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ARTICLE

Effects of biocontrol with an atyid shrimp (*Caridina denticulata*) and a bagrid catfish (*Pseudobagrus fulvidraco*) on toxic cyanobacteria bloom (*Microcystis aeruginosa*) in a eutrophic agricultural reservoir

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Abstract The biocontrol effects of *Caridina denticulata,* an atyid shrimp, on toxic cyanobacterial bloom (*Microcystis aeruginosa*) were evaluated in a mesocosm study with stable isotope tracers (^{13}C and ^{15}N) in a eutrophic agricultural reservoir. The accumulated assimilation (at.%) of *M. aeruginosa* into *C. denticulata* was increased, causing a significant reduction in the concentration of Chlorophyll-*a*. The ingestion rate of *M. aeruginosa* by *C. denticulata* was influenced by predation pressure exerted by bagrid catfish *Pseudobagrus fulvidraco* and was dependent on biomass ratio. *C. denticulata* affected zooplankton density, species composition, and ingestion rate, demonstrating that the number of small-sized cladocerans (*Bosmina coregoni* and *Bosmina longispina*) increased because they grazed *M. aeruginosa* for a food source. This study suggests that *C. denticulata* and *P. fulvidraco* can be feasible material to control a nuisance *M. aeruginosa* bloom in eutrophic agricultural reservoir.

Keywords Biocontrol · *Microcystis aeruginosa* · Nuisance bloom · *Caridina denticulata* · *Pseudobagrus fulvidraco* · Stable isotope tracer · Agricultural reservoir

Introduction

The occurrence of nuisance cyanobacteria blooms is a global concern in many freshwater ecosystems (Pearl et al. 2001; Pearl and Huisman 2008). Particularly, agricultural reservoirs located in the watershed of cultivated land are likely to become eutrophic and suffering from deterioration of water quality and ecosystem health, which causes a detrimental

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effect of agricultural and aesthetic water use (Hwang et al., 2003; Kim and Hwang 2004). Bloom-forming cyanobacteria, such as *Microcystis, Anabaena*, *Aphanizomenon*, and *Oscillatoria*, increasingly dominate phytoplankton assemblages as lakes and reservoirs become nutrient enriched and, at times, may comprise close to almost entire summer phytoplankton biomass (Sarnelle 1993; Kim et al. 2007).

Cyanobacteria could be a source of food for heterotrophs such as copepods (Koski et al. 1999), shrimps (Engstrom et al. 2001), fish (Mohamed et al. 2003), and bivalves (Bontes et al. 2007). However, cyanobacterial blooms can be harmful to aquatic organisms because various bloom-forming species synthesize toxic secondary metabolites, including cyanotoxins and microcystins (Dittmann and Wiegand 2006). Direct and indirect assimilation of toxic cyanobacteria into the aquatic food web may result in the removal of functional taxa crucial to ecosystem health and a decline in important food sources (Piola et al. 2008). Therefore, effective control of nuisance cyanobacteria blooms is crucial for the conservation of water quality and aquatic ecosystem health.

The biomanipulation was introduced as an alternative approach to control eutrophication (Shapiro et al. 1975). This approach is largely based on top-down control to reduce algal biomass (Perrow et al. 1997). The "top-down" cascading approach is widely accepted and is frequently used to improve water quality and ecosystem health (Mehner et al. 2004), to control algal blooms (Shapiro and Wright 1984) and to enhance water transparency and species diversity (Jeppesen et al. 1997). For example, reduction of planktivorous fishes increases the biomass of zooplankton and consequently results in a lowered density of phytoplankton via zooplankton grazing (Shapiro et al. 1975). However, many researchers have debated about controlling algal biomass using grazing by zooplankton, especially under toxic cyanobacteria bloom conditions (Bernardi and Giussani 1990; Degans and De Meestser 2002), because of their detrimental effect to the growth and survival rate of zooplankton (Ghadouani et al. 2004).

