Zooplankton biomass to chlorophyll ratios in relation to trophic status within and between ten South African reservoirs: Causal inferences, and implications for biomanipulation

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Abstract

Rising eutrophication in South African reservoirs is of major concern, leading to the consideration of top-down biomanipulation as a management option – reducing zooplankton-eating fish to sustain zooplankton grazing pressure and thus restrict autotrophic plankton that proliferate with nutrient increases. The biomass ratio of zooplankton to phytoplankton (ZB/PB) is used as an index of the likely value of biomanipulation to achieve this outcome, but values have not been explored for South African systems. Using chlorophyll (Chl) as a surrogate for PB, available ZB/Chl data are assembled for the first time for ten reservoirs of three types (minerally-turbid systems, oligo/mesotrophic clear water systems, and eutrophic/hypertrophic systems), and the results are discussed in relation to a generalised conceptual model proposed. With the exception of one minerally-turbid system, ZB/Chl values decline quasi-exponentially with rising chlorophyll within individual reservoirs. Conversely, between individual systems, median (or mean) values of ZB/Chl conversely increase rather than decline with rising trophic status – broadly contradicting observations reported elsewhere. Underlying causal reasons for the observed pattern and its implications for biomanipulation are considered. This assessment evaluates: the negative impacts of general declines in food quality that stem from rising eutrophication on zooplankton feeding ability and resulting seasonal changes in ZB and community structure; prospects of food sources other than living autochthonous autotrophs in sustaining ZB between systems; and inferences about fish predation pressure on zooplankton, derived from empirical data regarding the large body sizes of species and individuals of *Daphnia* that occur in the reservoirs. Observed increases in median ZB/Chl ratios with rising nutrient status are consistent with the inference that obligate visual zooplanktivorous fishes are scarce or absent, particularly in eutrophic reservoirs, suggesting that biomanipulative management is unlikely to assist in controlling the consequences of nutrient enrichment in local reservoirs.

Keywords: Biomanipulation, eutrophication, food webs, food quality, interactions, plankton communities

Introduction

Cultural eutrophication is a familiar phenomenon known for decades (e.g. OECD, 1982; Schindler, 2006). Smith and Schindler (2009) state that it has become the primary water quality issue in most of the freshwater and coastal marine ecosystems in the world. Its impact is of growing global concern in view of its multiple adverse consequences on the structure and functioning of affected ecosystems (e.g. Holdren, 2001; Jeppesen et al., 2003b; Osborne, 2005; Phillips, 2005; Søndergaard and Jeppesen, 2007). Harmful algal blooms (HABs) with adverse ecosystem implications and potential human health problems commonly emerge (Graham, 2007). Krantzberg et al. (2010) indicate that 20% of the world's population (more than one billion people) are at risk of water-related diseases associated with water pollution, while pathogens can benefit from the higher nutrient levels in eutrophic waters (Smith and Schindler, 2009). The greater vulnerability of warm and tropical waters to eutrophication problems (Jeppesen et al., 2003b, 2005; Hart, 2006b) is an emerging concern of particular relevance to South Africa, a water-scarce country, largely dependent on water stored in man-made reservoirs (reservoir-lakes) for the sustained supply of raw potable and irrigation water.

South African reservoirs impound at least 50% of the mean annual runoff in the country (DWAF, 2004). Some 35% of this stored water is currently classified as eutrophic or hypertrophic – with nutrient levels greatly exceeding generally-accepted trophic boundaries (Harding et al., 2009). Bulk nutrient loading of many inland South African reservoirs derives from wastewater return flows, leading in many cases to cyanobacterial blooms (Van Ginkel et al., 2000, 2006; Harding et al., 2009). Harding (2008) has estimated that nutrient load reductions of between 25 and 96% will be necessary to attain *in situ* threshold concentrations amenable to an acceptable reduction in the frequency of cyanobacterial blooms. However, the prospects of such reductions are poor, given the parlous state of increasingly over-loaded wastewater treatment plants in the country (DWA, 2009). Accordingly, alternative in-lake management options attract growing consideration, with food web modification (biomanipulation) emerging as a possible prospect (e.g. Harding et al., 2009).

The basic principles behind the biomanipulation approach to lake restoration are widely known (e.g. Gulati et al., 1990; Moss, 1998a; Hansson et al., 1998), and are not elaborated here. While the approach has been widely applied internationally, its successes are outnumbered by failures, certainly in the longer term (Gulati and Van Donk, 2002; Søndergaard and Jeppesen, 2007; Søndergaard et al., 2007; Gulati et al., 2008). Successful outcomes are more frequent in shallow natural lakes where submerged hydrophytes compete with phytoplankton for nutrients, and also provide a visual refuge

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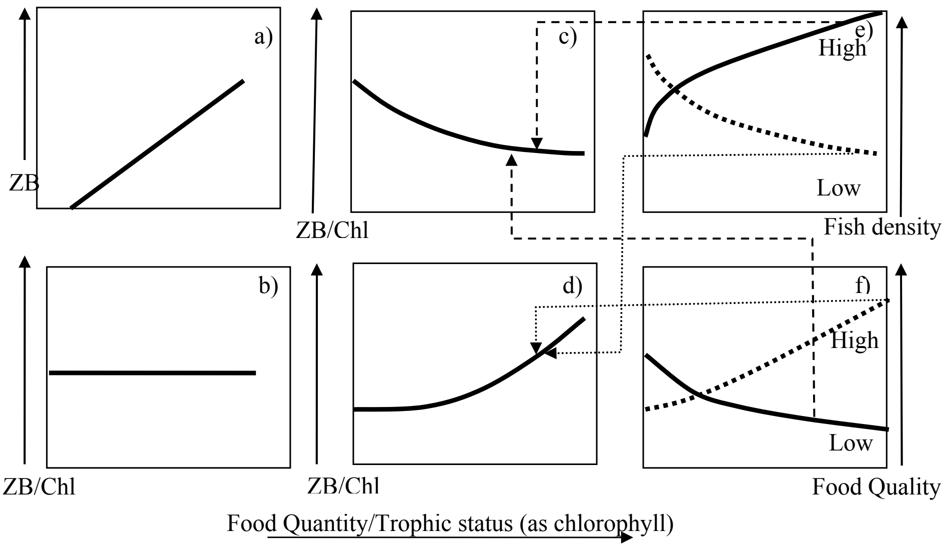

