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ZOOPLANKTON GROWTH RESPONSES TO THE CYANOBACTERIA *MICROCYSTIS* AND *ANABAENA* IN EAGLE CREEK RESERVOIR IN INDIANA

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ABSTRACT. Eagle Creek Reservoir is a small, eutrophic reservoir located on the northwest side of Indianapolis. Recent assessments by the Indiana Department of Environmental Management (IDEM) have shown that ECR is impaired due to persistent nuisance algal blooms (IDEM 303(d) list; 2002, 2004, and 2006). Research presented here explored the relationship between zooplankton feeding behavior and cyanobacteria morphology, specifically, how resident ECR zooplankton growth was affected by filamentous versus coccid algal morphologies. In August of 2003, *in situ* mesocosms were deployed in the reservior to observe zooplankton growth given two different algal food sources: *Anabaena* sp., a filamentous heterocyst-forming cyanobacteria, and *Microcystis* sp., a coccid non-heterocyst forming cyanobacteria. No statistical difference between the overall zooplankton growth in the enriched mesocosms was observed. However, a taxa-treatment effect was seen as rotifer populations grew significantly faster in the *Microcystis*-enriched mesocosm and the copepod populations were significantly greater in the *Anabaena*-enriched mesocosm. These taxa-specific trends show that different zooplankton taxa prefer and/or tolerate different phytoplankton morphologies.

Keywords: Zooplankton, Cyanobacteria, grazing preference, physical inhibition, Eagle Creek Reservoir

Cultural eutrophication of drinking water reservoirs continues to be a major threat to drinking water supplies. Watershed nutrient loading spurs greater productivity in these systems, changing the environment to favor the exponential growth of nuisance algae that can be a problem for both recreation and municipal uses. Scums of nuisance algae will deter swimmers, and high oxygen demand in the reservoir's bottom waters can stress fish populations and lead to fish kills of sport fish. In terms of municipal uses, nuisance algae can interfere with water treatment: some filamentous algae can clog filters, while other algae can produce secondary metabolites such as the taste and odor-causing compounds 2-methylisoborneol (MIB) and geosmin ((E)-1,10-dimethyl-9-decalol) or toxins (e.g., anatoxin-a, microcystin-LR, and cylindrospermopsin). As Eagle Creek Reservior (ECR) is a drinking water resource for ~80,000 Indianapolis residents, these nuisance algal blooms are a problem since several genera of cyanobacteria in the reservoir such as *Pseudanabaena*, *Anabaena*, and *Aphanizomenon* can produce secondary metabolic compounds that cause taste and odor problems and/or toxicity. Due to the societal importance of drinking water, understanding the prerequisite conditions necessary for exponential growth and the food-web checks and balances that could naturally control nuisance algal growth are important for protecting and maintaining the health of these ecosystems.

In addition to the nutrient loading and bloom formation research at Eagle Creek Reservoir and other lakes world-wide, ecosystem bloom control needs be studied as these biotic interactions between phytoplankton and zooplankton during blooms can give insight into

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long term solutions: understanding how primary consumers and higher tropic levels cope with and/or suppress cyanobacterial blooms may not only aid in our understanding of the reciprocal influence that cyanobacteria-dominated algal communities and zooplankton communities exert on each other, but may also provide a top-down, natural control for algal blooms.

Studies by Lampert et al. (1986) and Sommer et al. (1986) have shown that while zooplankton herbivory can clear springtime blooms, causing a "Clear Water Phase," the use of zooplankton to control late summer blooms of cyanobacteria is not as promising. Such a clearing effect is not seen to the same degree in late summer when the cyanobacterial blooms occur. From this inability of the zooplankton community to clear a cyanobacterial bloom, many studies consider cyanobacteria to be a poor food quality for reasons of toxicity, nutrient inadequacies, and physical inhibitions (Haney 1987; Lampert 1987).

While toxicity to zooplankton has been a major research focus in these phytoplankton-zooplankton interactions, DeMott & Moxter (1991) concluded that cyanobacteria toxicity is perhaps overemphasized and zooplankton adaptations to coexist with toxic cyanobacteria are underestimated. In Gilbert (1990), this is seen as the strain of *Daphnia pulex* that had coexisted with toxic *Anabaena affinis* had evolved resistance to toxin (Gilbert 1990). In another study, *Bosmina longirostris* was found to be resistant to strains of *Microcystis aeruginosa* (Fulton 1988).