On the other hand, it has been illustrated that filter-feeding fishes, such as silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthys nobilis*), and tilapia (*Oreochromis niloticus*), are effective candidates for biocontrol of cyanobacteria through suppression of phytoplankton as well as zooplankton (Starling 1993; Xie and Yang 2000; Lu et al. 2002, 2006). However, the feces of these fishes are excreted into the water column, resulting in an excessive nutrient load. Another biocontrol candidate, the freshwater shrimp (*Paratya australiensis*), is known for its variety of feeding strategies, such as filter feeding on suspended particles (Gemmell 1978), browsing on detritus (*Paratya, Caridina*) (Bunn and Boon 1993), and grazing upon cyanobacterial complexes (*Piptoporus australiensis*) (Burns and Walker 2000). The species belonging to the genus *Caridina* generally occur in freshwater and are widely distributed throughout the world. Although their size is relatively small, these shrimps contribute to a subsistence fishery in certain freshwater and estuarine systems and are quite suitable for culture in the confined waters (Lakshmi 1975). The atyid shrimp, *Caridina denticulate*, is predominant in agricultural reservoirs with a high adaptability in eutrophic waters, and feed on algae in the water column (An et al. 2010). Recently, two endemic shrimps such as *Caridina denticulata* and *Palaemon paucidens* were reported to be effective biocontrol organisms for *Microcystis aeruginosa* bloom compared with various fishes in a mesocosm experiment (An et al. 2010). However, the efficiency of atyid shrimp in controlling toxic cyanobacteria bloom is still equivocal.

In this study, stable carbon (^{13}C) and nitrogen (^{15}N) isotope tracers were used to evaluate the bioaccumulation of cyanobacteria (*M. aeruginosa*) assimilated into *C. denticulata* in in situ mesocosm experiments. Isotope labeling techniques based on the enrichment of ^{13}C and ^{15}N stable isotope ratios are commonly used to determine carbon and nitrogen uptake rates and their allocation to various tissue compartments in the biota. These techniques could be used for tracing the fate of algal-derived organic matter in the natural biota, involving energy sources and pathways (Peterson and Fry 1987; Parker et al. 1989). With ^{13}C- and ^{15}N-labeled phytoplankton, it is possible to track the assimilation pathways of carbon and nitrogen in aquatic organisms directly, in contrast to previous studies that only monitored changes in environmental parameters such as chlorophyll-*a* (Chl-*a*), nutrients, turbidity, and microcystin concentration (Benndorf 1990; Jeppesen et al. 1997; An et al. 2010). The objective of this study was to test a hypothesis that atyid shrimp (*C. denticulata*) efficiently control a ubiquitous nuisance alga, *M. aeruginosa*, in eutrophic agricultural reservoirs, by evaluating the assimilation effects on a massive *M. aeruginosa* bloom. A potential application involving an atyid shrimp (*C. denticulata*) and its grazer (bagrid catfish: *Pseudobagrus fulvidraco*), which is widely distributed in Asian agricultural reservoirs as a carnivore, is also discussed to control cyanobacteria (*M. aeruginosa*) bloom.

Materials and methods

Study site

Shingu reservoir is a eutrophic agricultural reservoir (36°10′N, 126°37′E) located in the mid-western region of South Korea. The surface area of the reservoir is 0.1 km^2 and it has a maximum depth of 7.0 m and a mean depth of

3.5 m. The volume of water in the reservoir is 388,000 m^3 (Kim and Hwang 2004). This reservoir was in a eutrophic condition during the study period, as it had Chl-*a* concentrations greater than 100 μg L^{-1}. The predominant algal species in the summer and fall is a colonial cyanobacterium, *M. aeruginosa*.

Experimental designs for the mesocosms

To evaluate the effect of biocontrol on large bloom of *M. aeruginosa* in the reservoir, we conducted biomanipulation test through in situ mesocosm environments using freshwater organisms, such as atyid shrimp and bagrid catfish. The in situ mesocosm tests were carried out from 1st to 22nd October 2007 to simulate natural reservoir environment. The mesocosm enclosures were open at the surface and sealed at the bottom. They were constructed with transparent polyethylene and were suspended from frames made from PVC tubing. The mesocosms consisted of three series of 3300-L tanks (1.3 × 1.3 × 2 m) with duplicate, including one control and two treatments:

(1) control (C; in situ water containing predominantly *M. aeruginosa*);
(2) treatment with atyid shrimp (TM; *C. denticulata*); and
(3) treatment with atyid shrimp and bagrid catfish (TMF; *C. denticulate* + *P. fulvidraco*).