Figure 1
A general conceptual model showing the responses of different variables to rising chlorophyll as a measure of food supply and a proxy for increasing trophic/nutrient status(the abscissa for all panels): a) zooplankton biomass (ZB); b) zooplankton abundance standardised for food supply (ZB/Chl); c) and d) alternative responses of ZB/Chl to food supply; e) alternative changes in zooplanktivorous fish abundance and f) alternative changes in food quality, with changing trophic status. Dashed lines show that the common empirical pattern (e.g. Jeppesen et al., 2003a, 2007) of declining ZB/Chl can arise from increased predation by rising densities of fish (e), but can also or alternatively derive from declining food quality (f). Dotted lines reflect how obverse changes in e) and f) could account for a progressive increase in ZB/Chl with rising trophic status.

against obligate visually-feeding zooplanktivorous fishes (Jeppesen et al., 1997). Nevertheless, the sustainability of successful food web manipulation has been found wanting on several grounds, even in such natural lakes (Gliwicz 2005; Søndergaard et al., 2007; Gulati et al., 2008). In South African reservoirs, obligate visual zooplanktivores are effectively absent, and most reservoir systems are deep enough to stratify (Allanson et al., 1990), and thus exceed the 'arbitrary' deep/shallow depth threshold, of aprox. 6 m, associated with effective biomanipulation prospects (Jeppesen et al., 2003a). Extensive hydrophyte stands are also not characteristic of many South African reservoirs, the lake beds of which mostly lie below the trophogenic zone, and/or because seasonal water-level drawn-downs strand hydrophytes and/or desiccate suitable habitat for them.

On various grounds, the prospects of successful biomanipulation in South African reservoirs have already been questioned and seriously challenged (Hart, 2006b); the problem autotrophs that increase radically with nutrient enrichment are dominated by taxa such as *Microcystis* (Van Ginkel et al., 2000, 2006) and, increasingly, *Ceratium* (Van Ginkel et al., 2001; Hart and Wragg, 2009), which are too large for direct consumption by grazing zooplankton. In addition, zooplankton populations are not subjected to significant fish predation, since obligate zooplanktivorous fish are absent and young-of-year (YOY) facultative zooplanktivores are numerically, temporally and/or spatially restricted in South African reservoirs (Hart 2006b).

Here, a conceptual model of causal changes in ZB/PB, using chlorophyll (Chl) as a proxy for PB, is offered. Values of ZB/Chl are collated for the first time for a number of South African reservoirs, systems for which empirical evidence regarding fish abundance and composition is severely limited. These data show that ZB/Chl ratios decline with rising chlorophyll within most individual reservoirs, a trend that is partly attributable to the negative effect of declining food quality on ZB within systems. Conversely, however, the data also reveal that median (or mean) ZB/Chl ratios for individual systems actually rise with trophic status. In this paper, possible causes for these observations are considered and discussed, along with the implications of these for prospective 'corrective' top-down biomanipulation, especially within the eutrophic reservoirs.

Conceptual background to the ZB/PB ratio, and inferences regarding its causal control

Fundamentally, and all else being equal, 'grazing' zooplankton biomass (ZB) is expected to rise commensurately with the increase of phytoplankton biomass (PB) associated with nutrient (especially P) enrichment (Fig. 1a). Using total chlorophyll (Chl) as a proxy for PB, the ZB/Chl ratio should effectively standardise this food effect, and remain constant in relation to trophic status/food resource level (Fig. 1b) (disregarding food-saturation limitations (Gulati, 1990b)). Alternatively, however, this latter 'equilibrium' pattern can decrease (Fig. 1c) or increase (Fig. 1d). Empirical declines in this ratio with rising food levels (Fig. 1c) have been commonly observed, and attributed to rising predation of zooplankton (Fig. 1e) by known increases in zooplanktivorous fishes with rising nutrient status (e.g. Jeppesen et al., 2003a). Such reductions in ZB/PB associated with rising fish predation were especially evident in shallow lakes across a temperate-arctic latitudinal range (Fig. 3 in Jeppesen et al., 2003a), where the ZB/PB dry weight ratio declined from 0.35 (equivalent ZB/Chl = ~23.45) in the most oligotrophic lakes to below roughly 0.15 (ZB/Chl= ~10.05) in the most eutrophic of 466 study lakes.

Equally logically, however, reductions in zooplankton feeding ability related to adverse changes in food type/quality with rising trophic status (Fig. 1f) can result in a similar inverse relationship, regardless of fish predation. Such reduction in food quality is a well-known outcome of eutrophication (e.g. Sommer et al., 1986; Gulati, 1990b; Moss, 1998b; Wetzel, 2001; Kalff, 2002; Lampert and Sommer, 2007); edible, palatable and nutritionally adequate phytoplankton are increasingly replaced by large colonial and other nutritionally deficient cyanoplankton (see Hart and Bychek (2011) for a contemporary synoptic overview of these nutritional deficiencies). In addition, these large particles depress feeding rates of large cladocerans in particular (Lampert, 1987), potentially reducing ZB and thus the ZB/PB ratio, regardless of any predatory impacts of zooplanktivorous fish (Fig. 1e). Since the depressive impacts of the cyanophytic autotrophs that increasingly predominate with rising trophic status are strongest on the large-bodied daphniid zooplankton (Gliwicz and Siedlar, 1980; Lampert, 1987; Gliwicz, 1990) that exert highest grazing pressures (Lampert, 1987), a decline in food quality can lead to disproportionately

Table 1
Best-fit linear (Y=*a* + *b*X) or power (Y=*a*X^b) regression statistics for zooplankton biomass (ZB) as functions of concurrent chlorophyll levels (Chl) in South African reservoirs. Suffixes for each system identify whether the best-fit regression is linear (–L) or power (– P). Data sources are listed in Table 2.

