TOP-DOWN CONTROL OF PHYTOPLANKTON BY ZOOPLANKTON IN TROPICAL RESERVOIRS IN SINGAPORE?

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ABSTRACT. – The potential for top-down control of phytoplankton populations by zooplankton in tropical lentic systems was examined in 12 shallow reservoirs using a 15 year data set. Regression analyses showed that calanoid, cyclopoid, and rotifer, but not cladoceran, abundances were important in influencing the structure of phytoplankton communities. Counts of chlorophytes *Ankistrodesmus, Cosmarium* and *Peridinium* decreased with increasing calanoid, cyclopoid and rotifer numbers while populations of the diatoms *Melosira* and *Synedra*, *Planktotrix* and *Scenedesmus* were inversely correlated with the abundance of calanoid copepods. Cyanobacteria populations, with the exception of *Planktotrix*, were not negatively affected by increasing zooplankton numbers. This study supports the hypothesis that zooplankton exert 'top-down' control on certain algal communities in tropical lentic systems, however, the use of broad taxonomic groups (calanoids, cyclopoids, cladocerans, and rotifers) potentially masks information on how specific zooplankton exert control on phytoplankton communities. We suggest that a greater taxonomic resolution of the zooplankton fauna is necessary to further understand the complex associations between phytoplankton and zooplankton communities within tropical reservoirs. Nevertheless, even at this coarse scale of investigation, this paper presents clear trends that support the importance of zooplankton in the control of freshwater algal abundance.

KEYWORDS. – Top-down control, zooplankton-phytoplankton relationships, cyanobacteria, tropical reservoirs, Singapore.

INTRODUCTION

Top-down control (i.e., the effects of a higher trophic level on those below it) of phytoplankton by planktivorous fish and zooplankton in lakes and reservoirs is one of the key ecological processes in lake ecosystems (Sommer and Sommer, 2006), contributing to the maintenance of dynamic balance between alternative stable states of plant-dominated clear water and phytoplankton-dominated turbid water (Scheffer et al., 1993). In temperate lentic systems, zooplankton are known to be efficient controls of phytoplankton biomass (Carvalho, 1994; Jeppesen et al., 2007) and community structure (Lampert et al., 1986).

Top-down control of phytoplankton by zooplankters occur by two principle mechanisms: i) grazing pressure, and ii) nutrient recycling (Vanni & Layne, 1997). Zooplankton have been shown to exert selective grazing pressure on standing crops of algae (Timms & Moss, 1984; Butler et al., 1989). This is largely a function of their filtering rates (Peters & Downing, 1984) and and their preferences for different species, morphologies and size of phytoplankton (Brooks & Dodson, 1965; Stemberger & Gilbert, 1985; DeMott, 1986). Behavioural and physiological mechanisms that effectively deter zooplankton grazing include toxin production in cyanobacteria such as *Aphanizomenon* and

Microcystis (Agrawal, 1998) and the formation of colonies by single-celled phytoplankton such as *Scenedesmus* (Holm et al., 1983; Lürling & van Donk, 1997). Biased feeding can lead to the decline of certain phytoplankton genera (Lehman & Sandgren, 1985) and indirectly promote the growth of competitors (Lynch & Sharpiro, 1981). Changes in the composition of zooplankters can therefore lead to shifts in phytoplankton community structure (Bergquist et al., 1985; Bergquist & Carpenter, 1986; Vanni, 1987). Conversely, declines in the abundance of favoured phytoplankton can subsequently result in the collapse of the dominant zooplankton (Lampert et al., 1986).

Zooplankters affect nutrient availability to phytoplankton via two main processes (Vanni & Layne 1997). First, the community composition has a direct effect on nutrients due to unequal rates of release and cycling of nitrogen (N), phosphorus (P) and silicon (Si) by different zooplankton grazers (Lehman, 1980; Sterner, 1990). For example, a critical element for diatom growth, silicate, is recycled by many zooplankton less efficiently than nitrogen and phosphorus, therefore creating an environment that favours the growth and proliferation of non-Si-limited genera of phytoplankton (Sterner, 1990). Second, zooplankters mediate phytoplankton community shifts between nitrogen and phosphate limited systems, for example, a system can move from N-limited to P-limited when the dominant zooplankton are relatively large cladocerans (Elser et al., 1988). This is because different types of zooplankton have different nitrogen or phosphorus requirements, which affects N:P ratios in the aquatic environment (Balseiro et al., 1997). As cladocerans have a low N:P ratio but high P content, they require more P from their diet and excrete less P than N, pushing the phytoplankton community towards being P-limited (Sterner et al., 1992).

High temperatures coupled with high concentrations of nutrients in tropical shallow lakes means that phytoplankton biomass typically remains greater than minimum threshold food concentrations; therefore top-down effects of grazers can be difficult to detect (Jeppesen et al., 2005; Rückert & Giani, 2008). Constant high annual temperatures correspond to an increase in filtering and metabolic rates but also lead to smaller forms of zooplankton (Dumont et al., 1994). The absence of certain large predatory zooplankton in equatorial regions could influence the structure of both zooplankton and phytoplankton communities (Dumont, 1994). Higher temperatures also limit the amount of energy stored by zooplankton. Increasing metabolic activities and high energy requirements could be further compounded by lower availability of nutritious phytoplanktonic food sources (Pinto-Coelho et al., 2005). Unfortunately, very few zooplankton-phytoplankton studies have been undertaken in the tropics and knowledge compared to the Northern Hemisphere is poor (Dussart et al., 1984.). The strength of top-down pressure exerted by zooplankters in tropical systems might therefore differ significantly from the zooplankton regulation of phytoplankton biomass in temperate aquatic ecosystems.

