

Phytoplankton dynamics and periodicity in two cascading warm-water reservoirs from 1989 to 1997 – taxonomic and functional (C-S-R) patterns, and determining factors

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Abstract

The composition and abundance of distinctive planktonic autotrophs (ca 60 taxa) were examined at roughly fortnightly intervals in two sizeable reservoirs (Midmar and Albert Falls) on the uMngeni River, KwaZulu-Natal, between 1989 and 1997. The dynamics of community structure and abundance were examined in both taxonomic and functional (C-S-R) terms in relation to physical abiotic variables (thermal stratification, light climate, water level) and biotic influences of predation (zooplankton abundance).

Annual periodicity was exhibited by most taxa apart from *Cryptomonas*, although patterns tended to be indistinct and inter-annual repeatability was generally weak – in line with year-to-year and between-system environmental variability. Water level fluctuation, with concomitant change in stratification intensity and hydraulic mixing and accompanying changes in water clarity associated with suspended sediment levels was clearly a major (direct and indirect) determinant of phytoplankton composition and abundance. The influence of top-down controls as inferred from phytoplankton-zooplankton relationships was fundamentally different in the two reservoirs – potentially stimulatory in Midmar, but clearly regulatory in Albert Falls, where episodic collapses of *Daphnia* populations resulted in chlorophyll values well into the eutrophic level range. In addition to annual patterns, changes in chlorophyll content implied progressive long-term changes in trophic status, especially in Albert Falls, with the emergence of various ‘new’ taxa (and/or higher peak densities of others).

Consideration of phytoplankton dynamics in terms of functional groups offers certain advantages over conventional phyletic taxonomic analyses, although algal response forecasting by either approach appears potentially constrained by hydrological variability. Site-specific bio-monitoring, possibly using new rapid technologies, is likely to be necessary for ongoing management purposes until predictive capabilities under regionally characteristic conditions improve. Despite limitations, functional classification proffers faster advances to this end than conventional taxonomic appraisal.

Keywords: algae, plankton, dynamics, community assemblage, reservoir limnology, water quality, bio-monitoring

Introduction

By virtue of high taxonomic diversity, and rapid response of most of its constituent members to environmental actuators and drivers (nutrients, light, temperature, turbulence, and pollutants), phytoplankton (in its collective sense of all planktonic autotrophs including cyanobacteria) has become widely recognised as a reliable ‘bio-indicator’ of water quality for a variety of purposes (Dubelaar et al., 2004). Man-made lakes (river-impoundments or river-reservoirs, colloquially referred to as “Dams”) are the predominant source of freshwater for all uses (irrigation, industry, etc.), including human consumption (drinking water) in South Africa (DWA 1986). Despite this, little information exists concerning the composition and periodicity of their phytoplankton (Allanson et al., 1990). Investigations into this topic in South Africa commenced on natural coastal lakes – the pristine L. Sibaya (Hart and Hart, 1977), and subsequently Princess Vlei, an anthropogenically perturbed system (Harding, 1992). Studies published on this collective topic for South African reservoirs have been limited in number and/or temporal extent. These mostly involve ‘extreme’ environments

such as the hypertrophic Hartbeespoort Dam (NIWR, 1985; Chutter and Roussouw, 1992), the eutrophic Roodeplaat Dam (Pieterse and Röhrbeck, 1990) and Loch Lomond (Vos and Roos, 2005), as well as certain water-bodies with high sediment turbidity – Lake le Roux (Allanson and Jackson, 1983) and Spioenkop (Hart, 1999). Extended algal studies of planktonic algae in the slow-flowing Vaal River Barrage have also involved eutrophic waters with elevated salinity (Roos and Pieterse, 1996; Pieterse and Janse van Vuuren, 1997). General concerns regarding water quality in SA impoundments have been largely subsumed in determinations of chlorophyll content – an integral measure of autotroph abundance – rather than in systematic analyses of its constituent members. Substantial regional databases containing such information exist (e.g. Graham et al., 1998) but appear not to have been interrogated regarding intrinsic temporal detail.

Water treatment costs and protocols are well known to vary according to its constituent suspended particles – biogenic autotrophs, and, commonly in South Africa – suspended mineral sediments. These attributes influence the filtration efficiency and capacity of water treatment plants, and may impose the need to combat objectionable tastes and odours (e.g. Graham et al., 1998; Barrell et al., 2004). Internationally, there is increasing prominence and concern about the growing and almost ubiquitous presence of toxins including geosmin, microcystin and cylindrospermopsin derived from cyanophytes (Baker et al., 1994; Shaw et al., 1999; Steffensen et al., 1999; Frank and

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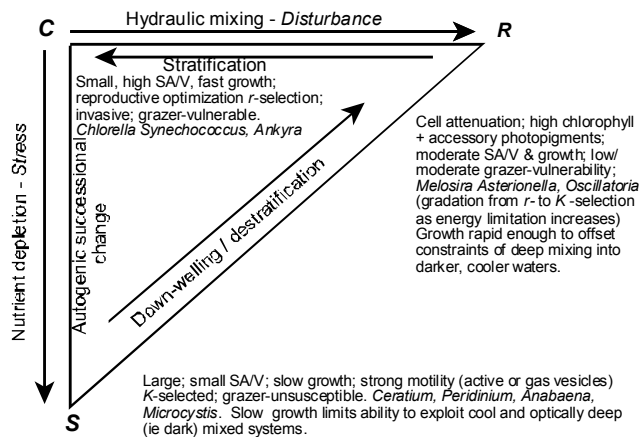


Figure 1
Graphical representation of the C-S-R functional concept as applicable to phytoplankton (after Reynolds, 1996)

Wolf, 2002). “The tiny cyanobacteria, being a geological force in the dynamics of the globe, will continually become more central to the modern world and be applied more closely, affecting our lives” (Skulberg, 2005). With growing awareness of the increasing socio-economic risks posed by toxic algae and Harmful Algal Blooms (HAB) to aquatic organisms, human health (Falconer and Humpage, 1996, 2001) and aquatic environments (Fitzgerald et al., 1999), the acronym HAB has become a contextually familiar term in water management circles (e.g. Hallegraeff, 1993; Anderson et al., 2002; Hoagland et al., 2002). Overall, predictive understanding of temporal changes in composition and abundance of phytoplankton is accordingly a valuable tool in water resource management.

Here, seasonal changes in phytoplankton in two cascading reservoirs are reported, and the concordance of observed changes in broad taxonomic composition with the theoretical constructs embraced in the C-S-R functional models of pelagic vegetation is explored (Reynolds, 1996; 1997; 1999). Periodicity patterns in these non-eutrophic monomictic systems are documented and examined to expand locally relevant ecological information on phytoplankton under conditions of contrasting stratification intensity and during different phases of hydrological regime (flood, drought). The value of functional C-S-R monitoring to monitoring is explored as a general alternative to specialist systematic analyses, potentially opening prospects for submersible FluoroProbe technology and/or flow cytometry (Dubelaar et al., 2004; See et al., 2005) as shortcuts to routine phytoplankton categorisation.

Conceptual framework

Building on a framework established for terrestrial plants (Grime, 1979), the seminal work of Reynolds (1984; 1996; 1997) has led to the common recognition today of three classes of planktonic autotrophs (Fig. 1), namely – the competitive Colonist (C), the acquisitive Stress tolerant (S) and the disturbance-tolerant or attuning Ruderal (R) elements, the respective morphologies, physiologies and ‘behaviours’ of which accord with these respective life-styles, and appositely, with his initials – Colin Stanley Reynolds. These classes are positional apices of a triangular space matrix (Fig. 1) whose primary axes reflect energy availability, resource availability, and disturbance. However, classes are not necessarily discrete or exclusive. Rather, species show adaptive and evolutionary trends that bias their performances

towards one or other of the primary strategies, within which gradations and intermediates exist. Taxa can occupy the apices themselves (C, R or S), or range between the C and R (C-R), the C and S (C-S) or the S and R (S-R) apices (Fig. 1), depending on their adaptability to and selection by the controlling influences of temporal changes in resource and/or energy availability.