Dam system	Regression statistics					Notes
	a	*b*	*r*^{2}	*n*	*P*	
Clear water (Oligo/mesotrophic) systems						
Midmar – L	21.1	4.22	0.120	195	***	
Albert Falls – P	30.5	0.26	0.093	195	**	
Nagle – L	9.3	12.92	0.373	14	*	
Inanda – P	93.7	-0.59	0.192	13	ns	
Biogenically turbid (eutrophic) systems						
Hartbeespoort – P	288.3	-0.08	0.010	133	ns	Jarvis, 1987 (Figs 2.0A & 2.2D)
Roodeplaat – P	367.1	-0.17	0.026	86	ns	
Rietvlei – L	286.4	6.40	0.561	8	*	Not all readings concurrent
Minerally turbid systems						
Vanderkloof – P	182.3	0.31	0.127	7	ns	Annual means-open lake
Vanderkloof – P	5.9	1.15	0.381	86	***	Shallow embayment
Spioenkop – L	-0.7	4.22	0.251	9	ns	
Wagendrift – L	-13.6	10.05	0.637	10	**	

**** P < 0.001 ** P < 0.01 * P < 0.05 ns – not significant*

rapid decreases in ZB, and thus in ZB/Chl ratios.

Alternatively, the ZB/PB ratio could theoretically rise with trophic status (Fig. 1d), an increase plausibly attributable to one or more of three causes: declining fish predation (Fig. 1e), increasing food quality (Fig. 1f), and, most likely, increases in autochthonous and/or allochthonous detritus particles, and/or non-autotrophic food particles, as trophic status rises.

Materials and methods

General

A comparative evaluation was made of zooplankton-chlorophyll (ZB/Chl) ratios in South African reservoirs for which appropriate data exist. Information was extracted from the author's own original raw data used in various publications, and from other sources (see Table 2). In the absence of original raw data for systems independently studied by other authors, their published figures were photo-enlarged to allow measurements of values of interest with a digital micrometer read to 0.1 mm. All data for Hartbeespoort Dam were derived from plots of 3-point moving mean values of weekly measurements over 6 years (Jarvis, 1987). These smoothed estimates obviously obscure some intrinsic temporal variability, and are not precise concurrent estimates. However, the error associated with this approach is unlikely to negate the general underlying trends described. Sampling frequency varied from weekly (Hartbeespoort), to fortnightly (Midmar, Albert Falls) with monthly sampling for all other systems apart from Rietvlei, where sampling mostly varied between 4 and 6 weeks

The median, rather than the mean, was selected as a measure of central tendency, principally to offset the effect of outlying high and low values within the data. However, some average values are explicitly given (Table 3) and used (Fig. 7b) to emphasise one point. General procedures used to obtain original information are outlined below.

Zooplankton biomass (ZB)

Zooplankton was collected in vertical hauls through the entire water column, or the upper 15 m thereof. Nets with mesh apertures of between 63 and 160 µm were used in different studies, and samples were preserved with formalin for subsequent microscopic enumeration. Resulting (species- or genus-specific) counts of copepod instars were converted to biomass using uniform instar biomass coefficients (see original publications, as noted in Table 2), while cladoceran counts were converted to biomass using published (e.g. Bottrell et al., 1976) or original length-weight regressions (Hart, unpublished data) applied to sample mean lengths (geometric means where available). For Hartbeespoort and Roodeplaat Dams, fresh sample wet weights (WW) were determined. Dry weight (DW) was estimated as one-sixth of fresh weight for Hartbeespoort Dam (NIWR, 1985); for consistency, a similar conversion was made for the WW values reported for Roodeplaat Dam by Van Ginkel (1987).

All resulting biomass estimates (mg/m^2) are reported as water column integrated volumetric values as mg/m^3 (µg/ℓ) DW, using corrections based on site- and date-specific records of net haul length, or from graphical plots given in these units by the original authors.

Phytoplankton biomass (PB)

Direct determinations of PB as dry weight are not available concurrently with ZB values for any of the study dams. Accordingly, total chlorophyll (Chl, µg/ℓ) was used as a surrogate measure, with values generally determined from integral hose-pipe samples through the upper 3 or 5 m of the water column. Chlorophyll has been multiplied by 67 to estimate PB (as µg/ℓ dry weight) (Jeppesen et al., 2003a). This approach can progressively underestimate PB as chlorophyll rises between 1 and 150 µg/ℓ chlorophyll *a*, since chlorophyll declines from approximately 0.7% to merely 0.15% of phytoplankton wet weight (Kasprzak et al., 2008), largely as cyanophytes with inherently more chlorophyll per unit weight than eukaryotic autotrophs predominate at high chlorophyll levels. To avoid this confounding prospect, chlorophyll was used as a direct proxy for PB. Obviously, not all chlorophyll reflects edible food species, and it disregards non-autotrophic foods. However, it is inferred here as a direct measure of food supply (as used for other published PB values determined from chlorophyll – e.g., Jeppesen et al. (2003a)).

Table 2
The biomass ratio of zooplankton (ZB) to chlorophyll (Chl) (as a surrogate of phytoplankton biomass) in various South African reservoirs. Ratios for all reservoirs are based on ZB estimates of dry weight per unit volume.