Low et al. (in review) showed that phytoplankton populations in the 15 reservoirs maintained by the Public Utilities Board were only marginally influenced by nutrient concentrations (but they appeared to respond to underlying geology). This present study aimed to add to our understanding of tropical lentic phytoplankton dynamics by examining the potential importance of top-down control by zooplankters. We used data available from long-term monitoring to elucidate the relationships between abundances of functional zooplankton groups (rotifers, cladocerans, adult forms of calanoid and cyclopoid copepods) and phytoplankton populations. Our main objectives were to i) characterise phytoplankton community structure and, ii) establish the effect of zooplankton abundance on phytoplankton community structure. The results of this study not only have direct implications for ecosystem function, but may also have applications for the management of water quality.

MATERIALS AND METHODS

Study sites. – Singapore is located in Southeast Asia, one degree north of the equator. It currently has 15 drinking water reservoirs with two more under construction, however, the most complete phytoplankton and zooplankton data set is only available for 12 of these lakes and only these shall be discussed here (Fig. 1). All the reservoirs are shallow (2–22 m deep) and range from eutrophic to hypertrophic hypertrophic states as defined by Forsberg & Ryding (1980), with phosphate and nitrate levels ranging between <0.01 to 1.5 mgl^{-1}. They are highly managed and serve multiple purposes including recreational activities and flood control in addition to holding the nation's drinking water supply. The reservoirs are managed as three types of catchments; unprotected, western military protected and central protected. In the unprotected catchment (Kranji, Pandan, Bedok, Marina and Lower Seletar reservoirs) land use is not strictly controlled. Access to the western military protected catchment, and hence the reservoirs within it (Tengeh, Poyan and Murai reservoirs), is restricted (Wee & Corlett, 1986). In the central protected catchment (Upper and Lower Peirce, Upper Seletar and MacRitchie reservoirs), certain recreational activities such as canoeing and golfing are allowed in or around the reservoirs, but large-scale commercial activities on adjacent land is prohibited. Water is transferred between reservoirs to maintain volume or to discharge excess storage. Eight out of the 12 reservoirs studied have an artificial mixing system installed in them to help keep dissolved oxygen levels above 3mg L^{-1}.

Sample collection and data treatment. – Sampling was conducted as part of a long-term monitoring programme and therefore subject to changes in historical sample handling and refinements to phytoplankton identification. The list of phytoplankton taxa monitored was revised in 2009 (Mitrovic & Croome, 2009). The phytoplankton previously identified as *Oscillatoria* was in actual fact comprised of two species of *Planktotrix*, thereafter labelled *Planktotrix* sp. 1 and 2. *Raphidiopsis* was found to be a mixture of both *Raphidiopsis* and *Cylindrospermopsis*. Samples previously

labelled *Oscillatoria* and *Raphidiopsis* were each treated as a single genus in all statistical analyses.

Between January 1992 and December 2006, phytoplankton and zooplankton were sampled on a monthly basis from a fixed site at each of the 12 reservoirs (Fig. 1). Samples were collected at a depth of 0.3 m from the water surface and kept in a cooler with ice while transported to the laboratory. Phytoplankton samples were fixed with 5 ml of Lugol's solution and agitated before 100 ml of the mixture was transferred to a graduated measuring cylinder and allowed to stand overnight for sedimentation. The supernatant was siphoned away to obtain a concentrated sample of 10 ml of which 1 ml was pipetted onto a Sedgwick Rafter counting cell. Usually, 20–50 microscopic fields were counted per slide and up to two slides were counted if algal counts exceeded 300 counts ml^{-1}. If the algal density in the sample was lower than 300 counts ml^{-1}, up to 300 fields were counted. Only 32 algae were identified to genus-level; in addition, 'coccoid greens' were also included (see Low et al., in review). Algae not identified to genus-level were recorded as Chlorophyta, Cyanophyta, Flagellata, Bacillariophyta (diatoms) and a category 'others' for any unidentified phytoplankton. Algal counts were expressed as number ml^{-1}. Phytoplankton genera, *Kirchneriela* and *Sphaerocystis*, together with the group 'coccoid greens', were omitted from the analyses as they were present in less than 10% of the samples and did not contribute to high loadings on any axes in the Principal Component Analysis (score range: 0.05–0.12).

For zooplankton, 0.1 m^3 of reservoir water in 10 L pails was filtered through a 40 μm net to obtain a sample of approximately 40 ml. On return to the laboratory, the sample was fixed with 3 ml of Lugol's solution. This fixed sample was diluted to 100 ml of which a 1 ml subsample was transferred onto a Sedgwick Rafter counting cell. The subsample was allowed to settle before being examined under 100× or 150× magnification, with at least 200 fields counted. A duplicate subsample was similarly examined and the median of the two reported. Zooplankton counts were expressed as number per m^3. Due to the lack of suitable keys for zooplankton identification in Southeast Asia, samples

were only differentiated into six general groups: calanoids, harpacticoids, cyclopoids, cladocerans, ostracods and rotifers. Whereas calanoid, cyclopoid, cladocerans and rotifers were represented in over 98% of samples, harpacticoids and ostracods were rarely present and so were omitted from the analyses. Utilisation of higher taxonomic levels has been successful in a number of ecological studies (Pace, 1986; Zhao et al., 2008). The four functional groups used in this research (rotifers, cladocerans, adult forms of calanoid and cyclopoid copepods) are often chosen as indicators of environmental condition in aquatic ecosystems, and demonstrate strong responses to nutrient levels. With nutrient enrichment, the relative abundance of calanoid copepods generally decreases, while small-bodied cyclopoid copepods and cladocerans usually become dominant macrozooplankton in eutrophic lakes (Brooks 1969). Eutrophication also leads to an increased importance of rotifers (Pace & Orcutt 1981, Attayde & Bozelli, 1998).