Midmar and Albert Falls Dams, the study sites for this investigation (see below) differ in stratification intensity and susceptibility to hydraulic disturbance, while inter-annual differences in suspended sediment loadings and variations in water depth impart additional dimensions of variability. All these factors serve to create a variable habitat template (Southwood, 1977) against which to examine and test the veracity of the C-S-R functional model (Reynolds, loc cit). The predictions amenable to comparative testing within and between these reservoirs include the following:

- Relatively more of the community will consist (both intra- and inter-annually) of ruderals in Midmar than in Albert Falls
- Stress tolerators will contribute relatively more to the community in Albert Falls than in Midmar
- In both lakes, ruderals will assume greater relative importance during drought conditions of lowered water-level (higher suspended sediment contents, and reduced stratification intensity) than during high water levels
- Within each lake, an inverse relationship will exist between the abundance of grazing zooplankton and small (colonist) phytoplankton taxa, while the abundance of large (stress-tolerant) autotrophs will either be unrelated or directly related to the abundance of grazing zooplankton.

It was additionally expected that the resolution of confounding influences of nutrient limitation imposed by reservoir trophic status per se (i.e. extrinsic consequence of general reservoir nutrient status) as opposed to limitation associated with stratification (i.e. intrinsic temporal effects within a reservoir) might be assisted by the comparative study. On this basis it can be premised that:

- Stress-tolerant taxa will either be more abundant:
 - In Midmar than Albert Falls (if lower extrinsic nutrient level is the principal selective influence);
 - In Albert Falls than Midmar (if selection principally reflects the intrinsic limitation imposed by stratification); or
 - Will make quasi comparable contributions to assemblages in both reservoirs (if the distinction between intrinsic and extrinsic factors is blurred or confounded).

Materials and methods

Study sites

Midmar (MID) and Albert Falls (ALF) are two consecutive reservoirs on the upper uMngeni River, in KwaZulu-Natal (Fig. 2). Their comparative morphometry at full supply level (FSL) and relevant biophysical information is compared in Table 1. The most salient differences relate to reservoir age (MID>ALF), elevation (MID>ALF), catchment area and lake surface area (ALF>MID), volume (ALF>MID) and theoretical flushing times (ALF>MID); conversely, mean depths are remarkably similar. Largely as a result of differences in physiographic elevation, water temperatures of Albert Falls are consistently warmer than Midmar by around 1.8 to 2.0°C (Hart, 1994; 2000), with resultant increases in stratification intensity and relative physical

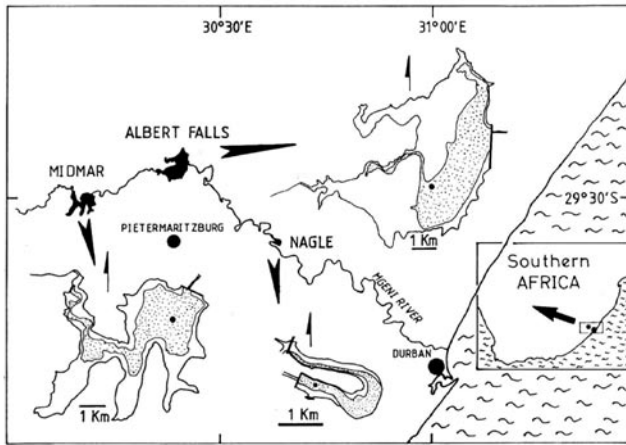


Figure 2

Location and outline maps of the study reservoirs, showing routine sampling sites (●) in relation to general bathymetry. Water deeper than 13.5 m is stippled.

stability (Hart, 2001;2004). A comparative summary of variables for these lakes listed by Graham et al. (1998) includes useful chemical information.

Sampling

Routine sampling was undertaken at a single deep-water offshore site broadly representative of each lake's open waters (29°30'S, 30°12'E on Midmar, and 29°26'S, 30°26'E on Albert Falls) at roughly fortnightly intervals from mid-1989 to mid-1998. Sampling generally took place between 10:00 and 14:00. Vertical profiles of temperature and dissolved oxygen were measured with an air-calibrated YSI model 58 electronic meter. Secchi depth transparency (SD) was measured using a white disk of 250 mm diameter. Vertical profiles of radiation at appropriate depth intervals were made with a Lambda model LI 188B radiometer to yield measures of underwater attenuation of light (PAR; 400–700 nm). Spectral characteristics were determined intermittently using selective red (540–750, midpoint 670 nm), green (470–690, midpoint 550 nm) and blue (370–510, midpoint 443 nm) Jena-Schott filters to identify the most penetrating component (K_{mpc}). Downwelling attenuation coefficients ($K_d \cdot m^{-1}$) were determined as:

$$K_d = \frac{\ln I_0 - \ln I_z}{z}$$

where:

- I_0 = light intensity at depth 0 m
- I_z = light intensity at depth z m
- z = depth interval between measured values.

Integral water samples of the uppermost 3 m were collected in a tube sampler (Zohary and Ashton, 1985) at a single offshore deep-water site in each lake (see Hart, 1992). After shaking to homogenise it, the sample was decanted into a freshly washed opaque 2 l plastic container, and a new 50 ml plastic bottle for subsequent chlorophyll extraction and phytoplankton analysis, respectively. The smaller bottle was fixed on site with 1.0 ml Lugol's solution; the larger was stored in the dark in an insulated 'cold-box'.

Sample analyses

Chlorophyll content was determined by vacuum filtration generally of 1 000 ml of the hose-pipe sample through glass fibre filter pads (GF/C) within 3h of collection. Filter pads were immediately immersed in 95% methanol and stored in the dark. Chlorophyll was extracted by boiling, and spectrophotometric measurements of optical absorbance (E) of the extract were made at 665 and 750 nm in a 40 mm light path after centrifugation. Chlorophyll concentration ($\mu g \cdot l^{-1}$) was determined, disregarding degradation products as:

$$\text{Chlorophyll } a = \frac{13.9 \times 8.9 \times (E_{665} - E_{750}) \times v}{V \times l}$$

where:

- v = volume of solvent (ml)
- V = volume of sample filtered (l)
- l = photometric light-path length (mm).

Phytoplankton abundance and composition was determined using conventional (Ütermohl) inverted microscopy (Lund et al., 1958). Sample aliquots of 10 ml were left overnight for particle sedimentation, and thereafter successive transects were examined microscopically at 400X until at least 200 'units', or roughly 100 'units' of the numerically dominant taxon on each sample date had been counted. 'Units' comprised individual uni-cells, filaments and other colony types as applicable, with no routine distinction of colony size within a taxon, although subjective rankings of colony size were noted. Taxa were routinely identified to generic level, and further distinguished to (unnamed) morpho-species level. Additionally, on the basis of published data and/or morphological inference they were assigned to an appropriate functional class – C, S or R (Reynolds, 1996; 1997), as detailed in Table 2 (modified from Hart (1996) after Reynolds, 2005). Counts were translated into density estimates of cells and colonies, per ml. No correction was made for counting biases associated with the obscuring influence (especially on smaller taxa) of variable levels of mineral turbidity, which was high on some sampling dates. Some 60 taxa were recorded during the study. Only the more frequently present and/or abundant taxa are considered in the following account. Taxa were selected for consideration on the basis of an "inclusion threshold" index, calculated as the product of their percentage occurrence and mean density m^{-1} on all 183 sampling dates. Across all taxa, this