Reservoir system (dam)	Sampling information		Haul depth range (m)	ZB/Chl ratio		Chlorophyll (µg/ℓ)		Zooplankton biomass (µg/ℓ dry weight)		
	Dates	*n*		Median	Mean	Median	Mean	Median	Mean	Source
Clear-water (Oligo/meso-trophic) systems										
Nagle	Jan 91- Sep 91	14	15	13.74	23.17	1.87	2.19	33.3	37.5	Original data (Hart,1996)
Inanda	Aug 92 - Aug 93	13	15	7.59	15.4	3.74	4.35	33.1	51.3	Original data (Hart, unpubl. data)
Midmar	Aug 89 - Sep 98	195	10-21	8.70	10.06	3.75	4.10	36.5	38.5	Original data (Hart, 1992, 1996)
Albert Falls	Aug 89 - Aug 98	195	5-21	10.05	11.84	4.38	5.83	45.7	53.7	Original data (Hart, 1992, 1996)
Biogenically turbid (eutrophic/hypertrophic) systems										
Hartbeespoort	Jan 81 - Dec 86	132	20-30	26.26	47.10	9.11	11.74	262.1	292.6	NIWR (1985); Jarvis (1987)
Rietvlei[1]	Jul 09 - Jul 10	8	14-17	27.05	36.82	12.7	30.45	439.8	607.8	Original data (Hart, unpubl. data; Coetzee, pers. comm., 2010)
Roodeplaat [2]	Jan 80 - Dec 81	86	7-20	12.97	88.12	26.6	31.36	248.4	392.6	Van Ginkel (1987)
Minerally turbid systems										
Vanderkloof [3]	Aug 81 - Sep 83	86	4-12	6.43	14.04	1.27	2.67	13.3	26.4	Original data (Hart, 1987)
Vanderkloof [4]	Aug 77 - Jul 84	7	70[5]	6.47	9.04	1.56	-	-	-	Original data (Hart, 1986)
Spioenkop	Jul 89 - May 90	9	15	3.22	3.82	2.61	2.68	11.5	10.7	Original data (Hart, 1999)
Wagendrift	Jul 89 - May 90	10	13-15	4.75	5.11	2.91	3.05	14.2	17.1	Original data (Hart, 2001)

[1] Ratio is approximation based on median values of chlorophyll and zooplankton collected on separate dates within the same overall annual period.
[2] Data for Stations 1 to 4.
[3] Average haul-depth corrected estimates for 5 sites in a shallow embayment.
[4] Determinations based on weighted annual mean values at a deep (70 m) offshore site, derived from a total of n=253 samples.
[5] Haul counts assumed to derive from 15 m, as zooplankton are concentrated in upper 10 m (Hart, 1986)

'Phytoplankton' edibility

Using species and cell or colony types and sizes, Jarvis (1987) distinguished between % biovolumes of 'edible' (*Cryptomonas*, *Chroomonas*, *Coelastrum*, *Ankistrodesmus*, *Cyclotella* and non-sheathed *Oocystis*), 'partly edible' (*Aulacoseira*, and sheathed *Oocystis*) and 'largely inedible' (predominantly *Microcystis*) 'fractions' of total 'phytoplankton' in Hartbeespoort Dam. Here, I partitioned chlorophyll into corresponding edibility classes, simplistically assuming a direct equivalence of chlorophyll and total phytoplankton bio-volume, in order to explore certain features relevant to this account (see 'Results' section).

Zooplankton-phytoplankton ratios (ZB/PB)

To avoid artefacts in PB associated with changes in proportionate contributions of chlorophyll to mass (see above), the proxy measure of ZB/Chl was used. This ratio is qualitatively but not quantitatively comparable to published values of ZB/PB, but an approximate conversion can be obtained as ZB/PB = ZB/Chl*67 for comparative purposes.

Phosphorus content/trophic status

As direct values of *in situ* phosphorus content concurrent with the zooplankton and chlorophyll data reported here are unavailable or inaccessible, chlorophyll is used as a standard general proxy for nutrient content (especially P). This approach is based on the well-established interdependency of these variables, as per classic Vollenweider (1975) and related modelling approaches (e.g. OECD, 1982; Walmsley and Thornton, 1984), despite potential confounding increases of chlorophyll to P when cyanophyte abundance increases with rising trophic status.

Results

ZB in relation to chlorophyll level

Table 1 gives the regression statistics for total ZB in relation to total chlorophyll (as a proxy measure of food supply). As expected, ZB increases with rising food supply (i.e. Fig. 1a), except in the eutrophic reservoirs in which the change to a negative regression slope (significant or not) is consistent with declining food quality (see below), or rising fish predation (for which no empirical data exist in South African reservoirs). The one system with empirical food quality data (Fig. 2, Hartbeespoort Dam) supports the former 'food quality' explanation. In this system, ZB declines with 'inedible' chlorophyll, in contrast to its increases with 'partly edible' and 'edible' chlorophyll fractions (see further the section on 'ZB and ZB/Chl ratios in relation to phytoplankton edibility' below).

Table 3
Adult carapace lengths (mm) of different species of *Daphnia* recorded in the specified reservoirs. Values are averages for n sampling dates (at multiple sites in the case of Rietvlei). The number of individuals measured on each sampling date generally ranged from 25 to 60. Data sources indicated.

	Parameter	Midmar	Albert Falls	Nagle	Inanda	Wagendrift	Vanderkloof	Spioenkop	Hartbeespoort	Rietvlei
D. gibba	Mean	-	-	-	-	-	2.94	X	-	-
	Range						2.31-3.90			
	n						191			
D. pulex	Mean	2.17	1.92	1.98	X	X	-	1.95	X	
	Range	1.38-2.84	1.04-2.60	1.80-2.30				1.63-2.28		
	n	205	195	14				6		
D. longispina	Mean	1.45	1.38	1.41	1.27	X			X	
	Range	1.19-1.94	0.93-1.89	1.26-1.57	1.20-1.56					
	n	106	193	14	15					
D. barbata	Mean	-	-	-	-	-	1.58	1.82	-	-
	Range						1.22-2.20	1.56-1.96		
	n						231	5		
D. laevis	Mean	X	X	1.65	1.62	-	-	-	-	-
	Range			1.52-1.80	1.57-1.80					
	n			7	15					
D. pulex/ longispina	Mean					1.69			-	2.25
	Range					1.36-1.94			up to 2.5	1.41-3.21
	n					9			-	43

The negative relationship for Inanda Dam (Table 1), although weak, is an interesting exception. Although classed as a 'clear-water' system on account of its low median chlorophyll value in the present data set, it is the most downstream and, correspondingly, enriched system in the Umgeni River reservoir cascade (Midmar, Albert Falls, Nagle and Inanda). Inanda is commonly viewed as functionally eutrophic, exhibiting prominent open-water blooms of *Microcystis*, generally high chlorophyll values, and extensive rafts of floating hydrophytes (*Eichornia* and/or *Pistia*) in its littoral margins.