For both zooplankton and phytoplankton, missing values were replaced with the annual mean number for each reservoir. All data were log (n+1) transformed to minimise skewness and kurtosis (Hair et al., 2005).

Statistical analyses. – Principal Components Analysis (PCA) was used to generate compound variables that captured the data dynamics across the large number of phytoplankton genera without losing information (McMarigal et al., 2000). PCA provides a meaningful interpretation of each principal component based on the variables that are most important in defining that dimension (McMarigal et al., 2000). The factor scores for each case were extracted from the PCA and used as the composite variables in subsequent analyses.

In order to identify correlations between zooplankton and phytoplankton abundances, log-transformed principle component scores were regressed against log-transformed abundance of zooplankton functional groups via stepwise regression. Stepwise regression is a procedure in which the order of the variables entered is based solely on a predetermined statistical criteria (Tabachnick & Fidel, 2006), that is, variables can be omitted at any point if they no longer contribute significantly to the regression (Tabachnick & Fidel, 2006). All analyses were performed in PASW 18.0 (formerly SPSS, IBM, 2009).

RESULTS

The first three Principal Component axes explained 39% of the total variation in phytoplankton abundance from all reservoirs across all sampling times (Table 1). The first PC axis (PC1) accounted for 20.4% of the total variation (Table 1) and all strong loadings on this axis were were positive. PC1 indicated that major sources in the phytoplankton community variation were driven by the abundance of the cyanobacteria *Planktotrix* sp. 1 and 2, the green algae *Scenedesmus*, and two diatoms, *Melosira* and *Synedra*. PC2 correlated positively with *Peridinium*, *Cosmarium*, *Ankistrodesmus* and negatively with *Trachelomonas*. PC3 was inversely correlated with

Fig. 1. Location of reservoirs within Singapore within which zooplankton and phytoplankton samples were monitored every month between 1992 and 2006. 1. Bedok, 2. Lower Seletar, 3. Upper Seletar, 4. Lower Peirce, 5. Upper Peirce, 6. MacRitchie, 7. Kranji, 8. Pandan, 9. Jurong Lake, 10. Murai, 11. Poyan and 12. Tengeh.

Table 1. Loadings of phytoplankton genera on Principal Component axes describing the major source of variation amongst reservoirs and time. Phytoplankton genera with high contribution to the PC axes are in bold. Loadings above 0.6 for PC1, 0.5 for PC2, and 0.4 for PC3, were considered high.–

Variable	PC1	PC2	PC3
% Variation	20.4	11.4	7.2
Actinastrum	0.289	–0.348	0.082
Anabaena	0.311	–0.414	**–0.521**
Anabaenopsis	0.510	–0.221	0.351
Ankistrodesmus	0.309	**0.585**	–0.344
Botryococcus	0.124	0.074	0.223
Ceratium	0.169	–0.234	–0.199
Cosmarium	0.335	**0.625**	0.012
Crucigenia	0.520	–0.158	0.088
Cyclotella	0.371	–0.313	0.003
Dictyosphaerium	0.320	0.211	**–0.460**
Euglena	–0.036	0.038	0.227
Glenodinium	–0.089	–0.021	0.213
Planktolyngbya	0.580	–0.377	0.078
Melosira	**0.674**	–0.184	–0.448
Merismopedia	0.579	0.177	0.138
Microcystis	0.564	–0.479	–0.364
Navicula	0.451	0.370	0.388
Pseudoanabaena	0.392	–0.043	0.280
Nephrocytium	0.039	–0.082	0.073
Nitzschia	0.197	–0.337	0.359
***Planktotrix* 1 & 2**	**0.770**	–0.101	0.093
Other cyanobacteria	0.532	–0.049	**–0.450**
Other diatoms	0.507	0.287	0.331
Other flagellates	0.035	0.133	0.241
Other greens	0.547	0.160	0.284
Others	0.400	0.602	–0.159
Pediastrum	0.578	–0.085	0.070
Peridinium	0.183	**0.689**	0.056
Raphidiopsis	0.580	–0.432	0.097
Scenedesmus	**0.747**	–0.043	–0.170
Staurastrum	0.464	0.377	–0.292
Synedra	**0.679**	–0.038	0.180
Tetraedon	0.592	0.504	0.180
Trachelomonas	0.133	**–0.552**	0.341

Anabaena, chlorophyte *Dictyosphaerum*, *Melosira* and "other cyanobacteria" (Table 1).