Caridina denticulata and *P. fulvidraco* were captured from agricultural reservoirs using hand nets (mesh size < 2 × 2 mm) and were maintained for 2 weeks in water tanks at a temperature of 25 ± 1 °C, a DO level of 6 ± 1 mg L^{-1}, a pH level of 7–8, and a photoperiod of approximately 16 L to 8 D. The mean size (length) and biomass (wet weight) of *C. denticulata* and *P. fulvidraco* were 3.19 ± 0.28 cm, 0.41 ± 0.08 g and 9.54 ± 0.75 cm, 5.48 ± 0.05 g, respectively. All *C. denticulata* and *P. fulvidraco* were starved for 48 h prior to the experiment.

For each mesocosm, the numbers of individual organisms were determined in preliminary experiments. The mean densities of *C. denticulate* and *P. fulvidraco* were individuals m^{-3} respectively.

In situ mesocosm experiment using ^{13}C and ^{15}N tracers

The in situ mesocosm experiment was conducted in Shingu Reservoir during the period of a massive bloom of *M. aeruginosa*, which comprised 97% of the total phytoplankton density. The enclosures were filled with reservoir water. Each enclosure was maintained for 2 days to stabilize water conditions. $NaHCO_3$ (Isotech; $^{13}C > 99\%$) and $(NH_4)_2SO_4$ (Isotech; $^{15}N > 99\%$) were added to each mesocosm and maintained for 1 day. The ^{13}C at.% of the dissolved inorganic carbon (DIC) pool and the ^{15}N at.% of the ammonium pool were increased to about 15% in a set of mesocosms. Both treatment organisms were added to each mesocosm. Samples of water and planktonic organisms were collected for analysis from each mesocosm on days 1, 2, 3, 4, 6, 8, 10, 14, and 22 after treatment.

Analysis of water quality parameters

Triplicate water samples were collected to determine concentrations of dissolved inorganic nitrogen (DIN: NH_4^+, NO_3^-, NO_2^-) and phosphate (PO_4^{3-}) in each mesocosm. The concentrations of DIN and phosphate were measured using standard colorimetric techniques according to the methods of Strickland and Parsons (1968) using an UV spectrophotometer (Carry 50, Varian USA). A fluorescence spectrophotometer (Turner Design, 10R, USA) was used to determine the Chl-*a* concentrations of the 90% acetone extract (Sigma, CAS 67-64-1; 24 h). Chl-*a* concentration was determined by standard method (APHA 2005) using the absorbance value at 750, 665, 645, and 630 nm. Dissolved oxygen (DO), turbidity (NTU), and water temperature were measured using a multiparameter water quality sensor (YSI Environmental Monitoring System 660, USA). All environmental parameters, including nutrients, Chl-*a*, DO, and turbidity were monitored during the entire experimental period.

Calculation of Chl-*a* removal rate (%)

In each grazing test, removal rates of Chl-*a* by the organisms tested were calculated as follows:

$$\text{Removal rate}(\%) = (\text{Chl}_i - \text{Chl}_f)/\text{Chl}_i \times 100,$$

where Chl_i is the initial concentration of Chl-*a* and Chl_f is the final concentration of Chl-*a*.

Enumeration of phytoplankton and zooplankton

Triplicate water samples for enumeration of phytoplankton cells were taken with an integrated sampler made by opaque PVC pipe (7 cm in diameter, 150 cm in length). An aliquot of 100 mL from the well-mixed water sample was sedimented for 24 h in the volumetric cylinder, and a known volume of the concentrated sample was placed in a Sedgewick-Rafter counting chamber in which at least 300 cells (or units) were counted under ×200–400 magnification. It was difficult to count some taxa (e.g., *Microcystis, Oscillatoria*) on an individual cell basis; therefore, the larger units were enumerated and then measured colonies

and filaments were converted into cell density. Protozoans were counted during phytoplankton enumeration. Phytoflagellates were included in the phytoplankton.

The rest of water sample (ca. 5L) taken for phytoplankton was filtered through 64-μm net by which zooplankton was collected. Collected zooplankton was enumerated in a Sedgewick–Rafter counting chamber in which at least 100 individuals were counted under ×50–100 magnification. In addition, specific zooplankton taxa (Cladocerans) were collected for stable isotope analyses using a microscope and a micropipette, placed on a combusted 25 mm GF/F filter and stored at −20 °C.