ZB/Chl ratios in relation to within-reservoir chlorophyll levels, and between-system trophic status

Figure 3 shows estimates of the ZB/Chl ratio within 4 reservoirs of progressively lower trophic status (i.e. declining maximal chlorophyll levels in concurrent data sets). In each reservoir, ZB/Chl declines as chlorophyll increases, contrary to the standardising effect expected of this division procedure (i.e. Fig. 1b). The declines are best described as power regressions, in which the negative exponents decline progressively with declining trophic status (Figs 3a to 3d), with broadly parallel declines in coefficients of determination. In effect, the standardising procedure effectively weakens with rising trophic status, resulting in correspondingly greater declines in ZB/Chl, (and thus ZB/PB) ratios. Although not illustrated, a comparable inverse trend, best described by negative power regressions, is evident for all other reservoir data sets, apart from Spioenkop, where a positive linear relationship exists. However, it is notable that the maximal ZB/Chl values within each system decline markedly as trophic status drops (Fig. 3).

ZB and ZB/Chl ratios in relation to phytoplankton edibility

Changes in ZB with chlorophyll edibility indicated above (Fig. 2) are also reflected in disparate differences in the rates of decline of the ZB/Chl ratio with rising chlorophyll, according to edibility class (Fig. 4). Although ZB/Chl ratios are high at low chlorophyll levels regardless of edibility, the sharpest decline of the ratio and its predominantly low values at higher chlorophyll levels are both associated with inedible chlorophyll. However, as noted above, the ZB/Chl ratio also declines with rising edible and partly edible chlorophyll, invoking a cause-effect dilemma. Are the high ZB/Chl ratios at low chlorophyll levels a consequence of chlorophyll reduction by ZB grazing, and/or is zooplankton food-limited? Overall, however, Figs 2 and 4 conform to the hypothesis that declining ZB is associated with poor food quality, certainly not an unexpected trend. Especially in eutrophic systems, however, the role of detrital food derived from high autotroph abundance adds an unquantifiable confounding effect to this evaluation.

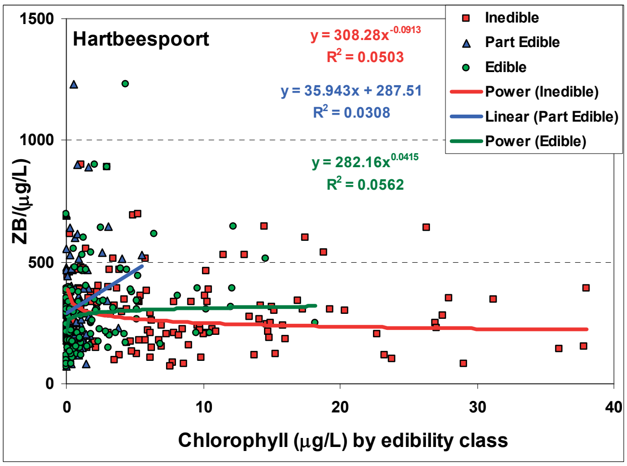

Figure 2
Changes in ZB in Hartbeespoort Dam in relation to concurrent chlorophyll levels differentiated according to edibility classes. Accompanying best fit linear or power regression relationships indicate positive relationships apply except for 'inedible' chlorophyll. Data extracted from Jarvis (1987).

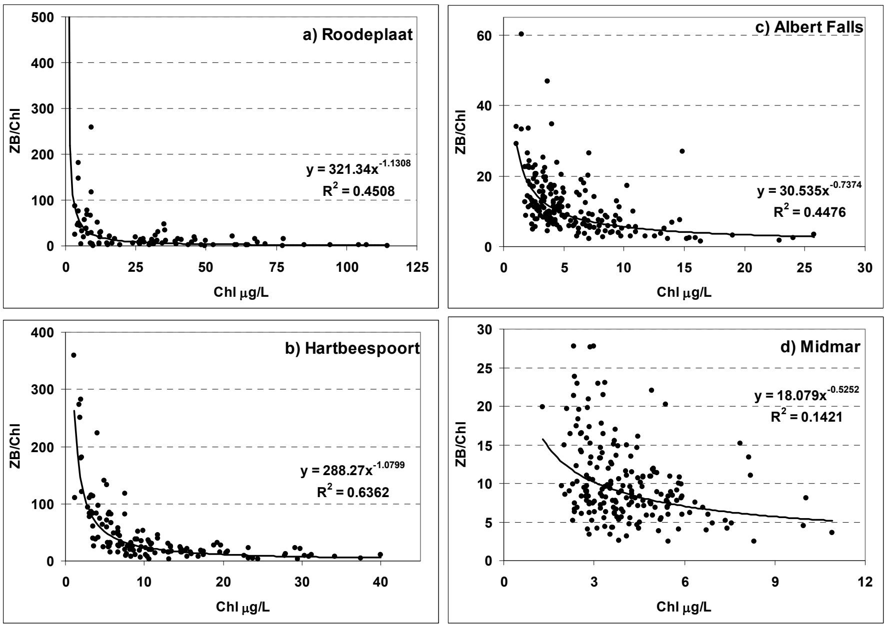

Figure 3

ZB/Chl ratios in relation to concurrent chlorophyll levels within 4 South African reservoirs of declining trophic status (Panels a to d). Note the sequential decline in exponents and most regression coefficients of the power curves fitted for each system.