In the field, toxicity may not be the most significant factor in shaping zooplankton community structure. Various studies have found filamentous morphology inhibits feeding and growth rates for daphnids (Arnold 1971; Holm et al. 1983; Gliwicz & Lampert 1990). In one study, *Daphnia* responded to the dominance of a filamentous, non-toxic strand of *Aphanizomenon* with reduced growth rates (Kurmayer 2001).

This mesocosm study attempts to understand the phytoplankton-zooplankton interactions in blooms that are not necessarily toxic to natural zooplankton populations by examining the impact of physical inhibition on zooplankton communities by using two morphologically different cyanobacteria present in the reservior, e.g., the filamentous *Anabaena* sp. and the coccid *Microcystis* sp. We hypothesize that zooplankton populations will be more adversely affected in the mesocosm enriched with the filamentous *Anabaena* sp.

METHODS

Study site.—ECR is a small (area of 5.0 km^2), shallow reservoir (mean depth of 4.2 m) with an estimated reservoir volume is 20,954,000 m^3 (Tedesco et al. 2003). Located northwest of Indianapolis, Indiana (39.83°N, 86.31°W; 39.87°N, 86.30°W) the reservoir was created by impounding Big Eagle Creek. Originally constructed as a method for flood control, the reservoir became a direct drinking water source in 1976 when the T.W. Moses Drinking Water Plant came on-line. The reservoir is fed by three streams in Eagle Creek Watershed (420 km^2, HUC 05120201120): Eagle Creek, Fishback Creek, and School Branch with the largest flow contribution coming from the trunk stream, Eagle Creek. Eagle Creek is a small stream with a median daily instantaneous flow of 0.9 m^3/s (USGS Stream Gage #03353200, 1957–2003). Water balance estimates of Eagle Creek Reservoir resulted in a calculated residence time of 43 days (Pascual et al. 2006). An average watershed slope of <5% and the presence of productive soils allowed for crop production in the watershed, resulting in the majority of Eagle Creek Watershed land to be cultivated as agricultural land, 60.1% in 2003 (Tedesco et al. 2005). Central Indiana Water Resources Partnership (CIWRP) bi-weekly monitoring during the growing season from 2003–2005 showed a reservoir mean total phosphorus concentration of 94 μg P/L (Pascual et al. 2006). The 2003 assessments using the Indiana Trophic State Index categorize ECR as eutrophic.

In August 2003, the ECR phytoplankton community was composed of chrysophytes, chlorophytes, and cyanobacteria. The diatoms present were *Asterionella, Aulacoseira,* while *Cyclotella. Ankistrodesmus, Actinastrum, Closterium, Coelastrum,* and *Pediastrum* represented the chlorophytes. *Merismopedia, Microcystis, Anabaena, Aphanizomenon,* and *Cylindrospermops*is represented the cyanobacteria. The cyanobacteria used to inoculate the experimental mesocosms (*Anabaena* sp. and *Microcystis* sp.) were naturally found in the reservoir at the time of the study.

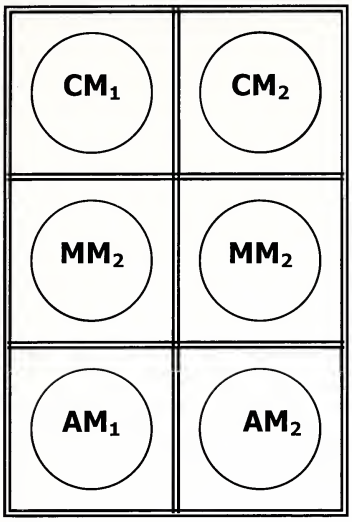

Figure 1.—Mesocosm experimental design.

Experimental design.—Mesocosms were deployed off a secluded dock in Eagle Creek Reservoir from 7 August to 12 August 2003 (5 days). Mesocosms were built using 45–50 gallon husky high density clear polyethylene bags (Poly-America) suspended from a PVC frame. Each bag provided a depth of 0.8 m and contained approximately 165 L of water. Two control mesocosms (CM) were filled with approximately 165 L of reservoir water filtered through an 80 μm mesh net to remove zooplankton and most of the larger filamentous algae. Four treatment mesocosms were filled with approximately 160 L of reservoir water filtered through a 20 μm mesh net to remove zooplankton and most of the resident algae. Two of the mesocosms were then inoculated with 5 L of cultured *Microcystis* sp., and designated as the *Microcystis* Mesocosm (MM). The other two exposure mesocosms were inoculated with 5 L of cultured *Anabaena* sp. and designated as the *Anabaena* Mesocosm (AM) (Fig. 1). Original cultures were obtained from Carolina Biological Supply in January 2003 and cultured using modified Guillards F/2 media. Cultures were verified as named genera prior to mesocosm inoculation.