Attribute:	Reservoir	
	Midmar	Albert Falls
Latitude and Longitude	29°30'S 30°12'E	29°26'S 30°25'E
Year of impoundment	1964	1976
Catchment area (km ²)	928	728
Altitude (m amsl)	1 044	656
Surface area at full supply (ha)	1 559	2 385
Mean depth at full supply (m)	11.4	12.3
Maximum depth at full supply (m)	22.3	24.6
Storage capacity at full supply (10 ⁶ m ³)	177.2	293.6
Theoretical mean water retention time (d)	318/367*	562/512*

Ruderals (R)	Colonists (C)	Stress tolerators (S)
<i>Cyclotella</i>	<i>Ankistrodesmus</i>	(C↔S) <i>Anabaena</i>
<i>Aulacoseira</i>	<i>Closteriopsis</i>	(C↔S) <i>Merismopedia</i>
<i>Fragilaria</i>	<i>Crucigena</i>	<i>Microcystis</i>
<i>Tabellaria</i>	<i>Shröderia</i>	<i>Nodularia</i>
<i>Closterium</i>	<i>Tetraëdron</i>	<i>Ceratium</i>
<i>Cosmarium</i>	<i>Oocystis</i> (C↔S)	<i>Peridinium</i>
<i>Staurastrum</i>	(R↔C) <i>Arthrospira</i>	<i>Trachelomonas</i>
	(R↔C) <i>Coelastrum</i>	
	(R↔C) <i>Scenedesmus</i>	
	(R↔C) <i>Cryptomonas</i> (C↔S)	

index averaged 1 656 in MID (range of 4 to 18 150), and 2 297 (1 to 24 927) in ALB. An arbitrary cut-off threshold value of 50 for this index was applied to all taxa other than *Ceratium* and *Peridinium*.

Detailed enumeration of zooplankton collected in vertical net hauls was undertaken as described elsewhere (Hart, 2001, 2004). For the present study, counts were converted to estimates of biomass ($\text{mg} \cdot \text{m}^{-2}$ DW) using the following coefficients: *Daphnia pulex* and *D. longispina* – individuals collectively assigned 35% of the date-specific mean biomass values of egg-bearing females, computed as $1.51 + 2.76 \ln L$ (where L = body length, mm); *D. laevis* – $7.5 \mu\text{g} \cdot \text{ind}^{-1}$; *Ceriodaphnia*, *Diaphanosoma* and *Moina* – $2.5 \mu\text{g} \cdot \text{ind}^{-1}$; rotifers – $0.1 \mu\text{g} \cdot \text{ind}^{-1}$; nauplii, ovigerous female and other life stages of cyclopoid copepods – 0.25, 2 and $1 \mu\text{g} \cdot \text{ind}^{-1}$; nauplii, C1-C3, C4-C5, adult male and adult female stages of calanoid copepods – 1, 3.7, 5.9, 10 and $20 \mu\text{g} \cdot \text{ind}^{-1}$. As obligate predators, *Chaoborus* larvae were excluded from the zooplankton biomass calculation.

Data analysis

Conventional parametric and non-parametric statistical tests (Zar, 1984; Quinn and Keough, 2002) were made using SPSS11.5 for Windows. Graphs were compiled using SigmaPlot V9.

Results and discussion

Thermal, hydrological and optical background conditions

Clear cyclical seasonal changes in water temperature and thermal stratification were evident in both lakes (Fig. 3a), with some additional inter-annual variability in thermal conditions understandably associated with hydrology (Fig. 3b). Between-lake

differences in annual temperature range, and stratification intensity are consistent with differences in lake elevation and wind-shelter aspect; ALF was consistently warmer, and showed stronger accompanying stratification than MID.

Water transparency varied considerably, as evidenced by the wide variations in Secchi depth visibility (Fig. 3b). Transparency varied seasonally, broadly in relation to thermal stratification events; autumnal overturn in particular, was mirrored in rapid reductions of Secchi depth. Water clarity also increased sharply following rising water levels after prolonged drought – partly owing to reduced sediment re-suspension in increasingly deep waters, and despite inflow-related sediment inputs (especially into MID, which effectively functions as a pre-impoundment for ALF downstream). Significant hydrological variability was evident during the study period, which commenced and terminated in ‘wet’ year phases effectively bracketing a prolonged ‘low water phase’, especially pronounced in ALF (Fig. 3b).

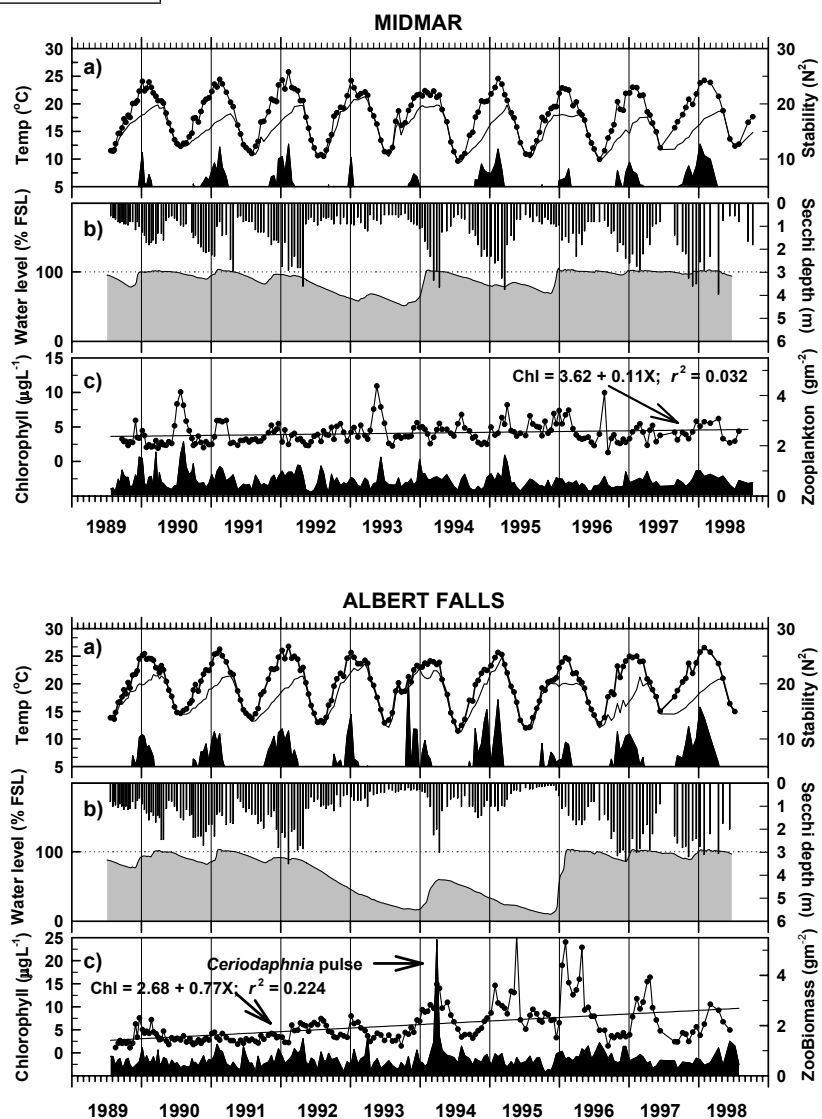


Figure 3

Synopsis of limnological conditions in Midmar and Albert Falls (upper and lower panels respectively) during the study period. a) Temporal changes in upper (1-5m mean) and bottom temperatures, with estimates of physical stability (N^2 , shaded plot); b) Secchi depth transparency in relation to water level; c) Chlorophyll concentrations (shaded plot, with overall temporal trend plotted as a linear regression, where X is years from start of study) and estimated zooplankton biomass.