Daphnia *biomass in relation to food supply and food type*

Contrasts in relationships between *Daphnia* biomass and chlorophyll among reservoirs provide further indications for the role of declining food quality as a factor reducing ZB with rising chlorophyll. Figure 5 shows a clear switch from a positive to a negative relationship between Midmar and Albert Falls. Importantly, total zooplankton (and total cladoceran biomass) rose with food supply in both systems (Table 1), with a negative relationship only appearing for total *Daphnia* biomass (Fig. 5). The same pattern is apparent in Hartbeespoort Dam, in which *Daphnia* density also declined as inedible chlorophyll increased, but increased with rising quantities of edible, and especially partly edible chlorophyll (Fig. 6). This trend is consistent with the well-known susceptibility of *Daphnia* to the disruptive influences of large inedible particles like *Microcystis* on its feeding ability (Sommer et al., 1986; Jarvis et al., 1987). *Microcystis* is numerically more prominent in Albert Falls than Midmar (Hart, 2006a), and predominates in Hartbeespoort Dam (NIWR, 1985; Jarvis 1987), while blooms of *Ceratium*, another large inedible taxon, have also appeared more recently in Hartbeespoort (Van Ginkel et al., 2001) as well as Albert Falls (Hart and Wragg, 2009).

Median ZB/PB ratios between reservoirs of different trophic status

Median ZB/Chl ratios for the 10 study reservoirs in 3 turbidity and/or trophic status groupings are

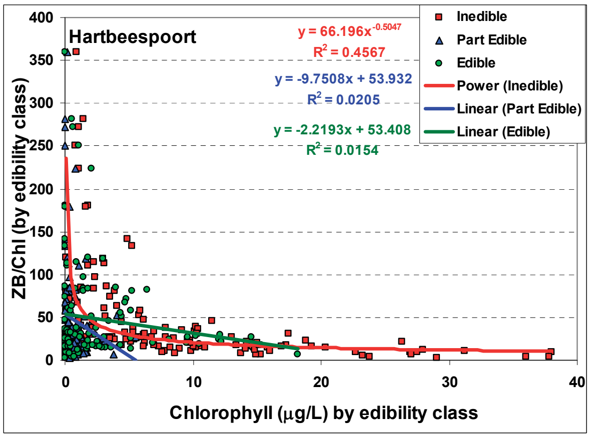

Figure 4

Changes in the ZB/Chl ratio in Hartbeespoort Dam in relation to concurrent chlorophyll levels differentiated according to edibility classes. Best fit linear or power regressions for each chlorophyll class are plotted. Note that the most significant decline is associated with inedible chlorophyll.

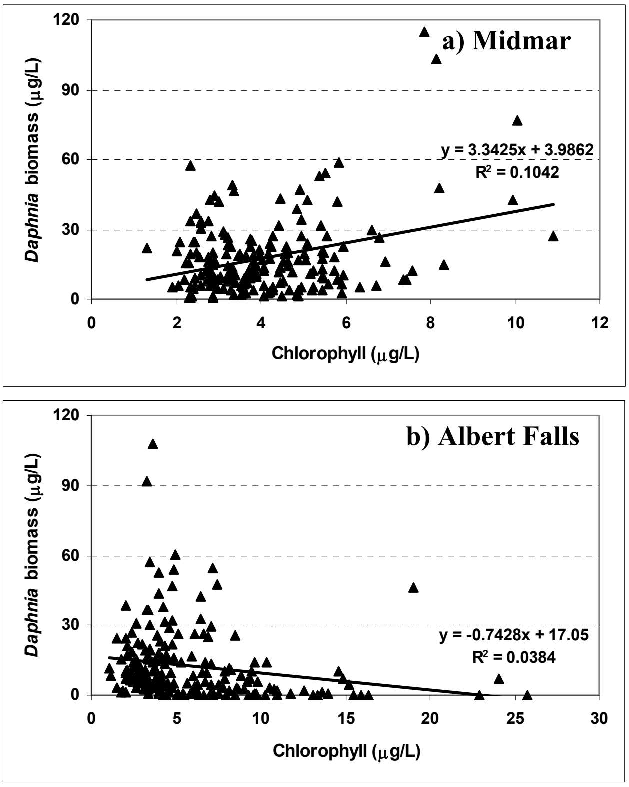

Figure 5

Daphnia *biomass in relation to concurrent chlorophyll values in 2 adjacent reservoirs. The inversion from a positive relationship in Midmar to a negative relationship in Albert Falls is attributed to a decline in food quality in the latter, associated with greater quantities of large inedible taxa such as* Microcystis*.*
Both regressions are significant: P << 0.001 for Midmar, and P < 0.01 for Albert Falls.

http://dx.doi.org/10.4314/wsa.v37i4.9
Available on website http://www.wrc.org.za

given in Table 2. Ratios are arrayed according to median concurrent chlorophyll values within each reservoir class. Apart from Roodeplaat Dam, median values of ZB/Chl between individual systems (Fig. 7a) unexpectedly rise (to nearly 30, as median chlorophyll rises to around 15 µg/ℓ), rather than declining with chlorophyll as they do within individual systems. Roodeplaat's position becomes less discordant if average rather than median values are used (Fig. 7b), but the trend remains the same – an increase in ZB/Chl with chlorophyll before an inflection (based on only 1 data point) drops the ratio with further increases in chlorophyll. Importantly, the relationships are described by strongly positive but slightly less significant linear regressions.

This generally positive relationship between average ZB/Chl ratios and average ambient chlorophyll levels used to approximate trophic status has important implications regarding the prospective utility of biomanipulation. It also raises the question of how or why ZB increases with trophic status, given the associated general decline in food quality. These points are discussed below.