Analysis of stable isotope ratios

To analyze the stable isotope ratios of particulate organic matter (mostly phytoplankton), water samples were passed through a 20-μm mesh to remove zooplankton, and the remaining water was filtered using precombusted (450 °C, 24 h) glass fiber filters (Whatman GF/F) and a gentle vacuum. Zooplankton and particulate organic matter samples were fumed for 24 h with saturated HCl to remove inorganic carbon and were dried using a freeze drier.

Biota sampling was carried out using hand nets (mesh size: 2 × 2 mm) in each mesocosm. The *C. denticulata* and *P. fulvidraco* samples were dissected to separate the digestive gland from the muscle (three samples for each biota). The muscle and gland samples were freeze-dried and then ground to a fine powder using a grinder (FRITSCH-planetary mono mill, Pulverisette 6, Germany). The freezing and storage processes do not affect the $\delta^{13}C$ and $\delta^{15}N$ values of biota tissue (Sweeting et al. 2004). Homogenized powder samples of each tissue were decalcified with 1 N HCl for at least 24 h to remove possible carbonates. However, subsamples for $\delta^{15}N$ analysis were not treated with acid because it has been reported that HCl treatment affects $\delta^{15}N$ values (Kim et al. 2016). After the acid treatment, the samples were redried using a freeze drier and were ground to a fine powder, which was thoroughly mixed prior to analysis. Measurements of stable carbon and nitrogen isotopic ratios were performed using a continuous-flow isotope-ratio mass spectrometer (Isoprime; GV Instrument, UK) coupled with an elemental analyzer (Euro EA 3000-D, Italy). Isotopic ratios are presented as δ values (‰), expressed relative to the Vienna PeeDee Belemnite (VPDB) standard and to atmospheric N_2 for carbon and nitrogen, respectively. The reference materials were IAEA-CH6 ($\delta^{13}C = -0.45 \pm 0.04$‰) and IAEA-N1 ($\delta^{15}N = 0.4 \pm 0.2$‰). The analytical precision was within 0.2 and 0.5 ‰ for carbon and nitrogen, respectively. Isotope ratios were reported in per mil (‰) using standard delta notation (Eq. 1):

$$\delta X = \left\{ \left(R_{\text{sample}} - R_{\text{std}} \right) / R_{\text{std}} \right\} \times 1000\,(‰), \quad (1)$$

where X = ^{13}C or ^{15}N, R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and std (standard) = VPDB for carbon and air N_2 for nitrogen.

For this study, the δ values were converted to at.%, which is more appropriate for labeled samples. Conversion was performed according to Eq. (2):

$$A(\text{atom}\%) = 100/[1/\{(\delta\,\text{sample}/1000 + 1) \times a_{\text{ns}}\} + 1], \quad (2)$$

where the a_{ns} for carbon is 0.011180 and that for nitrogen is 0.0036765.

Microcystin analysis

The purification and analysis of microcystin were carried out by the methods developed by Harada et al. (1988). From each sample of freeze-dried GF/F filters and atyid shrimp, the microcystins were extracted twice with 20 ml of 5% (v/v) acetic acid for 12 h while shaking at 140 rpm. The extract was centrifuged at 12,000×*g*, and then the supernatant was applied to a C18 cartridge (Sep-Pak; Waters Association). The cartridge was rinsed with water and 20% methanol in water. The eluate from the cartridge with 90% methanol water was evaporated to dryness, and the residue was dissolved in methanol. Finally, the solution was analyzed on an HPLC (Agilent Technologies 1200 series). The separation was performed on an ODS (Cosmosil 5C18-AR, 4.6 mm × 150 mm) reverse-phase column and the mobile phase consisted of 0.1% formic acid and acetonitrile with a constant flow at 1 ml min^{-1}. The measurement was determined at 238 nm using an Agilent DAD detector (G1315D).

Statistical analysis

All data were tested for normality and homogeneity of variances (Levene's median test). Pearson's correlation was used to analyze the relationship between two factors. The significance of differences between the control and the treatment was statistically evaluated with one-way ANOVA using the SPSS Statistics 21 software.