All the zooplankton groups examined had significant effects on phytoplankton populations (Table 2). Calanoids consistently had negative influences on PC1 (see calanoid vs PC1 in Table 2; Fig. 2) and thus *Planktotrix*, sp. 1 and 2, *Melosira*, *Synedra* and *Scenedsemus*. Rotifers correlated positively to PC1 but negatively to PC2 while cyclopoid regressed negatively to both PC1 and 2 (see zooplankton groups vs. PC2 in Table 2). Calanoid, cyclopoid and rotifer abundances were associated with a reduction of *Peridium*,

Cosmarium and *Ankistrodesmus* but elevated numbers of *Trachelomonas* (Figs. 2–4). Rotifer and cyclopoid counts were also linked with higher counts of *Planktotrix*, *Scenedesmus*, *Melosira* and *Synedra* (PC1) (Figs. 3, 4). Cladocerans were unusual in that they were the only zooplankter that did not significantly influence either PC1 or PC2; but they did significantly affect PC 3 (Table 2). "Other cyanobacteria", *Dictyosphaerum* and *Melosira* increased with cladoceran abundance (Fig. 5).

DISCUSSION

This analysis of zooplankton and phytoplankton populations in 12 tropical reservoirs over a 15 year period showed that calanoids, rotifers and cyclopoids abundances were negatively correlated with chlorophytes *Ankistrodesmus* and *Scenedesmus*; the desmid *Cosmarium*; and the flagellate *Peridinium*, while cladocerans did not covary inversely with any of the phytoplankton genera monitored. Cyanobacteria abundances, with the exception of *Planktotrix*, did not appear to be negatively affected by increasing counts of zooplankters. These results fit the hypothesis that zooplankton were exerting top-down control on phytoplankton biomass.

Decreases in the abundance of chlorophytes such as *Scenedesmus* and *Ankistrodesmus* were correlated with increases in the abundances of rotifers, cyclopoids and calanoids. Most groups of zooplankton readily accept *Scenedesmus* and *Ankistrodesmus* as a part of their intake (Sterner, 1993; Lürling et al., 1997; Kilham et al., 1997), possibly due to the relatively high concentrations of polyunsaturated fatty acids, eicospaentaenoic acids and docosahexaenoic acids possessed by these taxa (DeMott & Müller-Navarra, 1997; Macedo & Pinto-Coelho, 2001). Calanoid copepods were the only group of zooplankton among the four studied that showed a negative correlation with abundances of the diatoms *Synedra* and *Melosira*. Calanoid copepods are known to be efficient grazers of these diatom genera (Vanderploeg et al., 1988) as compared to other crustaceans which tend to avoid them (potentially a result of their ability to release repellent odour compounds) (Jütter, 2005; Leflaive & Ten-Hage, 2009).