Discussion

Converting the median ZB/Chl ratios given for South African reservoirs in Table 2 into corresponding ZB/PB values indicates that the South African values are broadly comparable with those reported by Jeppesen et al. (2003a) for 466 higher latitude (north temperate to arctic) systems. However, they tend to rise (Fig. 7) from 0.05-0.1 (i.e. 5-10%) to ~0.4 (40%) across the trophic spectrum, rather than declining from a mean ratio value of 35% in the most oligotrophic lakes to less than 0- to 20% in the most eutrophic lakes in Jeppesen et al.'s (2003a) data set. The decline observed by these authors was attributed to empirically determined rises in fish density and associated predation pressure. Almost all South African values are higher than 2 natural lake values reported by Havens et al. (2009) for the shallow temperate Lago Trasimeno (~6.5%) and the cyanophyte-dominated subtropical Lake Apopka (~1%). The latter value led the authors to argue that their findings 'support an emerging view that fish predation limits the biomass of crustacean zooplankton in subtropical lakes'. (The ZB/PB ratios for these 2 lakes are averages 'eye-balled' from their Fig. 2c, and adjusted by ~1.28 to correct for differences between their ZB/PB ratios which are based on carbon (viz. 0.48*ZB/25*Chlorophyll), using the Chl:C ratio proposed by Perga et al. (2006) and Taipale et al. (2008), rather than the dry weight ratios determined here (viz. ZB/67*Chlorophyll)).

Notably, a fundamental difference exists within and between South African reservoirs. Within individual systems, the ZB/Chl ratio declines with rising chlorophyll (Fig. 3), whereas, conversely, median (Fig. 7a) or mean (Fig. 7b) ZB/Chl ratios rise with increasing chlorophyll between systems (Fig 7). This contrast merits appraisal.

As the decline in ZB/Chl with rising chlorophyll within individual reservoirs occurs regardless of trophic status (Fig. 3), it is difficult to attribute the overall pattern to a declining food quality effect. Rather, the changes may reflect temporal dynamics within individual systems. The high ZB/Chl ratios at low chlorophyll plausibly reflect a relatively high ZB grazing on a low standing stock of chlorophyll with a relatively high turnover rate – the classic 'inverted trophic pyramid' characteristic of pelagic systems. They also imply a food-limited zooplankton.

Subsequent declines of the ratio plausibly mirror the approach to a nominally 'standard' predator/prey state within

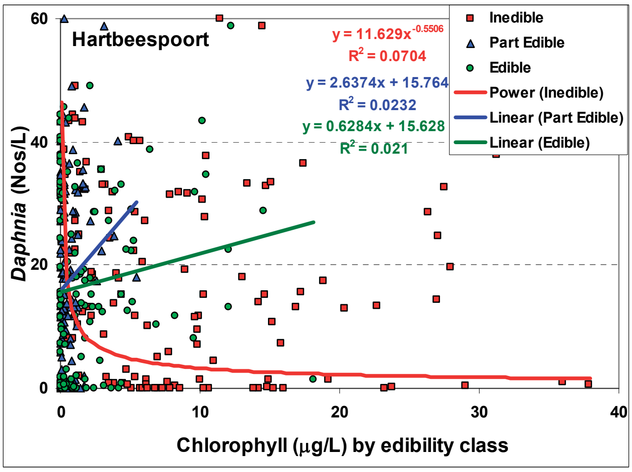

Figure 6

Daphnia *density in Hartbeespoort Dam in relation to concurrent levels of chlorophyll of different food quality. Positive relationships with edible and partly edible foods are replaced by a strong decline with inedible food. The presence/abundance of* Daphnia *at low levels of inedible food is attributable to the concurrent presence of edible and/or partly edible foods in natural food mixtures.*

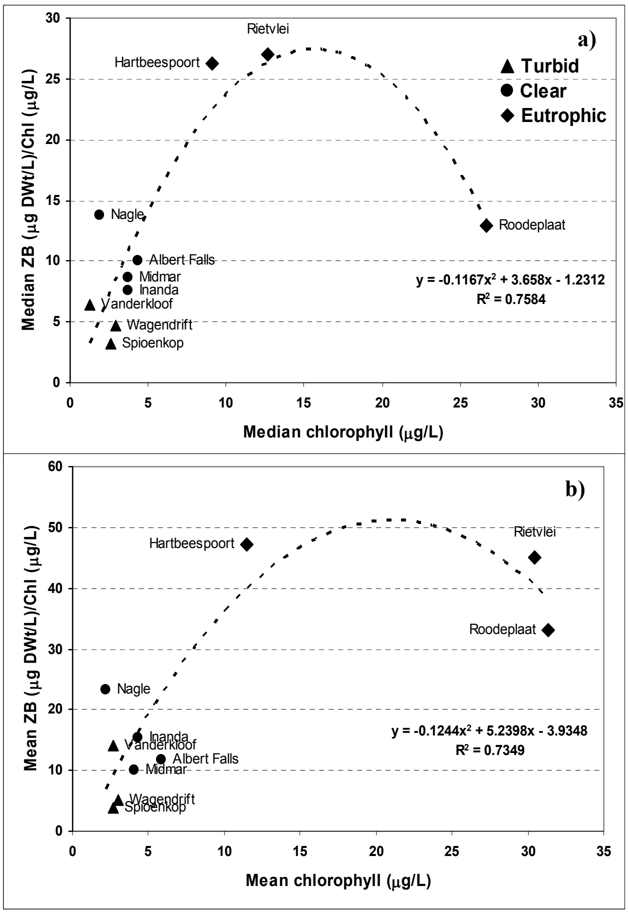

Figure 7

Reservoir-specific a) median and b) average values of ZB/Chl values in South African reservoirs of 3 trophic classes in relation to corresponding chlorophyll values. The strong positive relationship for medians is inflected by a single low value for Roodeplaat Dam. The reality of this inflection is discussed in the text.

the system, with further declines heralding the possible onset of food quality constraints. It is, however, implausible to attribute within-system changes in ZB/Chl to increasing fish predation as chlorophyll rises, since life-history constraints of the fish taxa known in the reservoirs will restrict short-term (intra-annual) changes in fish density.