To discern if zooplankton feeding behavior was influenced by toxicity, *Microcystis* culture samples were sent to State University of New York College of Environmental Science and Forestry in March 2004 for toxin analysis. Toxin concentrations were determined to be 103 μg microcystin-LR per gram chlorophyll *a*. Compared to microsystin-LR levels found in natural systems, our *Microcystis* culture had very low toxicity (G.L. Boyer pers. comm.). During non-bloom conditions, other studies have reported natural microsystin levels 100-fold greater than our culture (Wang et al. 2002). *Anabaena* cultures were not tested for toxicity.

A total of six mesocosms was deployed: two control, two MM, and two AM (Fig. 1). Resident ECR zooplankton were harvested using an 80 μm mesh plankton net, as done by Sterner (1989), drawn over a 2 m vertical depth and concentrated into a 125 ml collecting bottle at the end of the plankton net. After three vertical tows, the zooplankton were transferred into an amber 1 L glass bottle for transport to the mesocosm. Harvested zooplankton were introduced to their respective treatment mesocosm exposure within 10 minutes to minimalize stress. All six mesocosms were each inoculated with zooplankton from a total of 15 tows. The tows were spaced to prevent re-towing the same water column. After all mesocosms were inoculated, an additional tow was made in ECR to calculate initial zooplankton densities.

Sampling.—Zooplankton and phytoplankton communities interacted in the six mesocosms between 7–12 August 2003. Each morning, dissolved oxygen (DO), temperature, and pH were measured with a Hydrolab® multiparameter field probe (Hydrolab Corporation, Austin, Texas) inside and outside the mesocosms to ensure that environmental conditions remained within ranges for optimal phytoplankton and zooplankton growth as recommended by US EPA: DO of ≥ 6 mg/L, pH between 6–9, and temperature ranging between 20–25 °C (Lewis et al. 1994). Secchi disk readings were also taken to ensure that the mesocosm depths were consistently in the photic zone. After abiotic measurements were taken, the mesocosm bags were stirred to evenly distribute the zooplankton and algal populations. The mixed mesocosms were sampled for zooplankton and phytoplankton abundance.

At 0, 42, 65, and 89 hours, a 1 L sample was taken from the middle of each mixed mesocosm. This 1 L sample was concentrated into 125 ml using a 20 μm mesh plankton net

with the filtrate being returned to the mesocosm (Ferrão-Filho et al. 2002). The 125 ml sample was split into two 50 ml HDPE centrifuge tubes and preserved with Lugol's Solution.

Identification and enumeration.—Preserved samples were refrigerated at <4 °C for no longer than six months prior to analysis. Each duplicated sample was counted first for zooplankton and then phytoplankton. Zooplankton were counted using a 1 ml Sedgwrick-Rafter cell and identified based on these zooplankton groups: Calanoida, Cyclopodia, Bosminidae, Daphniidae, Leptodoridae, Acariformes, Certopogonidae, Chironomidae, Ostracoda, and Keratella (Rotifera). Zooplankton taxonomic categories are similar to those used by Newhouse & Stahl (2000). The entire Sedgwrick-Rafter cell was counted at 100×.

After zooplankton counts, preserved water samples were allowed to settle by gravity for 24 h and were concentrated. Phytoplankton were counted using a Palmer-Malone Nanoplankton Counting Chamber at 400× and identified to genus. In each sample, at least 100 natural units were counted. Later measurements and counts were made to convert *Anabaena* filaments and *Microcystis* colonies to densities on a per cell basis.

Statistical methods.—Before the experiment, the alpha level of 0.05 was chosen for the statistical analyses. A three-way ANOVA test for Treatment × Replicate Mesocosms × Taxa was run separately for both phytoplankton and zooplankton. Additional two-way ANOVA tests were run to analyze the Treatment × Day interaction for individual zooplankton taxa. Whenever appropriate, the Holm-Sidak (HS) *post hoc* tests were employed to further analyze statistical differences. All statistical tests were preformed on SYSTAT Software.