Results

Environmental variables in the mesocosms

The duplicate mesocosms showed similar variation in environmental factors during the whole experimental period; there were high correlations between duplicate

Table 1 Results of correlation analysis of environmental factors including temperature, pH, DO, turbidity, and Chl-*a*, TN, and TP concentrations in each duplicate mesocosm

	Temperature	pH	DO	Turbidity	Chl-*a*	TN	TP
Control	0.925***	0.994***	0.990***	0.992***	0.995***	0.855**	0.836**
TM	0.990***	0.670*	0.984***	0.965***	0.993***	0.671*	0.949***
TMF	0.990***	0.936***	0.877**	0.958***	0.995***	ns	ns

The adjusted r^2 and p values are given

C control, *TM* treatment with atyid shrimp (*C. denticulata*), *TMF* treatment with atyid shrimp and bagrid catfish (*C. denticulata* + *P. fulvidraco*), *ns* not significant

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

mesocosms except for TN and TP concentrations in the TMF mesocosm, possibly because of fish pellet effects (Table 1).

Water temperature in the outside water and in the mesocosms showed the same temporal changes (Fig. 1), decreasing after October 8 and ranging from 22.1 to 16.8 °C until October 22. The Chl-*a* concentrations in the outside water and in the control mesocosm were always higher than those in the treatment mesocosms (Fig. 1). Chl-*a* concentrations in the mesocosms decreased from October 6 and were the highest on October 4 in all mesocosms except the TM mesocosm, for which the highest concentration was on October 8. Chl-*a* concentration in the *C. denticulata*-only mesocosm (TM) was normally lower than that in the control mesocosm, except on October 8, indicating that its temporal variation differed from that of the TMF mesocosm. Combined treatment with *C. denticulata and P. fulvidraco* caused a significant decrease in Chl-*a* concentration in the TMF mesocosm compared with those in the other two mesocosms (C and TM), ranging from 112 to 45 μg L^{-1} (Fig. 1). These results demonstrate that *M. aeruginosa* biomass was reduced by *C. denticulata*. In addition, the removal rate of Chl-*a* in the TMF mesocosm was significantly greater than that in the TM mesocosm (Fig. 2). This indicates that combined treatment with *C. denticulata* and *P. fulvidraco* had a positive effect on the removal of algal biomass. The DO concentration was generally higher in the control mesocosm compared with the other mesocosms, but it increased abruptly on October 10 in the TM mesocosm, corresponding with an apparent increase in Chl-*a* concentration and turbidity on the same day. Turbidity was higher in the control mesocosm than in the other treatment mesocosms.

Biocontrol with *C. denticulata* and *P. fulvidraco* resulted in significant differences in water quality parameters such as Chl-*a*, DO, and turbidity in the cyanobacteria (*M. aeruginosa*) blooming environment, in comparison with those of the control mesocosm (Table 2). In addition, the DIN concentration (1.17 mg L^{-1}) in the control mesocosm was lower during the whole experimental period than those of the other mesocosms (from October 14 through 22). DIP concentration was slightly elevated in all mesocosms, but it increased markedly in the TMF mesocosm after October 14 (Fig. 1).

Species composition and cell density of phytoplankton and zooplankton

The relative proportions of phytoplankton species at the beginning of the mesocosm experiment showed that the predominant species was cyanophyceae (about 97.71%), followed by bacillariophyceae (1.32%), chlorophyceae (0.80%), euglenophyceae (0.13%), and cryptophyceae (0.04%) (Table 3). Among cyanophyceae, *M. aeruginosa* was predominant (97% of the total phytoplankton cell number) in all mesocosms (Table 3). The taxonomic composition of phytoplankton was not notably changed during the study period, but bacillariophyceae and chlorophyceae were increased in a small degree in TMF treatment. The cell density of phytoplankton in both TM and TMF mesocosms was fluctuated during the experiment; however, it was clearly decreased at the end of the experiment compared to the initial cell density (Fig. 3).

The zooplankton community composition varied between the control and treatment mesocosms during the study period. At the beginning of the mesocosm experiment, the predominant taxa were rotifers (70.72%), followed by copepods (14.30%), protozoans (10.42%), and cladocerans (4.54%) (Fig. 4). The zooplankton abundance and composition changed remarkably during the study period in each mesocosm (Fig. 4). In the control mesocosm, the total density of zooplankton decreased on October 2 and remained low throughout the experiment. Total zooplankton abundance differed between the TM and TMF mesocosms, and the total zooplankton density increased because of an increase in cladoceran density in the TMF mesocosm (30.0% on October 8, 45.4% on October 14, 50.3% on October 22) in the middle of the experimental period.