The marked decline in ZB/Chl values between eutrophic and oligo-mesotrophic systems (Fig. 3) appears consistent with and attributable to the differences in overall system productivity; eutrophic systems support higher standing stocks – as indicated clearly in the differences in median values of ZB and chlorophyll between systems of contrasting trophic status (Table 2).

The increase (with one exception) in reservoir-specific ZB/Chl ratios with rising productivity (Fig. 7a) raises the question of how ZB is able to increase with trophic status despite the accompanying decline in food quality. Detritus arising from autochthonous production is likely to increase, plausibly augmenting the food supply. Indeed, the importance of bacteria as a food resource for zooplankton, especially in eutrophic waters, was identified by Gliwicz (1969), although empirical evidence from *in situ* grazing experiments in Hartbeespoort Dam (Hart and Jarvis, 1993) indicated that bacteria accounted for barely 3% of total cladoceran dietary carbon intake, perhaps owing to the notably small size of natural free-living bacteria in this system (Robarts et al., 1986); the value also under-estimates the food value of bacteria in detritus-bacterial aggregates.

The microbial loop generated from autochthonous (and/or allochthonous) detritus adds additional food sources for particular zooplankton. Allochthonous terrestrial energy subsidies of aquatic food webs have been identified as important in small lakes (e.g. Cole et al., 2010). In reservoirs, with disproportionately high catchment areas, and especially point-source organic inputs from wastewater treatment works, such subsidies may assist strongly in the accumulation of ZB relative to ambient chlorophyll levels, and generate the parallel increases in ZB/Chl. No explanation can be offered for the deviation shown by Roodeplaat (Fig. 7a). Its outlying nature possibly reflects a systematic difference in sampling methodology. It is the only totally independent data point in the present collation – and the author of this paper was directly or indirectly involved in research on all of the other reservoirs examined herein. Alternatively, it may reflect limited habitat suitable for zooplankton occupancy, owing to the extent of seasonal hypolimnetic anoxia in this system, for which Van Ginkel (1987) proposed ‘space’ as the major constraint on zooplankton. However, similar space constraints apply in Hartbeespoort Dam where anoxic hypolimnia occur extensively (NIWR, 1985).

To date, zooplanktivory has been examined in only 2 comprehensive ecosystem studies of South African reservoirs – Vanderkloof (Tomasson, 1983) and Hartbeespoort (NIWR, 1985; Cochrane, 1985). In both these systems, overall fish predation on zooplankton was recorded as low or negligible. In line with this, the increases in ZB/Chl with rising productivity strongly counter prospects that fish predation on zooplankton becomes more significant as system productivity rises. This inference is empirically supported by the invariably large sizes of *Daphnia* spp. present in the reservoirs (Table 3). Such large daphniids (and other zooplankton components in some systems) strongly contraindicate the existence of strong, sustained visual zooplanktivory (Hrbáčeck and Hrbáčková-Esslová, 1960; Brooks and Dodson, 1965; Hart and Bychek, 2011), commonly evident in warm subtropical lakes (Jeppesen et al., 2007). Overall, biomanipulation-induced reductions in zooplanktivory are unlikely to manifest in major improvements in grazer control of large planktonic algae and/or cyanophytes that dominate the eutrophic and hypertrophic South African reservoirs, the inedibility and suppressive influence of which on daphniids in particular is ubiquitously acknowledged by all authorities.

Prospects for biomanipulation paradoxically appear theoretically or practically better in Australian reservoirs, in which zooplanktivorous fishes enigmatically appear important (Matveev et al., 2002; Hunt et al., 2003; Matveev, 2003; Sierp et al., 2009), in contrast to South African systems that are otherwise limnologically similar.

In natural lakes, planktivorous fish generally impact significantly on zooplankton, as observed in many cooler temperate lakes around the world (Jeppesen et al., 1997, 2003a; Vakkilainen et al., 2004), and the ZB/PB ratio commonly declines with rising trophic status (e.g. Jeppesen et al., 2003a). As fish stocks rise concurrently (e.g. Jeppesen et al., 2003a, 2005, 2007; Havens et al., 2009), the decline in ZB/PB ratio is plausibly attributable to rising top-down controls of fish on zooplankton; thus prospects of ameliorating the consequences of eutrophication by top-down biomanipulation – reducing zooplanktivorous fish – appear more promising.

Conversely, however, Vanni et al. (2006) effectively ascribe the reduction in ZB/PB to increases in PB in response to nutrient recycled by fish rather than ZB depletion by fish; in other words, a bottom-up rather than top-down effect. Their argument suggests that the most likely positive benefits of fish manipulation in eutrophic South African reservoirs are likely to derive from bottom-up rather than top-down effects of fish assemblage modifications. This would involve removal of overabundant ‘coarse’ fish species – particularly exotic common carp (*Cyprinus carpio*) whose bioturbation effects undoubtedly sustain strong internal nutrient loadings, along with indigenous catfish (*Clarias gariepinus*) that both dominate the ichthyomass in the eutrophic reservoirs studied (Harding et al., 2009).

Conclusions

In individual South African reservoirs, ZB/Chl ratios decline with rising ambient chlorophyll levels, regardless of trophic status. Conversely, disregarding Roodeplaat Dam, median (or mean) values of the ZB/Chl ratio for each separate system increase with rising median (or mean) chlorophyll levels, indicating a progressive increase of ZB/Chl with system trophic status.

Although evidence regarding fish abundance in reservoirs is severely limited, the increase in ZB/Chl ratios with rising trophic status between reservoirs implies that fish predation on zooplankton has little or no significant impact on ZB, and any such effect certainly does not increase progressively with trophic status. Accordingly, food web modifications to reduce fish predation on zooplankton will be futile to moderate/correct the consequences of eutrophication. In-lake management options other than top-down biomanipulation will be required to reduce the symptoms of eutrophication until such time as its root cause – excessive external nutrient loading – can be effectively controlled. Much greater attention to fish-zooplankton-phytoplankton interactions in reservoirs is also required to provide a secure platform for sustainable (and multi-purpose) management of South African river reservoirs.

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