		Midmar	Albert Falls
K_d PAR	Mean	1.383	1.954
	Median	1.341	1.345
	Max	2.715	13.253
	Min	0.464	0.517
	n	192	193
K_d RED		1.25	1.10
K_d GREEN	4 Sept 1991	1.53	1.29
K_d BLUE		2.72	2.07
K_d PAR		1.32	1.32

Variations in PAR attenuation coefficients were equally broad (summary values in Table 3). On various occasions that spectral characteristics were determined, red light was the most penetrating component in both reservoirs, followed by green and blue light. Spectral characteristics for MID during this study were comparable to those previously reported (Breen, 1983); no previous values for ALF are known. Deep penetration of red wavelengths is widely associated with the light-scattering effects of suspended clays (Kirk, 1983). The fact that red was also the most penetrating wavelength in this downstream reservoir was accordingly surprising, given MID's potential function as an upstream sedimentation basin. Rather, it indicates that sedimentation may instead be overwhelmed by re-suspension, a feature that likely pertained during the 'low water phase' conditions that occurred during much of the study (Fig. 3b).

Autotroph temporal dynamics – chlorophyll proxy

Changes in chlorophyll content in relation to selected abiotic factors, and potential grazer biomass, are reflected in Fig. 3c. While no clear long-term trend in chlorophyll content was evident in MID (Fig. 3c), linear regression analysis of mean annual values yielded an overall slight, but very significant positive slope with time (X, years from mid 1987): $\text{Chl } a = 3.62 + 0.11X$; $r^2 = 0.032$, $p = 0.012$. In contrast, a more distinct long-term increase occurred in ALF, for which a corresponding regression of $\text{Chl } a = 2.68 + 0.77X$; $r^2 = 0.224$, $p < 0.0001$ was obtained (Fig. 3c). Chlorophyll values reached eutrophic range levels during the middle of the study period. Intra-annual variation was evident in both lakes; in MID, chlorophyll peaks commonly occurred in mid-winter but timing of maxima showed rather weak periodicity in ALF.

Several peaks in zooplankton biomass roughly coincided with chlorophyll peaks, especially in MID in winter (Fig. 3c); closer scrutiny hints at a general lag of one sampling interval between these peaks (but see below). Pearson's direct and Spearman's rank correlations between chlorophyll and grazer zooplankton biomass were highly significant ($p \leq 0.001$) overall in both lakes, with respective r^2 and r_s values of 0.318 and 0.288 for MID, and 0.243 and 0.264 for ALF. Correlations with *Daphnia* biomass alone were inconsistent for MID (0.301 and 0.095^{ns}) but were both strongly negative for ALF (-0.207 and -0.369). Lagged correlations between total grazer or *Daphnia* biomass and

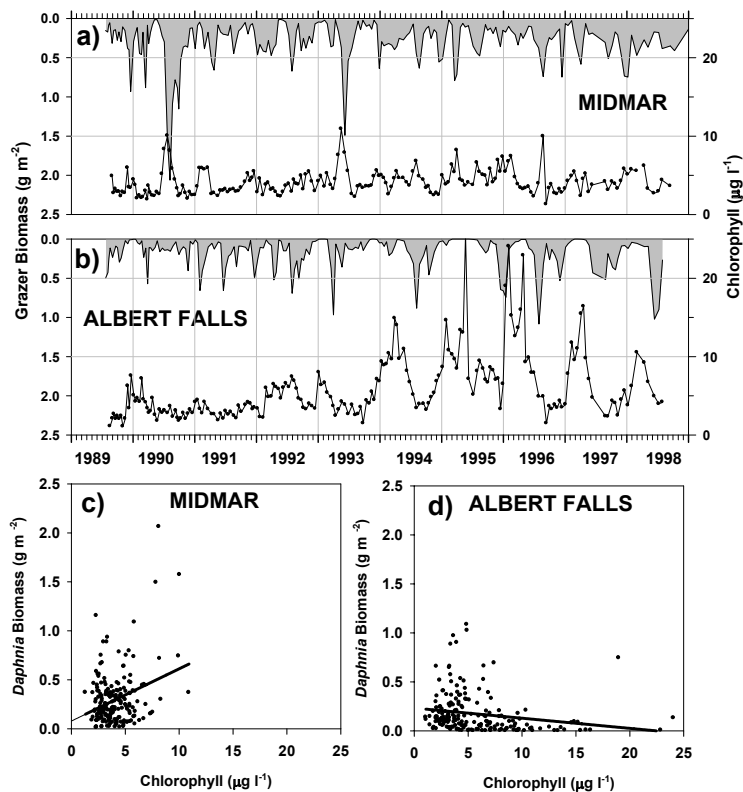


Figure 4
Temporal changes in chlorophyll in relation to concurrent standing stocks of *Daphnia* spp. in Midmar (a) and Albert Falls (b), and corresponding regression plots for these reservoirs (c and d).

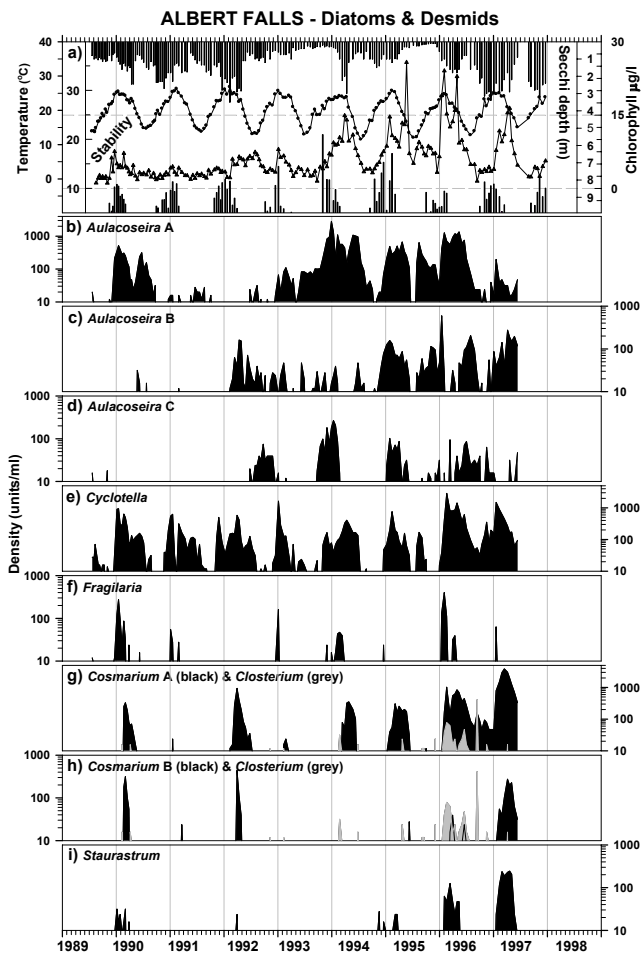
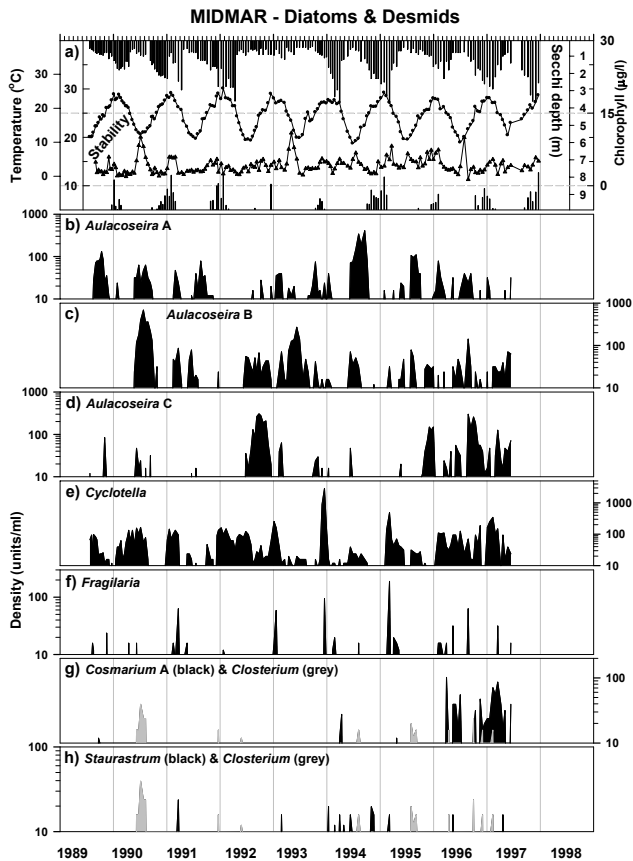
chlorophyll level on the preceding sampling date were variously stronger or weaker than, but generally comparable to their unlagged equivalents (corresponding values of 0.355, 0.286, 0.176 and 0.273 in the above sequence). However, very clear evidence of the regulation of algae by zooplankton grazers was manifest in ALB, where maximal chlorophyll values corresponded with severe reductions or disappearance of *Daphnia* in particular (Fig. 4), as well as the strong overall negative correlations.