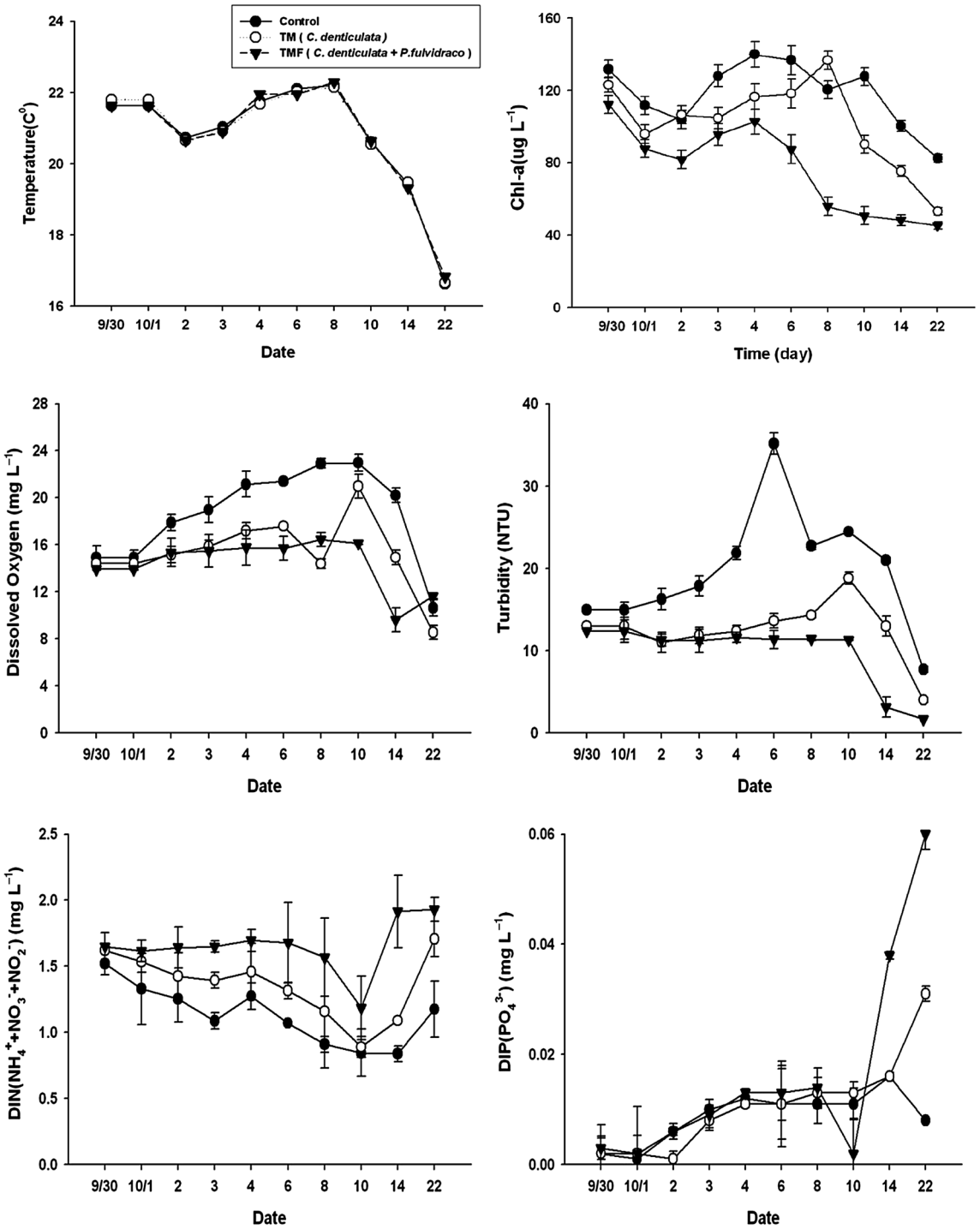

Fig. 1 Change of water environmental parameters (water temperature, Chl-*a*, DO, turbidity, TN, and TP) in each mesocosm. *C* control, *TM* treatment with atyid shrimp (*C. denticulata*), and *TMF* treatment with atyid shrimp and bagrid catfish (*C. denticulata* + *P. fulvidraco*). Values represent mean ± SE

The ^{13}C and ^{15}N at.% in POM, zooplankton, and treatment organisms

The ^{13}C and ^{15}N at.% of the particulate organic carbon (POC) and particulate organic nitrogen (PON) in the particulate organic matter (POM) (mostly phytoplankton) in the control and in both treatment mesocosms showed similar variation (Fig. 5). Within 1 day of the addition of the tracers, ^{13}C and ^{15}N at.% were remarkably enriched in the POM through active phytoplankton assimilation.