RESULTS

Physical parameters.—All mesocosms stayed within the optimum growing ranges as determined by EPA. The temperatures of the mesocosms were similar to the temperature of ECR, ranging from 24.9–27.6 °C. The pH and DO within the mesocosms ranged from 8.2–8.7 and 7.0–9.1 mg/L, respectively. Secchi disk measurements taken outside the mesocosms indicated that the exposures were always within the photic zone (as estimated by 1.7× Secchi disk reading). While nutrient restraints within the mesocosms were not known during the experiment, limiting nutrients such as NO^-_3, NH^+_4 and TP were abundant in a surface reservoir sample located in the same basin as the mesocosms: [NO^-_3] = 1.4 mg N/L, [NH^+_4] = 0.30 mg N/L and [TP] = 0.063 mg P/L.

Biotic results.—Biotic data were analyzed for changes in both the phytoplankton and zooplankton community densities and in taxon specific populations. In analyzing the data, samples from replicate mesocosms were pooled as the replicate mesocosms were not determined to be significantly different for either the phytoplankton (F = 0.273, P = 0.601) or the zooplankton (F = 3.615, P = 0.058) (Tables 1 and 2, respectively).

Phytoplankton trends: The initial total phytoplankton concentrations for the CM, AM, and MM were 16,100, 16,200, and 31,800 cells/ml respectively (Fig. 2). The overall phytoplankton trends for the CM and AM are nearly identical with means always in the other's error bars for 0 h to 65 h. While the total phytoplankton in the AM increased to 23,000 cells/mL at 89 h, the CM phytoplankton decreased from 22,500 cells/ml at 65 h to 20,000 cells/ml by 89 h. Initial total population in the MM, 31,800 cells/ml, are nearly double that found in the CM (16,100 cells/ml) and decreased over time to 17,100 cells/ml (Fig. 2). While the three-way ANOVA test (Treatment × Replicate mesocosms × Taxon) showed no significant difference between treatments (F = 1.875, P = 0.154; Table 1), both the taxonomic interaction (Taxon) and Taxon × Treatment interactions were highly significant (F = 142.76, $P < 0.001$; Table 1).

Of the many phytoplankton taxa identified, this paper presents the results only for chlorophytes in general, *Anabaena* sp., and *Microcystis* sp. because of relevance to the experimental design. While *Merismopedia minima* was often the major cyanophyte on a per cell basis in the mesocosms, the biovolume of the eight celled colonies was substantially smaller than a cell of any other phytoplankton identified (<5 μm^3).

The results for the Chlorophyta showed population changes for the majority of non-cyanobacteria during the experiment. In the CM, Chlorophyta populations steadily decreased from initial populations of 900 cells/