Temporal dynamics – taxonomic account

General – A rather low total of nearly 60 different taxa were encountered during the study, with an overall diversity ranking of Chlorophytes > Bacillariophytes > Cyanophytes > Pyrrophytes. Roughly 25% of these taxa are excluded from further consideration by the inclusion index threshold described above. Distinctive taxa within a genus were distinguished by alphabetic labels. Where available, (tentative) species identifications are provided below at first mention.

Based on the intermediate disturbance hypothesis, which partly underpinned the research direction (Hart, 1992) of which the present account is a product, rather more taxa would be anticipated (Padišák et al., 1993; Reynolds, 1995). The relatively low number of taxa recorded may be partly attributable to inadequate distinction among morphologically closely similar taxa within a non-specialist study.

Diatoms and desmids – These groups are considered jointly since desmids function as "green diatoms" (Reynolds, 2005) Figures 5 and 6 show the temporal variability of dominant taxa in this category in Midmar and Albert Falls, respectively.



Aulacoseira was the dominant diatom in both lakes; two species (A = *A. granulata* and B = *A. granulata* var. *angustissima*) were present virtually through the entire study (Figs. 5b, 5c; 6b, 6c), while a third species (C = *Aulacoseira* sp.) rose in prominence in MID from 1992 (Fig. 5d), and appeared almost concurrently in ALF (Fig. 6d). Taxa in the genus showed extended (but not continuous) seasonal occurrences in ALF, but were generally more 'seasonal' in MID. Major annual peaks of *Aulacoseira* species A and B were quite consistently mid-winter events in MID (Figs. 5b, 5c), but less regular in ALF, where peaks variously occurred both in mid-summer and mid-winter in different years (Figs. 6b, 6c), with some indications of bimodal occurrences. Considerable between-year variability in abundance was evident, especially for *Aulacoseira* A; this diatom was sparse in ALF in 1991 and 1992, but increased radically in 1993 as water clarity dropped with the rise in suspended sediments corresponding with declining water levels (Fig. 3b), and thereafter tended to remain more abundant. Significant ($p < 0.001$) inverse correlations of *Aulacoseira* A density and Secchi depth transparency were evident both in MID ($r_s = -0.293$) and ALF ($r_s = -0.386$). Peak annual densities of both *Aulacoseira* species A and B also varied considerably in both lakes. Based on correlation analysis, *Aulacoseira* A was inferred to be the major contributor to chlorophyll concentration in ALF ($r = 0.499$; $r_s = 0.577$; $p < 0.001$), but less strongly in MID ($r = 0.099$, ns; $r_s = 0.212$; $p = 0.004$).

Cyclotella was seasonally the most persistent member of the diatom/desmid assemblage in both lakes, but reached consistently higher densities in ALF than MID (Figs. 5e, 6e). This diatom commonly peaked in late summer/autumn, often after a fairly consistent mid-summer decline from an irregular spring/early summer development. Although relatively sparse, *Fragilaria* peaked fairly consistently in mid-summer (Figs. 5f, 6f).

Several desmids – *Cosmarium*, *Staurastrum* and *Closterium* – occurred in significant numbers in some years, reaching consistently higher densities in ALF than in MID (Figs. 5g, 5h; 6g to 6i). Species of *Cosmarium* (species A in MID, and both A and B in ALF) and *Staurastrum* appeared inconsistently from year to year, but showed quite consistent brief late-summer developments in the years they were present. *Staurastrum* was much sparser in MID than in ALF, where its annual prominence increased in later years of the study (as too did *Cosmarium* A in both lakes). *Closterium* showed sparse autumn/winter peaks in both lakes, and as with *Cosmarium* A and *Staurastrum*, also increased in ALF in later years.

Cryptomonas and non-desmid chlorophytes – Figures 7 and 8 illustrate the seasonal and inter-annual variations in this Chrytophyte and the non-desmid members of the green algal assemblage in MID and ALF respectively. *Cryptomonas* was clearly the taxon with the most extended seasonal presence in both lakes, and was substantially more abundant in ALF than MID (Figs. 7b and 8b). Two species of *Crucigena* (spp. A and

Temporal changes in composition and abundance of specified taxa in relation to changes in selected abiotic and biotic variables:

Figure 5 (top left)

Bacillariophytes and desmid Chlorophytes (mostly ruderal taxa) in Midmar.

Figure 6 (bottom left)

Bacillariophytes and desmid Chlorophytes (mostly ruderal taxa) in Albert Falls.

B) and *Closteriopsis* assumed broadly comparable second-rank co-dominance in both lakes, although the density of all these three taxa generally tended to be marginally higher in ALF than in MID. No clear recurrent seasonal pattern was evident among these taxa, although all reached mid-year (winter) peaks in both lakes in certain years, and were often absent or present at greatly depressed densities in mid-summer. Seven additional taxa – *Scenedesmus*, *Schroderia*, *Tetraedron*, *Oocystis*, *Ankistrodesmus*, *Coelastrum* and *Trachelomonas* – contributed to this broad taxonomic assemblage in low densities. Several of these taxa increased in abundance in ALF in the latter half of the study; this feature was most clearly manifest in *Scenedesmus*, *Tetraedron* and *Ankistrodesmus* (Figs. 8f, 8g and 8h). A broadly parallel increase in MID was evident for *Ankistrodesmus*, which only reached significant densities in MID in the 1996/97 year (Fig. 7h). Of the four remaining taxa, *Trachelomonas* was seasonally most persistent, and more abundant in ALF than MID. An unresolved paradox is the absence of *Chlorella* in this record: Graham et al. (1998) identified it as an overwhelming dominant in both lakes.

Cyanophytes and Pyrrophytes – Temporal changes in cyanophytes and pyrrophytes in MID and ALF are shown in Figs. 9 and 10, respectively. Substantial increases in abundance and seasonal duration in the later years of study were evident in both lakes for several cyanophytes – especially *Microcystis* (= *M. aeruginosa*) and *Anabaena* species A and C. Brief and seasonally inconsistent peaks of *Nodularia* were observed in ALF; in contrast, this taxon was sporadic in MID (Fig. 9g). Surprisingly, several of the more prominent taxa showed substantial mid-summer declines and even effectively disappeared in some years although little consistency was evident between taxa and lakes – apart from the virtual absence of all taxa in this assemblage in both lakes at the end of 1996. Pyrrophytes barely featured in MID, in which only *Peridinium* reached the inclusion threshold in the final years of study (Fig. 9h). In ALF, *Ceratium* was the dominant member of this group but was absent or scarce in the initial years of the study. However, in the years when representation of this group was tangible, both taxa were seasonally restricted to late summer, except during 1992, when they featured in winter (Fig. 10i).