Cladocerans were the only group of zooplankton that did not have an inverse correlation with any of the phytoplankton monitored. As cladocerans are highly efficient and non-selective herbivores (Becker et al., 2004) this result is unusual, and is inconsistent with the large number of temperate studies demonstrating cladocerans exerting top-down control of phytoplankton (Schoenberg & Carlson, 1984; Lampert et al., 1986; Christoffersen et al., 1993). The marked contrast between published information for temperate regions and the results presented here may be linked to differences in cladoceran species composition. Larger species of cladocerans are notably absent or numerically rare in Southeast Asia (Fernando, 1980). The constraints imposed by the correspondingly small size of the feeding apparatus of smaller species could limit the intake of a large variety of phytoplankton. Cladocerans in local systems may be restricted
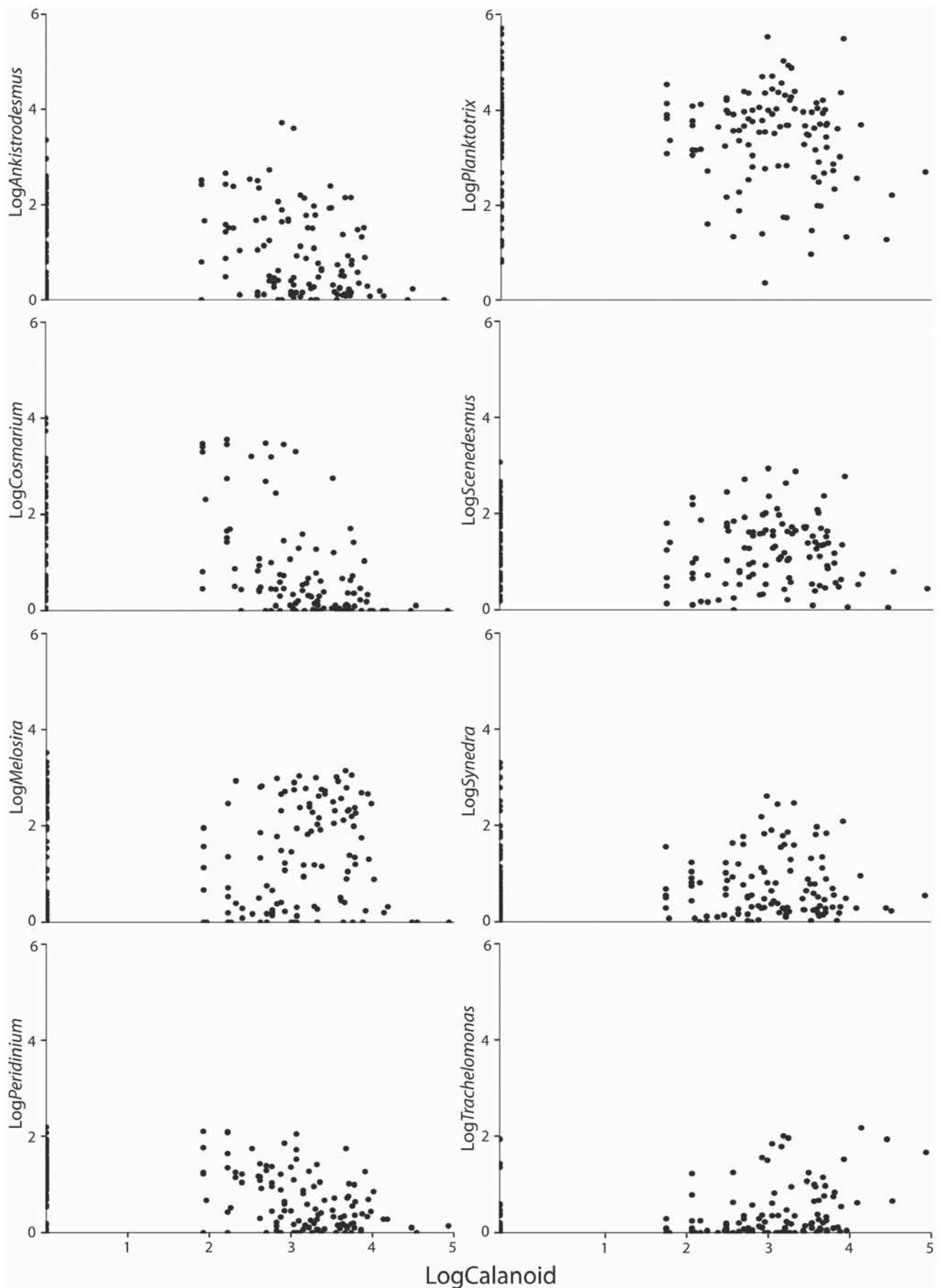
Fig. 2. The correlations of calanoid copepods with phytoplankton genera with high loadings on PC1 and PC2; i.e. *Ankistrodesmus*, *Cosmarium*, *Melosira*, *Peridinium*, *Planktotrix* sp. 1 and 2, *Scenedesmus*, *Synedra* and *Trachelomonas* (see Table 3). Calanoid counts were expressed in number per m^3 while phytoplankton counts were expressed as number per ml^3.