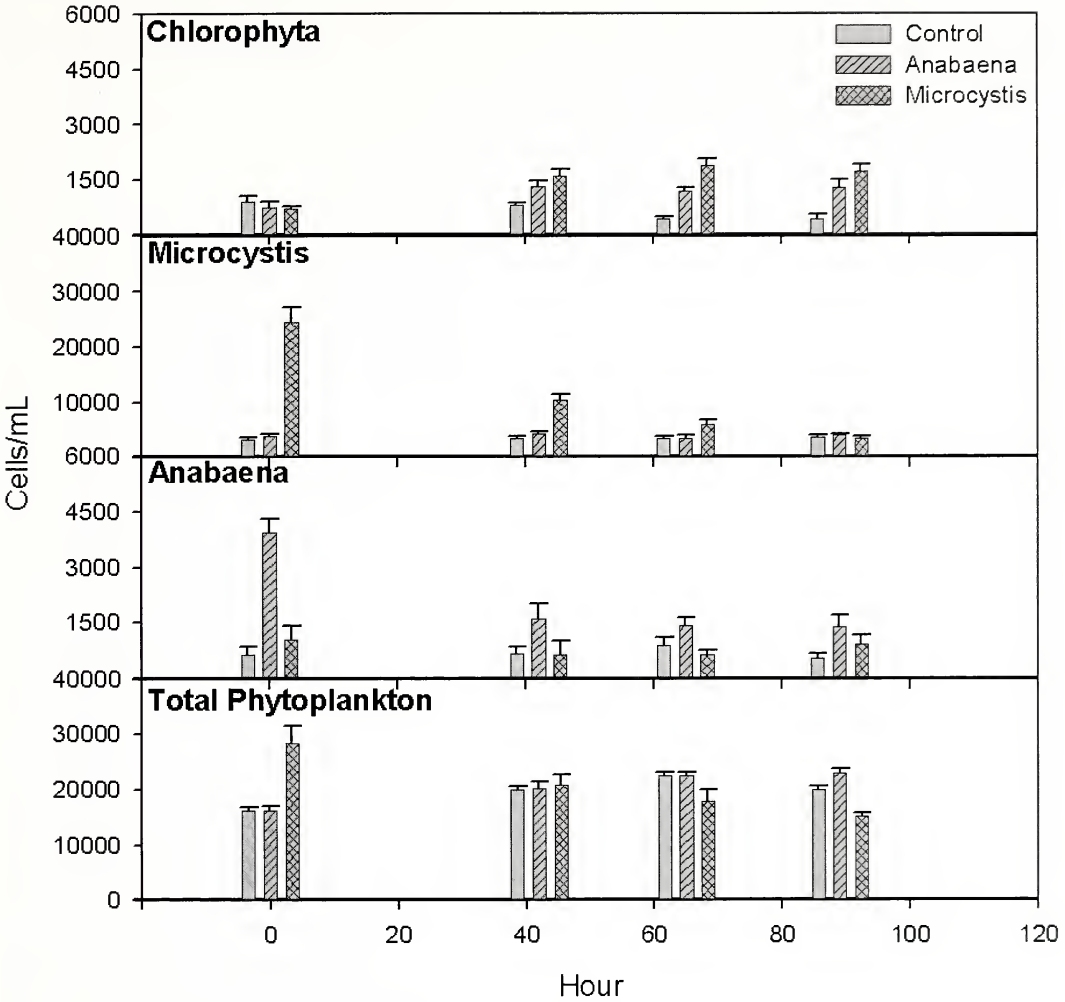

Figure 2.—Phytoplankton in different treatments. Solid bars represent the control mesocosm; diagonally-hashed bars represent the *Anabaena* mesocosms; and crosshatched bars represent the *Microcystis* mesocosms. Each value is a mean (±1 SE) of eight counts.

Table 1.—Results of three-way ANOVA testing the effects of treatment (Control, *Anabaena*, and *Microcystis* mesocosms), Replicate mesocosm, and time on Phytoplankton Densities. SS = sum of squares; df = degrees of freedom; MS = mean square; F = F-value; and P = P-value.

Source	SS	df	MS	F	P
Treatment	6.20×10^{7}	2	3.10×10^{7}	1.875	0.154
Replicate	4.52×10^{6}	1	4.52×10^{6}	0.273	0.601
Taxon	2.13×10^{10}	9	2.36×10^{9}	142.761	0.000
Treatment × Replicate	1.95×10^{6}	2	9.76×10^{5}	0.059	0.943
Treatment × Taxon	1.22×10^{9}	18	6.76×10^{7}	4.087	0.000
Replicate × Taxon	2.22×10^{7}	9	2.46×10^{6}	0.149	0.998
Treatment × Replicate × Taxon	1.25×10^{7}	18	6.93×10^{5}	0.042	1.000
Error	2.25×10^{10}	1359	1.65×10^{7}		

Table 2.—Results of three-way ANOVA testing the effects of treatment (Control, *Anabaena,*, and *Microcystis* mesocosms), Replicate mesocosm, and time on Zooplankton Densities. Abbreviations are the same as those defined in Table 1.

Source	SS	df	MS	*F*	*P*
Treatment	1.81×10^{9}	2	9.07×10^{8}	3.742	0.024
Replicate	8.76×10^{8}	1	8.76×10^{8}	3.615	0.058
Taxon	2.32×10^{9}	3	7.75×10^{8}	3.196	0.023
Treatment × Replicate	1.76×10^{9}	2	8.78×10^{8}	3.623	0.027
Treatment × Taxon	5.30×10^{9}	6	8.84×10^{8}	3.648	0.001
Replicate × Taxon	2.66×10^{9}	3	8.85×10^{8}	3.654	0.012
Treatment × Replicate × Taxon	5.36×10^{9}	6	8.93×10^{8}	3.686	0.001
Error	1.32×10^{11}	544	2.42×10^{8}		

ml to the final population of 430 cells/ml (Fig. 2). In the AM, the chlorophyte populations increased from 750 cells/ml to a peak of 1300 cells/ml at 42 hrs (Fig. 2). Unlike in the controls, Chlorophyta populations in the MM steadily increased for 65 h, then slightly decreased to the final population of 1730 cells/ml (Fig. 2).

Microcystis sp. and *Anabaena* sp. were prominent in the mesocosms to which they were inoculated. In the MM, the initial *Microcystis* sp. population was 24,400 cells/ml, more than five times the CM concentration of 3200 cells/ml. However, while *Microcystis* sp. dominated the phytoplankton at the start of the experiment, concentrations rapidly decreased to 3300 cells/ml by 89 h. In the CM and AM, *Microcystis* sp. remained fairly constant.