Temporal dynamics – functional categories

Ruderal taxa – The prime disturbance factor selecting for ruderal strategist taxa is that of vertical mixing. On this basis, ruderal taxa abundance should relate inversely to stability. While broadly true for MID (Fig. 5), some radical departures from this expectation were evident in ALF (Fig. 6), where *Aulacoseira* A for example, reached its peak abundance in mid-summer of 1993/94, and was common later in summer in several years, but conversely declined to mid-year insignificance in other years (Fig. 6b). Rank correlations between abundance and stability

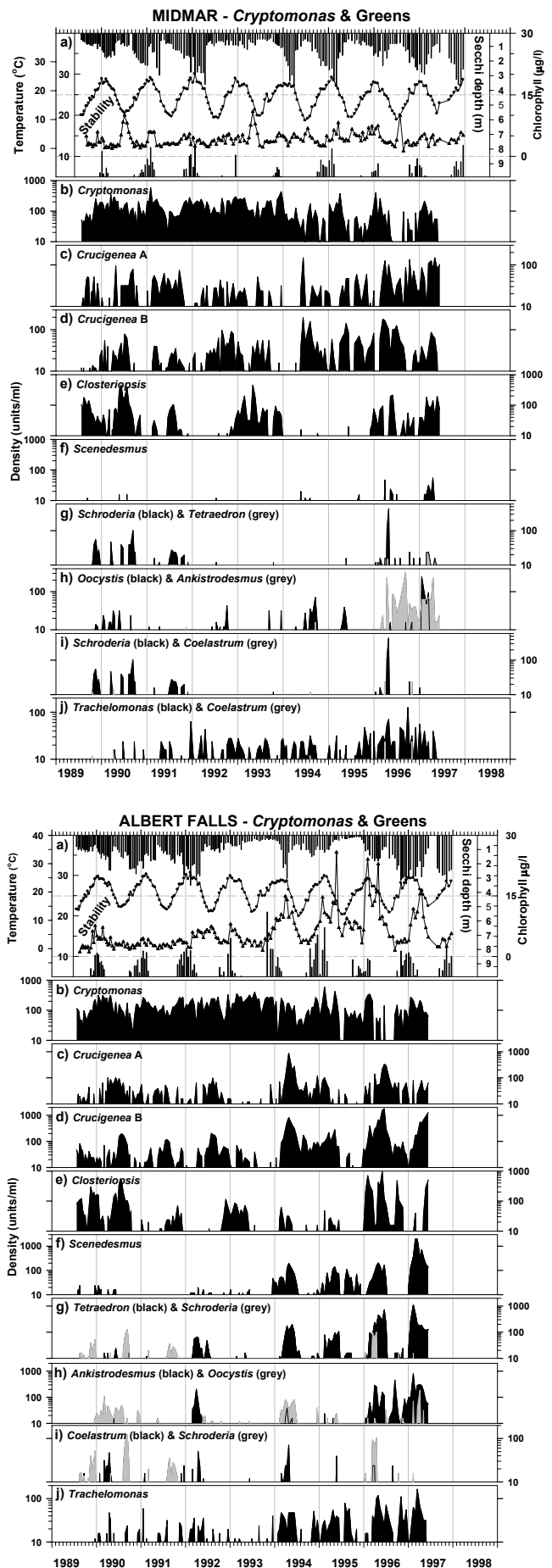
Temporal changes in composition and abundance of specified taxa in relation to changes in selected abiotic and biotic variables:

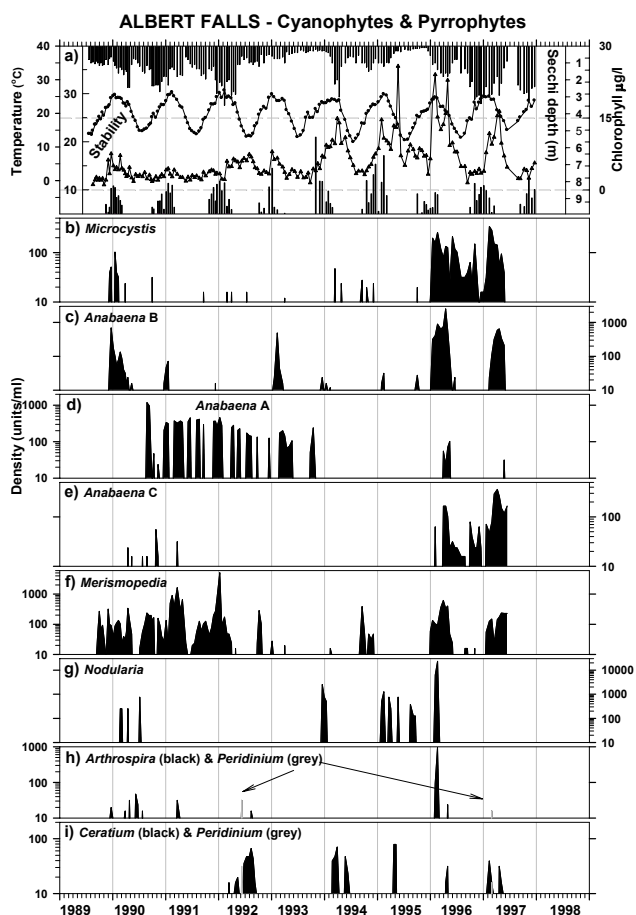
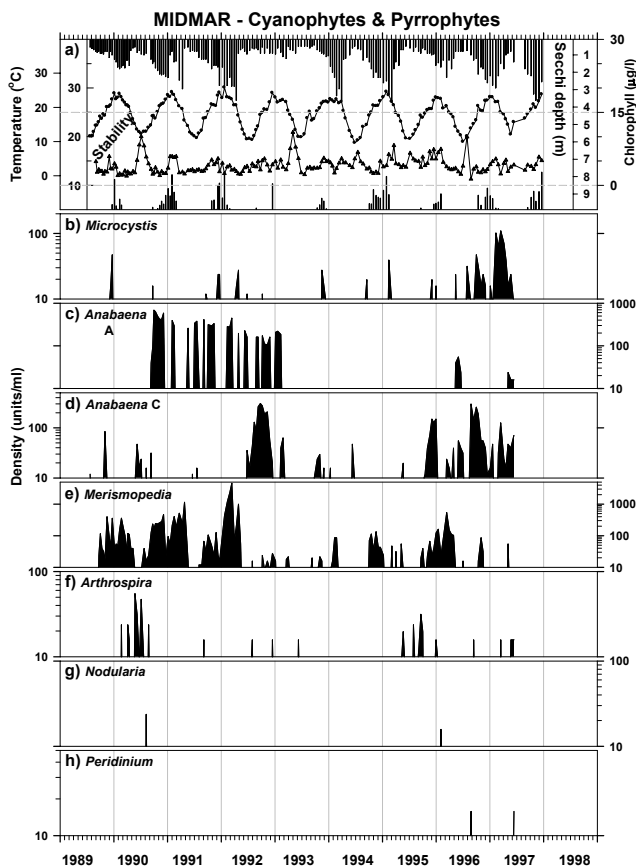
Figure 7 (top right)

Cryptomonas/Cryptophytes and non-desmid Chlorophytes (mostly colonist taxa) in Midmar.