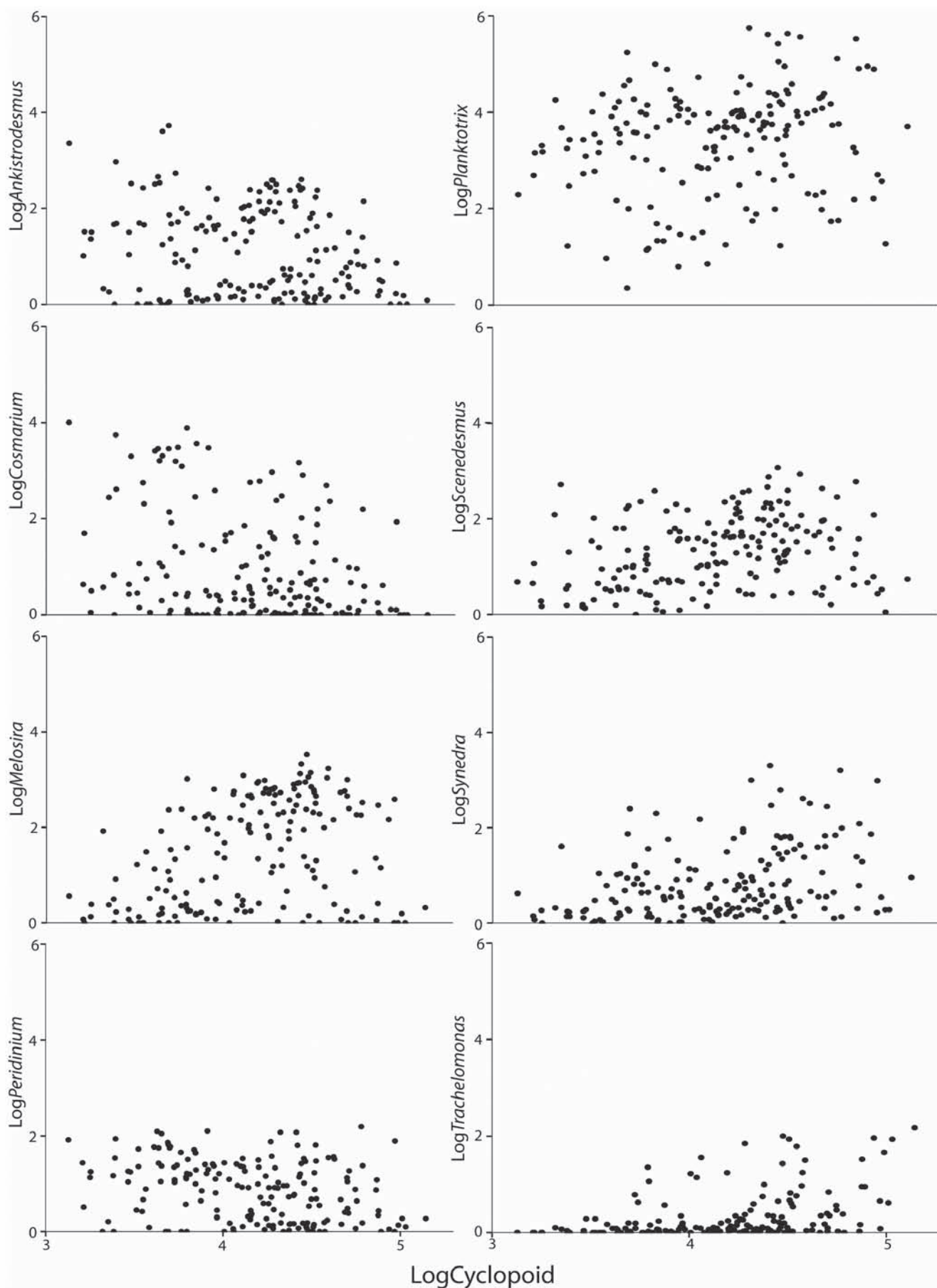
Fig. 3. The correlations of cyclopoid copepods with phytoplankton genera with high loadings on PC1 and PC2; i.e. *Ankistrodesmus*, *Cosmarium*, *Melosira*, *Peridinium*, *Planktotrix* sp. 1 and 2, *Scenedesmus*, *Synedra* and *Trachelomonas* (see Table 3). Cyclopoid counts were expressed in number per m³ while phytoplankton counts were expressed as number per ml³.
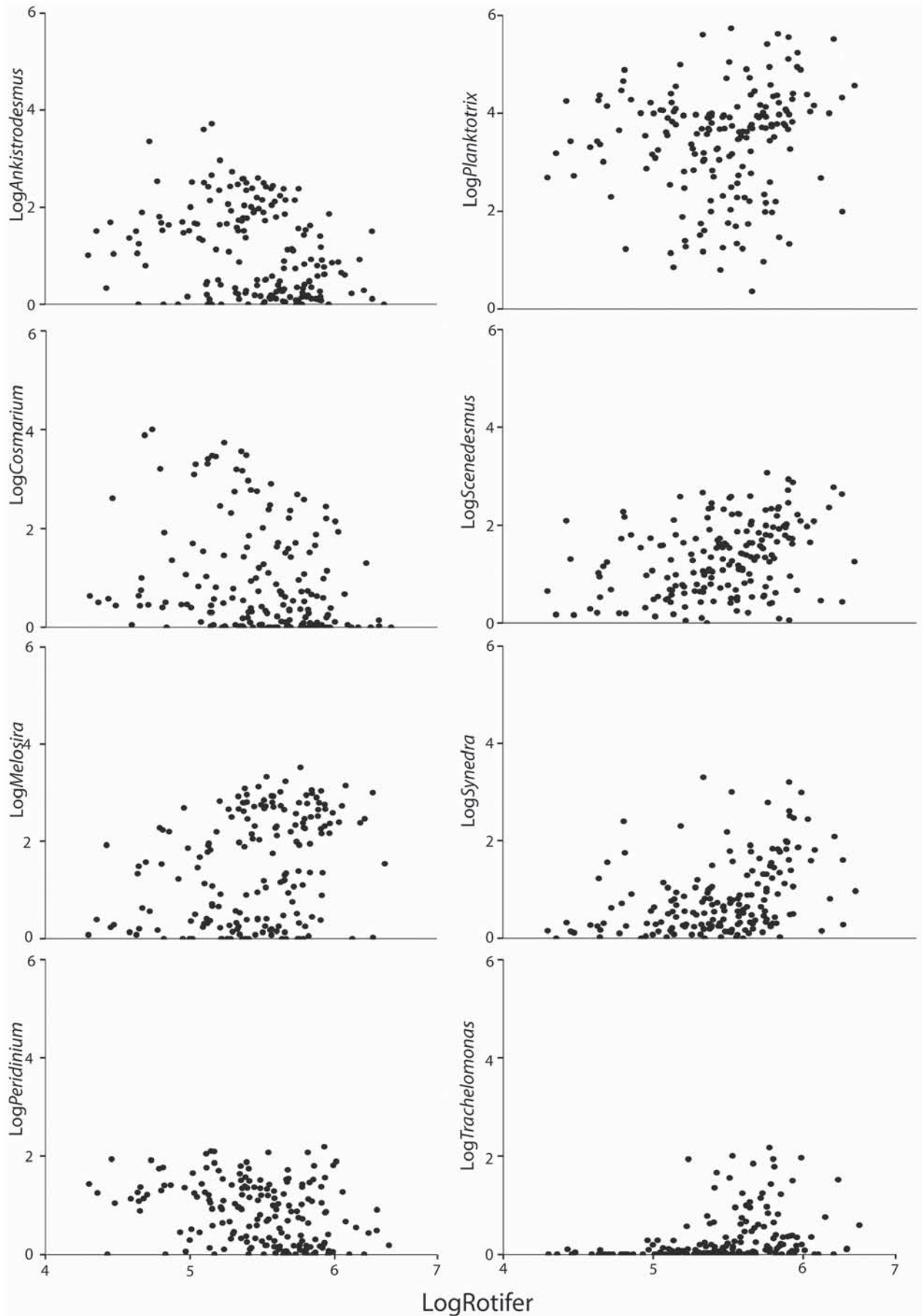
Fig. 4. The correlations of rotifers with phytoplankton genera with high loadings on PC1 and PC2; i.e. *Ankistrodesmus*, *Cosmarium*, *Melosira*, *Peridinium*, *Planktotrix* sp. 1 and 2, *Scenedesmus*, *Synedra* and *Trachelomonas* (see Table 3). Rotifer counts were expressed in number per m³ while phytoplankton counts were expressed as number per ml³.
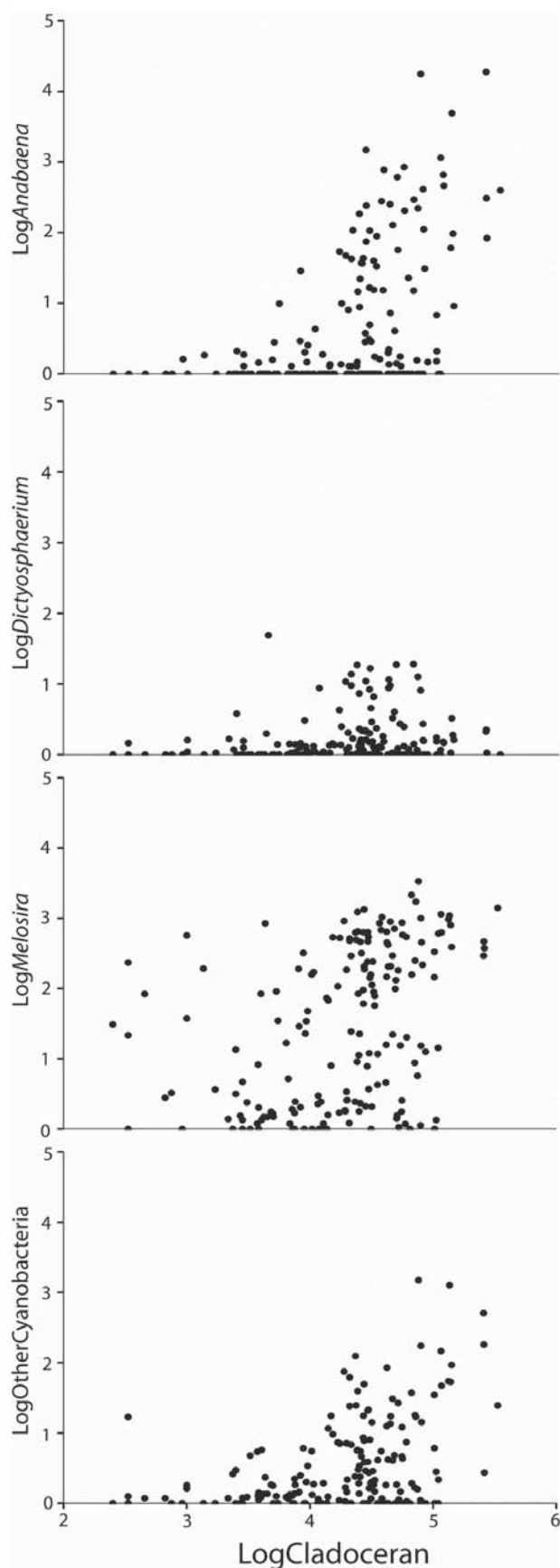
Fig. 5. The correlations of cladocerans with phytoplankton genera with high loadings on PC3; i.e. *Anabaena*, *Dictyosphaerium*, *Melosira* and "other cyanobacteria" (see Table 3). Cladoceran counts were expressed in number per m^3 while phytoplankton counts were expressed as number per ml^3.

