLFLWQLQWZ cascading warm-water reservoirs from 1989 to 1997 – taxonomic and functional (C-S-R) patterns, and determining factors. *Water SA* **32** (1) 81-92. +\$(=6.7ZSRUDODQGVSDWLDQGLVWULEXWLRQRWIKHLQRHJ ellate *Ceratium hirundinella*2000HHLKQVBOORRERZD lake. *Freshwater Biol.* **6** 531-542. +\$(=6.DQG)851667/DERUDWRU\PRGHVIRIGLH YHWLFDOPJUDWLRQLQWKHLQRHJHODWHEeratium.hirundinella *Freshwater Biol.* **10** 163-170.