Figure 8 (bottom right)

Cryptomonas/Cryptophytes and non-desmid Chlorophytes (mostly colonist taxa) in Albert Falls.





reflect this variability in response (Table 4). Correlations were negative for six of the nine taxa in MID, but for only three taxa in ALF, but were significant for only one taxon in each reservoir (Table 4). This pattern was maintained even when confounding influences of change in water depth were controlled for using partial correlation analysis.

Competitive/colonist taxa – The abundance of most C-strategist taxa correlated negatively with stability in both reservoirs (9 of 11 taxa), significantly so for 4 taxa in MID, and 3 taxa in ALF (Table 4). All significant correlations were directionally consistent for given taxa in both reservoirs; the only taxon that was significantly positively correlated to stability was *Cryptomonas* – a motile flagellate. Although somewhat unexpected, the predominance of negative correlations with stability in this functional subset is consistent with its ‘colonist’ nature – hydraulic disturbances that reset autogenic succession effectively create the ‘gap’ for colonist occupancy.

Stress-tolerant taxa – The positive correlations expected between abundance and stability for taxa in this assemblage were not unambiguously realised, although the only significant correlations (3 in MID, 1 in ALF) were correctly positive (Table 4). Several other taxa showed directionally opposite (but insignificant) correlations in the two reservoirs (Table 4).

Hypothesis interrogation

Influences of mixing and stratification on phytoplankton

The numerical proportional contributions of ruderal, colonist and stress-tolerant taxa over the entire study period respectively averaged 0.361, 0.328 and 0.311 in MID and 0.449, 0.292 and 0.258 in ALF. These relative proportions were not significantly different overall in MID (ANOVA; $F = 2.2$, $p = 0.108$), but differences were highly significant in ALF ($F = 32.185$, $p < 0.001$). Based on differences in stratification intensity between the reservoirs, initial predictions that a) the proportional dominance of ruderal taxa should be greater in MID than in ALF, while b) stress tolerant taxa should be more dominant in ALF than MID, were not realised overall. Comparative analyses of high (> 50% FSL) and low (< 50% FSL) water-level data confirmed that the postulated increase in proportion of ruderal taxa (prediction c) was highly significant ($p < 0.001$ both by ANOVA and t -tests) in both lakes: from 0.362 to 0.562 in MID, and from 0.366 to 0.474 in ALF, suggesting a controlling influence of hydrological variation as a major determinant of community structure. Predictability of algal dynamics requires the careful consideration and “factoring in” of such hydrological variability, as it is clearly an over-riding regional influence in reservoir functioning.

The extended presence of numerically strong populations of *Cryptomonas* in both lakes is especially notable. This feature is entirely in keeping with its status as a C-S-R “generalist”;

Temporal changes in composition and abundance of specified taxa in relation to changes in selected abiotic and biotic variables:

Figure 9 (top left)
Cyanophytes and Pyrrophytes (mostly stress-tolerant taxa) in Midmar.

Figure 10 (bottom left)
Cyanophytes and Pyrrophytes (mostly stress-tolerant taxa) in Albert Falls.

Cryptomonas virtually ruled the worlds of the two study reservoirs, affirming its position in successfully blending all three strategies (Reynolds, 2005). Its prolonged presence is in keeping with the very environmentally dynamic nature of these reservoirs, further emphasising the closing statement of the preceding paragraph.

Inferred grazer impacts on phytoplankton

The relationship between chlorophyll (i.e. algal biomass) and grazing zooplankton biomass was surprisingly discordant in the two reservoirs. A very significant negative relationship was apparent in ALF (Fig. 4d), in keeping with direct grazer control logically anticipated from typical general predator-prey interactions. The equally strong but direct relationship in MID (Fig. 4c) conversely implied that phytoplankton was stimulated rather than regulated by grazer activity in this upstream reservoir. The direct relationship in MID may be partly attributable to the dominance of large ruderal elements, especially of large filaments of *Aulacoseira*, that exceed the size range of easily ingestible foods for suspension feeding cladocerans. Furthermore, the negative consequences of suspended sediments on cladoceran suspension-feeding efficiency (e.g. Hart, 1988) are predictably expected to be greater in the sediment-richer waters (mirrored in lower water transparency – Fig. 3b) of this upstream reservoir. The ‘headwater’ location of MID further renders it nutrient-poorer than ALF, a speculated consequence of which is that nutrient recycling by grazers may provide a greater stimulation to phytoplankton growth in MID than in ALF (although this speculation is contradicted by the significantly higher average *Daphnia* biomass (0.293 vs. 0.176 g·m⁻²; $p < 0.001$, $n = 199$, paired *t*-test: although total cladoceran and total grazer biomass did not differ significantly), and implied higher resource repletion in MID. Regardless of causality, however, this fundamental contrast importantly emphasises the illusion of ecological generality (Dunham and Beaupre, 1998; Morin, 1998), and the corollary requirement for systems-specific analyses to unravel system-specific response.

Differential influences of grazing on specified categories of phytoplankton were also variable and generally inconsistent between the lakes. In MID, the proportional abundance of C, S and R taxa on given sampling dates was consistent with the initial prediction that small autotrophs (colonist taxa) would relate inversely while large (stress-tolerant taxa) would relate directly or not at all to grazer biomass, whereas parallel evidence in ALF

TABLE 4
Spearman rank correlations between abundance levels of specified algal taxa and water column stability in Midmar and Albert Falls. Significant correlations are highlighted.

Stability vs.	Midmar			Albert Falls		
	r_s	p	n	r_s	p	n
<i>Aulacoseira</i> sp. A	-0.138	0.115	131	0.031	0.698	159
<i>Aulacoseira</i> sp. B	-0.241	0.007	125	-0.017	0.854	122
<i>Aulacoseira</i> sp. C	0.083	0.434	91	0.091	0.412	84
<i>Aulacoseira</i> (all spp.)	-0.223	0.004	163	0.025	0.740	173
<i>Fragilaria</i>	-0.035	0.769	72	0.383	0.002	60
<i>Cyclotella</i>	-0.001	0.988	163	0.161	0.037	168
All diatoms	-0.145	0.051	180	0.043	0.571	174
<i>Cosmarium</i> sp. A	-0.089	0.618	34	-0.192	0.088	80
<i>Cosmarium</i> sp. B	0.894	0.104	4	0.134	0.479	30
<i>Staurastrum</i>	0.135	0.414	39	0.044	0.741	58
<i>Closterium</i>	-0.193	0.099	74	-0.208	0.125	56
All desmids	-0.073	0.440	114	-0.171	0.084	103
All ruderals	-0.167	0.023	184	0.107	.149	183
<i>Anabaena</i> sp. A	0.506	0.001	40	-0.081	0.581	49
<i>Anabaena</i> sp. B	-0.610	0.061	10	0.228	0.046	77
<i>Anabaena</i> sp. C	-0.278	0.137	30	0.176	0.276	40
<i>Anabaena</i> (all spp.)	0.184	0.138	66	0.040	0.660	125
<i>Microcystis</i>	0.078	0.538	65	-0.100	0.395	75
<i>Merismopedia</i>	0.327	0.000	123	0.137	0.156	108
<i>Nodularia</i>	0.203	0.700	6	0.344	0.176	17
All cyanophytes	0.132	0.100	156	0.195	0.015	165
<i>Ceratium</i>	n/a	n/a	n/a	-0.094	0.601	33
<i>Peridinium</i>	-0.414	0.414	6	-0.064	0.843	12
<i>Trachelomonas</i>	-0.185	0.029	138	-0.046	0.598	136
All stress tolerators	0.302	0.000	184	0.182	0.014	183
<i>Cryptomonas</i>	0.238	0.002	176	0.223	0.003	178
<i>Crucigenia</i> A	-0.240	0.002	158	-0.248	0.002	150
<i>Crucigenia</i> B	-0.248	0.002	157	-0.361	0.000	160
<i>Tetraëdron</i>	-0.283	0.077	40	-0.108	0.279	102
<i>Scenedesmus</i>	-0.193	0.143	59	-0.006	0.948	123
<i>Closteriopsis</i>	-0.309	0.000	132	-0.187	0.042	119
<i>Arthrospira</i>	-0.088	0.562	46	-0.134	0.480	30
<i>Ankistrodesmus</i>	0.046	0.727	59	-0.029	0.825	62
<i>Oocystis</i>	-0.036	0.736	92	-0.051	0.652	80
<i>Schröderia</i>	-0.120	0.421	47	0.047	0.784	37
<i>Coelastrum</i>	-0.043	0.798	38	-0.080	0.588	48
All colonists	-0.395	0.000	184	-0.252	0.001	183