to smaller prey such as nano- and pico-phytoplankton, groups not included in our routine monitoring programme (Sommer & Sommer, 2006). Another possible explanation for the apparent lack of correlation between cladoceran counts and phytoplankton biomass could be the variation in feeding traits among different families of cladocerans (McGill et al., 2006). For example, the cladoceran *Bosmina* has a markedly differing foraging mode to the filtering feeding *Daphnia*. *Bosmina* use their first two pairs of limbs to direct and capture food, thus enabling this taxon to feed on the phytoplankton flagellates that *Daphnia* cannot (DeMott & Kerfoot, 1982). Hence, a finer taxonomic resolution or the use of functional groups might aid in elucidating the top-down control of phytoplankton biomass among different genera of cladocerans.

Increases in cyanobacteria counts with zooplankton population growth, as found in Singapore's reservoirs, have been observed elsewhere (Burns, 1987; Abrantes et al., 2006; Wang et al., 2010). As zooplankton selectively graze on other genera of phytoplankton, they indirectly help cyanobacteria proliferate in two ways, one by reducing the (competing) phytoplankton standing crop, the other by excreting ammonium and soluble reactive phosphorus for the (now dominant) cyanobacteria to ultilise (Burns, 1987; Elser et al., 2001). This is exacerbated in ecosystems with low cladoceran counts as cladocerans recycle a greater proportion of nitrogen to phosphorus nutrients, with higher amount of ammonium released (Elser, 1999). The higher concentration of ammonium released reduces advantage that nitrogen-fixing cyanobacteria usually benefit from in nitrogen limited waters, leading to lower cyanobacteria counts (MacKay & Elser, 1998). Conversely, a lake with lower counts of cladocerans would have similar nitrogen and phosphorus recycling rates, thus allowing cyanobacteria to continue their dominance (MacKay & Elser, 1998; Elser, 1999).