While the *Anabaena* sp. population in the AM was not the dominant alga by cell count (second to *Merismopedia* sp.), the initial *Anabaena* density was more than five times that found in the CM (630 cells/ml). Starting at 3900 cells/ml, the AM *Anabaena* density decreased to 1400 cells/ml by 89 h. This is in contrast to the CM, where *Anabaena* sp. abundance steadily increased to 870 cells/ml at 65 h before decreasing to 540 cells/ml by 89 h.

Zooplankton trends: Overall zooplankton trends, like the overall phytoplankton trends, showed a broad picture that is further supplemented by the taxa specific trends. At the start of the experiment, the total zooplankton populations of the various treatments were not statistically different (Table 2). The initial densities for total zooplankton in CM, AM, and MM were respectively: 770 ± 131, 700 ± 112, and 920 ± 160 organisms/L (means ± 1 SE). Total zooplankton in all treatments experienced continual positive growth from 0 to 89 h. Results at 89 h showed a striking difference between densities in the CM, 1380 ± 100 organisms/L, and the enriched mesocosms with 2200 ± 337 organisms/L in the AM and 2700 ± 318 in the MM. While all treatments experienced growth, there was a significant difference ($F = 3.742$, $P = 0.024$) in overall zooplankton densities between the treatments (Table 2). Further, Holm-Sidak *post hoc* tests found the difference between the total zooplankton in CM from either enriched mesocosms AM or MM to be significant ($P < 0.05$). However, there was no significant difference ($F = 3.742$, $P = 0.24$) between the total zooplankton populations in AM and MM. There was a highly significant interaction ($F = 3.648$, $P = 0.001$) among the taxa and mesocosm treatments (Table 2).

Of the zooplankton taxa recorded, only the copepod and rotifer populations were at high enough densities to record distinct trends. The copepod trend in mesocosms was different from the Total Zooplankton Trend (Fig. 3). The initial densities for the copepods in the CM, AM, and MM were similar (respectively: 380 ± 65, 480 ± 104 and 480 ± 107 organisms/L; Fig. 3). The CM copepods peaked on 42 h at 480 ± 130 organisms/L, decreased to 230 ± 37 organisms/L by 65 h, and returned to 380 ± 58 organisms/L by 89 h. The copepods in the AM were the only population to increase to 810 ± 159 organisms/L by 89 h. The population in the MM decreased slightly to 392 ± 42 organisms/L. These fluctuations over the experimental period for any treatment did not show a significant change ($F = 0.987$, $P = 0.403$). Holm-Sidak *post hoc* tests found the copepod population in AM to