was not unequivocal. Relationships between C taxa and total grazer biomass, cladoceran biomass, and *Daphnia* biomass were all significant, and negative (as predicted) for MID ($r = -0.249^{**}$, -0.177^{*} and -0.143^{*} respectively), but insignificant (and positive) for ALF (in contrast to the opposite pattern shown for total grazer biomass and chlorophyll). Corresponding values for S taxa were 0.143*, 0.073 and 0.055 for MID, and -0.063, -0.030 and 0.132 for ALF. Only the (just) significant value is consistent with the initial prediction. Somewhat unexpectedly, *Daphnia* biomass and ruderal taxa in ALF demonstrated the strongest relationship overall (-0.207^{**}). While no relationships between any categories of grazer biomass and absolute (rather than relative)

Predictions:	Empirical observations					
	Overall Aug 1989 to June 1997		High-water Jan to Dec 1990		Low-water Jan to Dec 1993	
	MID	ALF	MID	ALF	MID	ALF
a) 'R' taxa proportionately commoner in MID than ALF	0.360	0.449	0.277	0.379	0.462	0.629
	N		N		N	
b) 'S' taxa proportionately commoner in ALF than MID	0.258	0.311	0.419	0.317	0.152	0.205
	Y		N		Y	
c) 'R' taxa proportionately commoner at low than high water level	0.474 0.331*	0.562 0.366*	0.277	0.379	0.462	0.629
	Y		Y		Y	
d) 'C' taxa vary inversely with grazers 'S' taxa vary directly or not at all with grazers	-0.249	0.109	-0.246	-0.429	-0.283	0.417
	Y		Y		Y	
	0.143	0.132	-0.096	-0.183	-0.120	0.566
	Y		N		Y	
e) proportionately more 'S' taxa:	0.258	0.311	0.419	0.317	0.152	0.205
i) in MID	N		N		N	
ii) in ALF	Y		Y		Y	
iii) comparable in both lakes	Y		Y		Y	
No. predictions upheld (of 16):	9		6		6	
Correct direction, but $p > 0.05$	6		4		6	
Correct direction; $p < 0.05$	3		2		3	
Significantly contradictory	1		0		1	

* Based on comparison of high (> 50%) and low (<50% FSL) water level phases through entire study.

abundance of C, S and R taxa were significant in MID, *Daphnia* biomass correlated inversely both with C and R taxa densities in ALF (-0.173*, -0.271**). Correlations between total grazer or cladoceran biomass and autotroph density did not approach significance.

Influences of trophic status on phytoplankton composition

Based on the premises of prediction e) (in Table 5), the greater proportional prominence of S taxa observed in MID than ALF (0.311 vs. 0.258; $p = 0.017$ – paired t -test) implies that extrinsic nutrient level constraints may exceed the intrinsic limitation imposed by stratification. Nutrient concentrations for MID and ALF reported by Graham et al. (1998) indicate comparable multi-annual mean levels ($\mu\text{g}\cdot\text{L}^{-1}$) of TP (24.1, 28.1) and $\text{TN}_{\text{inorganic}}$ (327, 358), with TN:TP ratios of 20.9 and 24.3 in MID and ALF respectively between (perhaps) 1990 and 1994. However, inter-annual changes and variability in stratification intensity within the reservoirs confound attempts to distinguish response causality within and between these water bodies during the present study. Alternatively, the limited degree of difference observed between the reservoirs may imply that causality cannot be ascribed independently to intrinsic nor extrinsic influences, but rather reflects their interactive influences, with blurred or confounded effects. Without contemporaneous chemical evidence regarding comparative nutrient concentrations, further deliberation of this point is conjectural.

Predictability of annual periodicity

Meaningful conclusions about the existence or otherwise of cyclical seasonal repetitions of phytoplankton dynamics in reservoirs under South African conditions are difficult to attempt on the basis of presently limited empirical data, which is especially poignant to the notional illusion of ecological generality (Dunham and Beupre, 1998; Morin, 1998). Available evidence does, however, suggest that inter-annual variability within single systems (Pieterse and Röhrbeck, 1990; Pieterse and Janse van Vuuren, 1997; Zohary et al., 1996; this study) is considerable, as is the variability between systems. While the fundamental determinants of periodicity and successional change are universal (Reynolds, 1996; 1997; 1999), environmental variability inherent within and between reservoirs in this geographical region will delay, and may compromise attempts to define repeatable patterns of species abundance and assemblage associations comparable to those already synthesised for temperate waters (e.g. Reynolds, 1996; Kruk et al., 2002). The relatively low-frequency monitoring undertaken for SA reservoirs is also seriously out-of-step with the increasing trend towards short interval, even daily sampling, undertaken in temperate climes, that has stimulated the introduction of various automated/semi-automated analytical tools (Dubelaar et al., 2004; See et al., 2005) to replace conventional microscopy.

Utility of C-S-R censusing

While several of the initial predictions based on functional responses were not supported by evidence from the study overall, ecologically logical explanations are offered in the foregoing discussion to account for several of the disparities between expected and observed features. As these hinge largely on variability of the physical environment, greater concordance between expectations and observations might be expected over shorter time-frames. With this in mind, I selected shorter segments of the record to re-examine the initial predictions.

As such selection is difficult to justify objectively *a priori*, the calendar years of 1990 and 1993 were chosen somewhat arbitrarily as representative high- and low-water phase conditions, respectively (see Fig. 3), in order to minimise longer-term temporal variability.

Table 5 summarises the comparative 'validity' of each prediction for each lake over the entire study period with these two years of contrasting water level. While these results are not examined here in any further detail, Table 5 reflects little comparative improvement in prediction conformity between the annual and the overall data. Initial predictions may be incorrectly formulated, or unfounded. Nevertheless, the monitoring of autotroph dynamics using a functional approach is believed to remain as a useful adjunct to conventional taxonomic analysis, as demonstrated statistically using CANOCA by Kruk et al. (2002). In any event, prospects of predicting individual taxon responses remain daunting at best, if not impossible for all but a very limited number of taxa – such as *Microcystis*. Prospects of forecasting diatom periodicity at even generic level will demand much better documentary evidence than presently exists for reservoirs in South Africa. Conversely, forecasting the responses of functional groups (such as 'ruderals'), already approaches practicality. As indicated by Kruk et al. (2002), cross-phyletic and often overlapping selective influences confound the prediction of the phyletic composition of species – constraints that are explicitly tempered or removed by the functional approach.

Perhaps most importantly, this study identifies widely disparate effects of similar grazer assemblages on phytoplankton under broadly similar conditions in comparable lakes. Several attempts to characterise phytoplankton assemblages on the basis of trophic status in particular (e.g. Seip and Reynolds, 1995; Rojo et al., 2000) have not incorporated this influence, perhaps contributing to the apparent 'lack of pattern' among assemblages (Rojo et al., 2000). The influence has been recognised (Watson et al., 1997), but merits explicit incorporation in future attempts to identify congruent assemblage structure and species temporal dynamics.

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