There are various other reasons why cyanobacteria might be expected to proliferate. Some cyanobacteria genera are able to produce toxins, a potential defence mechanism against grazers, especially cladocerans and calanoids (Lampert, 1981; DeMott et al., 1991). Hansson et al. (2007) showed that an increase in microcystin toxins in lakes corresponded to decreases in the numbers of calanoids; but smaller zooplankton such as rotifers were able to proliferate under such conditions. Certain filamentous cyanobacteria, e.g. *Anabaena*, and some species of Oscillatorales are known to inhibit the mechanical filtering of cladocerans, reducing their growth and reproduction (Webster & Peters, 1978; Haney, 1987), while the sheer sizes of other, colony-forming, cyanophytes such as *Aphanizomenon* and *Microcystis* cannot be ingested by zooplankton (Lampert, 1987). Rotifers and copepods are less likely to be affected by mechanical disturbance during uptake of cyanobacteria, but when ingested, cyanobacteria do not provide the essential nutrients required by these zooplankton (Lampert, 1987). Copepods, are able to selectively feed on smaller sized colonies and cyanobacteria with shorter filament lengths (Burns & Xu, 1990; DeMott & Moxter, 1991), in agreement with our results where an increase in calanoid copepods led to a

Table 2. Results of forward stepwise multiple regression for the effects of calanoid, cladoceran, cyclopoid and rotifer abundances on PC1, PC2 and PC3. Data are unstandardised regression coefficients for each independent variable retained in the final model, with standard errors (±) for each in parentheses. All R^2 values are adjusted for degrees of freedom. All dependent variables were statistically significant at $p < 0.01$.

Compound variable	Intercept	Rotifer	Calanoid	Cyclopoid	Cladoceran	R^2	Overall F	Overall p
PC1	-1.85 (0.18)	0.30 (0.04)	-0.11 (0.01)	0.09 (0.02)	-	0.076	59.8	<0.01
PC2	2.18 (0.18)	-0.35 (0.03)	-0.15 (0.01)	-0.04 (0.02)	-	0.119	98.7	<0.01
PC3	0.64 (0.05)	-	-	-	-0.18 (0.01)	0.084	198.3	<0.01

possible decline in *Pseudoanabaena*, *Planktotrix* sp. 1 and 2 abundances.

Some decreases in phytoplankton abundances might not be accounted for by zooplankton grazing but, instead, to changing water quality or trophic status (Naselli-Flores & Barone, 1994). Similarly, increases in certain zooplankton populations could also be attributed to increased primary productivity (Pace, 1986; Kasprzak & Koschel, 2000). As lakes increase in trophic status, the amount of detritus and bacteria increases, and larger populations of grazers can be supported (Pace, 1986; Carpenter et al., 1996; Auer et al., 2004). In Singapore, high counts of zooplankton groups were found in Kranji and Jurong. Both reservoirs are hypertrophic with high productivity and are thus probably able to support more zooplankton as compared to nutrient poor reservoirs such as MacRitchie (Low et al., in review). Other researchers have documented a shift in zooplankton community structure, from one dominated by calanoids to another dominated by cladocerans, with increasing eutrophication (e.g., McNaught, 1975). Decreasing calanoid-to-copepod ratio has even been proposed as an indicator of eutrophication as calanoids are typically found in low nutrient waters (Gannon & Stemberger, 1978).

Decreases in *Cosmarium* and *Peridinium* may also not be necessarily a result of zooplankton grazing. Conflicting accounts of the ingestibility and digestibility of these genera make it difficult to pinpoint grazing as the main reason for their declines in the reservoirs studied here (Porter, 1972; Burns, 1979; Bergquist et al., 1985; Edgar & Green, 1994). *Cosmarium* is usually found in acidic and phosphorus-poor waters (Huszar et al., 1998) in contrast to most of the lakes in Singapore (Low et al., in review). In the present study, this desmid genera was only found at large concentrations in MacRitchie reservoir. Their general scarcity could have led to a negative regression when data from all the reservoirs were compared as a whole. *Peridinium* (Phylum Dinophyta), is commonly found in mesotrophic to eutrophic conditions (Edgar & Green, 1994; Reynolds et al., 2002) as opposed to the eutrophic to hypereutrophic state in Singapore's reservoirs. The increasing trophic status could perhaps contribute to their declines instead of zooplankton grazing pressure, demonstrating possible bottom-up control of nutrient sensitive taxa.

To be able to determine if zooplankton are really exerting top-down control of phytoplankton standing crop, a number of obstacles have to be removed. First, the taxonomic resolution of zooplankton in tropical Southeast Asia must be improved if within-group variation in diets is to be resolved. Within each group of zooplankton examined here, the various families or genera could potentially graze on very different phytoplankton (Fryer, 1957; Lair, 1991). For example, different species of the cladoceran *Daphnia* have different diets. Some species, e.g., *D. hyaline*, are able to graze efficiently on filamentous cyanobacteria (Knisely and Geller, 1986) while others cannot (Haney, 1987). Second, laboratory-based experiments detailing the uptake rates and food choices of endemic zooplankton species (Lampert, 1974) should be carried out using tropical species of zooplankton. Third, field experiments should be undertaken to elucidate the effects of water quality on both zooplankton (Yang et al., 1999; Pedrozo & Rocha, 2005) and phytoplankton (Reynolds, 1998; Reynolds et al., 2002) community structures. Fourth, enclosure experiments in the natural habitats where specific taxa are excluded to determine the extent of top-down control of the remaining zooplankton should be carried out to compare the grazing efficacy among zooplankton groups (Bergquist et al., 1985).

This study used 15 yrs of zooplankton and phytoplankton data to illustrate some possible zooplankton-phytoplankton relationships in 12 shallow tropical reservoirs. Top down control of phytoplankton by zooplankton grazers was the most likely explanation for the decreases in certain phytoplankton genera, and the corresponding decreases in these gave other algae, especially cyanobacteria, the competitive advantage to thrive. However, other factors such as trophic status of the reservoirs could also explain some of the variations observed in both plankton communities. Further studies, such as food selection experiments, need to be carried out to determine the exact relationships between individual genera of zooplankton and phytoplankton.

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