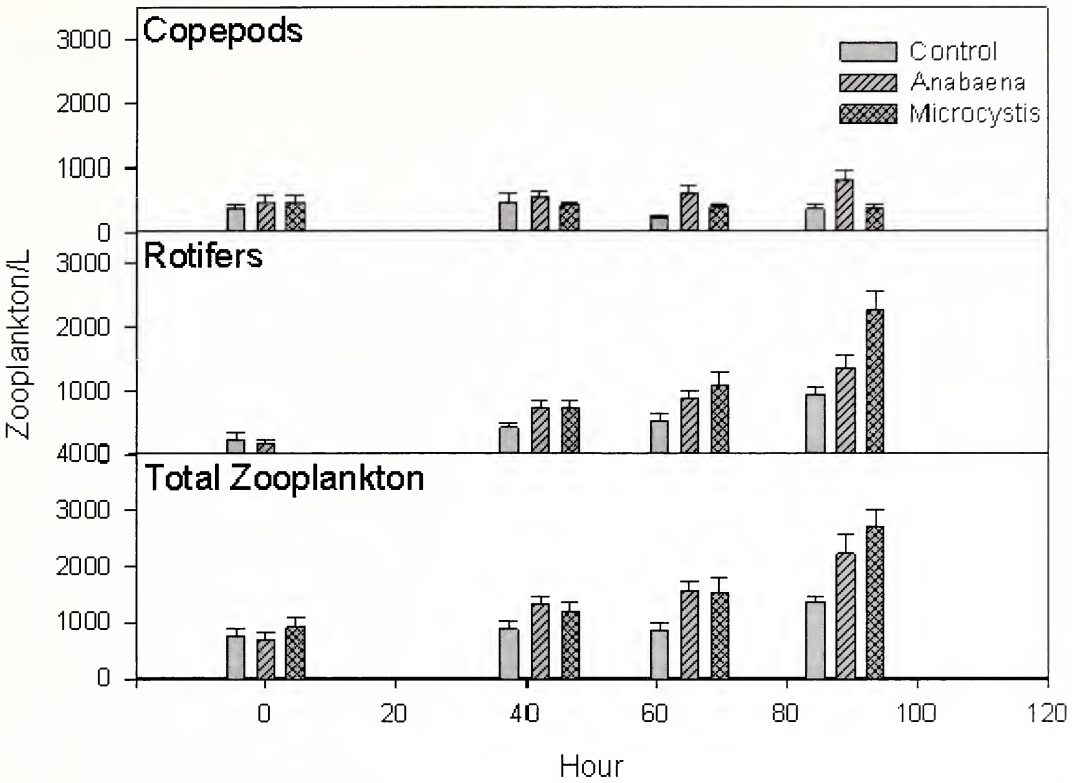

Figure 3.—Zooplankton in different treatments. Solid bars represent the control mesocosm; diagonally hashed bars represent the *Anabaena* mesocosms; and crosshatched bars represent the *Microcystis* mesocosms. Each value is a mean (±1 SE) of eight counts.

be significantly higher than the populations in both CM and MM for 65 h and 89 h ($P < 0.01$ for both days and treatments). No significant difference between the copepod populations in the CM and MM (HS $P = 0.92$) was observed.

Unlike the copepod trends, the rotifer trends closely resembled the total zooplankton treatment trends. The starting rotifer populations were distinct from each other, but the difference did not appear to inhibit the growth in the enriched exposures (Fig. 3). All treatments showed significant (HS $P < 0.05$) growth of rotifer populations from 0 to 89 h. By 89 h, rotifer densities for CM, AM, and MM reached 953 ± 108, 1359 ± 211, 2277 ± 278 organisms/L, respectively. As with the total zooplankton populations, rotifer populations in the enriched mesocosms were significantly different ($P < 0.01$ for both AM and MM) from the CM but not from each other ($P = 0.76$) except on the last day (HS $P < 0.05$).

DISCUSSION

Inoculated mesocosms resulted in higher zooplankton growth than the CM, which did not experience a statistically significant growth. However, different inoculations did not produce a statistically different effect on the total zooplankton from each other. This contradicts our hypothesis that the AM would more adversely affect zooplankton growth in comparison to the MM. However, AM and MM enrichments did exhibit taxa specific zooplankton trends. Copepods did significantly better in the AM by 65 h than in the other mesocosms, and rotifers did statistically better in the MM. These taxa specific trends reflect a preference for, or a tolerance towards, a certain algal morphology.

Although cladocerans made up such a small percentage of the zooplankton counted that they could not be accurately analyzed, this taxa is worth mentioning in context to this

study as a majority of zooplankton-cyanobacteria studies use cladocerans. Since cladocerans have high filtering rates and a parthenogenic lifecycle like the rotifers (Allan 1976), cladocerans have been known to quickly respond to spring algal blooms and consume large amounts of algae such that they visibly clear the water, causing what is called the "Clear Water Phase" (Lampert et al. 1986; Sommer et al. 1986). In these favorable conditions, the cladocerans can out-compete and suppress other zooplankton with overlapping niches such as the rotifers (Gilbert 1990). This clearing effect is unlikely to occur if the algae are inedible, as most filamentous cyanobacteria are considered to be (Lampert et al. 1986; Sommer et al. 1986). The literature suggests that the presence of filamentous algae reduces the food gathering capability of daphnids. This is most observed with large filaments: larger filaments entering the daphnid's feeding current are rejected, disrupting the feeding and consumption of edible algae (Burns 1968; Gliwicz 1977; Burns et al. 1989). By being unable to exhibit selection in what they ingest, cladocerans are considered generalist feeders and must reject all their food if something inedible such as a filament is ingested (Gilbert 1990). As summer blooms in ECR are often composed of filamentous, heterocyst-forming cyanobacteria, the absence of cladocerans during the experiment is reasonable and consistent with the literature.

The presence of other zooplankton, mainly copepods and rotifers, in ECR during the experimental period indicates a tolerance if not adaptation to the late summer cyanobacterial community not exhibited by the Cladocera. This is probably the reason why the zooplankton community in the *Anabaena* mesocosms was not negatively impacted by the enrichment.

Copepods, the largest taxon seen during the experiment, responded contrary to expectations since they thrived in the AM (Fig. 3). Copepods have a very different lifestyle from the cladocerans and rotifers in that they reproduce sexually. Because of the short time scale of the experiment, the copepod response to the inoculation may not have fully materialized as they have a longer reproductive cycle than do either the cladocerans or the rotifers (Allan 1976). In addition, they display a very different feeding behavior that shows selectivity not seen in cladocerans. Copepods are known to discriminate by size, taste, and toxicity (DeMott 1986, 1988). In one study, copepods strongly avoided consuming colonial *Microcystis aeruginosa* because of chemical compounds associated with these cyanobacteria (Fulton & Paerl 1987). This active selection is a mechanism that allows copepods to coexist with toxic algal blooms.

While primarily filter feeders, copepods can capture larger particles raptorially, thus giving the taxon the largest size range for food particles: 5–100 μm (Allan 1976; Pennak 1989). This size range allows them to access other food sources unavailable to both cladocerans and rotifers, such as larger filaments like *Anabaena* filaments. Some studies suggest that some species of copepods have a greater selectivity and feeding efficiency on larger food particles (Haney & Trout 1985; Vanderploeg et al. 1988; DeMott 1990). While it is unclear how efficient copepods are in handling filamentous cyanobacteria in comparison to a filamentous Chlorophyta or Bacillariophyta, Burns & Xu (1990) found calanoid copepods significantly reduced both density and trichome length of filamentous cyanobacteria. Regardless of their handling efficiency, copepods clearly benefited from the *Anabaena* sp. enrichment and are the only zooplankters morphologically capable of exerting enough grazing pressure to cause *Anabaena* densities and length to decrease.

Rotifers, like copepods, exhibit a greater selectivity over what they can consume. This selectivity is better attributed to their relative smaller size (0.2–0.6 mm, Allan 1976) than any capabilities to choose what they ingest based on toxicity or taste (Kirk & Gilbert 1992). Rotifers use coronal cilia for suspension feeding, which restricts their consumption size to 1–20 μm (Allan 1976). As a result, rotifers are not impeded from feeding by having to reject filaments as do the cladocerans because most filaments cannot enter their mouth (Gilbert 1994). This advantage against physical inhibition also seems beneficial against toxic species that are filamentous or form mats, as they are less likely to ingest those toxins as with larger cladocerans. Gilbert (1990) demonstrated that the growth rates of five rotifer species were unaffected by high concentrations of toxic *Anabaena affinis* while growth rates of large cladocerans were re-

duced. This tolerance to *Anabaena* filaments due to their small size could explain why rotifer growth in the AM was higher than their growth in the CM (Fig. 3). The inability of rotifers to utilize the inoculated *Anabaena* sp. could lead to the conclusion that rotifer populations in the mesocosm inoculated with *Anabaena* sp. would closely resemble the rotifer populations in the CM if their feeding behavior was the only factor. However, this was not the case. The increase in rotifer populations in the AM could be explained by a lack of competition with copepods for the same food source as copepods were likely to consume the *Anabaena* sp. filaments. Thus, the rotifers would have had an ample food source of chlorophytes and *Microcystis*.

The success of the rotifers in this experiment was aided in part by their highly opportunistic nature and parthenogenic reproduction. With an r_{max} range of 0.2–1.5 d^{-1}, rotifers are quicker in their response to the inoculations than cladocerans and copepods, whose maximum growth rate in ideal conditions (r_{max}) are respectively 0.2–0.6 d^{-1} and 0.1–0.4 d^{-1} (Allan 1976). Therefore, rotifer populations in the MM exploded when a food source within their size range was enriched to more than five times the natural concentrations (Fig. 3). Fulton & Paerl (1988) observed in their study that a rotifer's (*Brachionus calyciflorus*) ability to handle a non-toxic strain of *Microcystis aeruginosa* was superior to that of a cladoceran (*Daphnia ambigua*).

Successful short term coexistence or even population growth found in these taxa specific trends requires behavioral or physiological adaptations to select, reject or tolerate specific cyanobacteria. The morphology of an algal bloom can change the zooplankton community structure and can favor certain zooplankton taxa to excel due to their feeding behaviors and mechanisms. Therefore, while zooplankton graze upon nuisance algae in Eagle Creek Reservoir, this grazing stress may not have the same effect in reducing cyanobacterial populations during the late summer as in the spring-early summer "clear water phase." Future mesocosm studies would benefit from a longer experimental period, a more efficient way to measure zooplankton and phytoplankton populations as phytoplankton and zooplankton identification and enumeration were time-consuming, and nutrient flux measurements. More mesocosm studies are needed for ECR and other lakes to fully understand these interactions and to achieve a long term management plan for algal blooms.

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