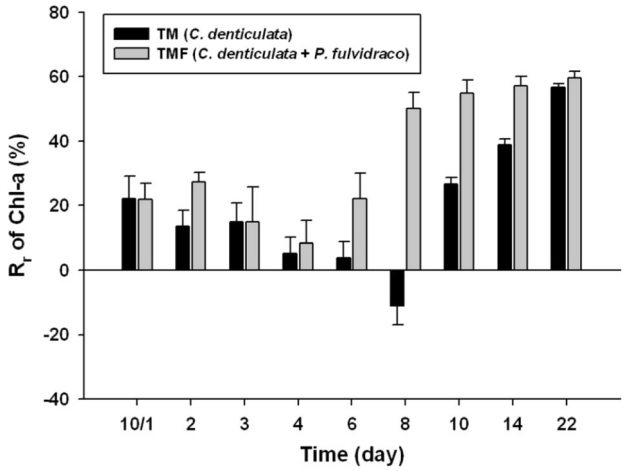

Fig. 2 Removal rate (R_r) of Chl-*a* by atyid shrimp (*C. denticulata*) in the absence (TM) and in the presence (TMF) of bagrid catfish (*P. fulvidraco*) during the experimental period. Values represent mean ± SE

However, the values were saturated and decreased slightly at the end of the trial. The at.% of incorporated ^{13}C and ^{15}N in cladocerans in all treatments showed clear enrichment on the first day and showed similar ranges to those of POM. ^{13}C and ^{15}N at.% in cladocerans were higher in the TMF mesocosm than in the other mesocosm (Fig. 5).

The accumulated incorporations of carbon and nitrogen into muscle and the digestive glands of the treatment organisms were indicated by the increase in ^{13}C and ^{15}N at.% through dietary assimilation. Most treatment organisms showed continuous apparent enrichment of ^{13}C and ^{15}N ratios in their tissues during the experimental period (Fig. 6). As it is a filter-feeding organism, the accumulated incorporation of *C. denticulata* differed between the TM and TMF mesocosms (Fig. 7): 1.08 ~ 2.41 at.% for ^{13}C and 0.36 ~ 2.55 at.% for ^{15}N in the TM mesocosm and 1.08 ~ 3.72 at.% for ^{13}C and 0.36 ~ 4.93 at.% for ^{15}N in the TMF mesocosm. The *P. fulvidraco* accumulated incorpo-

Table 2 Statistical results for environmental parameters for the outside, control, and treatment (TM and TMF) mesocosms (n = 7)

Parameters (unit)	*p* value			
	Outside	Control	TM	TMF
Water temperature (°C)		0.162	0.277	0.245
Dissolved oxygen (mg L^{-1})		0.245	0.768	0.102
pH		0.435	0.091	0.068
Turbidity (NTU)		0.511	0.007**	0.001***
Chl-*a* (μg L^{-1})		0.295	0.009**	0.000***
Total nitrogen (mg L^{-1})		0.365	0.001***	0.000***
Total phosphorus (mg L^{-1})		0.342	0.223	0.015*

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3 Phytoplankton taxa and relative proportions (%) during initial experimental condition in a study reservoir (on September 30, 2007)

Class	Species	Relative proportion (%)
Cyanophyceae	*M. aeruginosa*	97.71
	Oscillatoria sp.	
	Spirulina sp.	
Chlorophyceae	*Ankistrodesmus falcatus*	0.80
	Closterium aciculare	
	Pediastrum simplex	
	Scenedesmus quadricauda	
	Staurastrum sp.	
	Gloeocystis gigas	
Cryptophyceae	*Cryptomonas ovata*	0.04
Euglenophyceae	*Trachelomonas* sp.	0.13
Bacillariophyceae	*Aulacoseira varians*	1.32
	Cyclotella meneghiana	
	Navicula spp.	
	Synedra ulna	
	Nitzschia sp.	

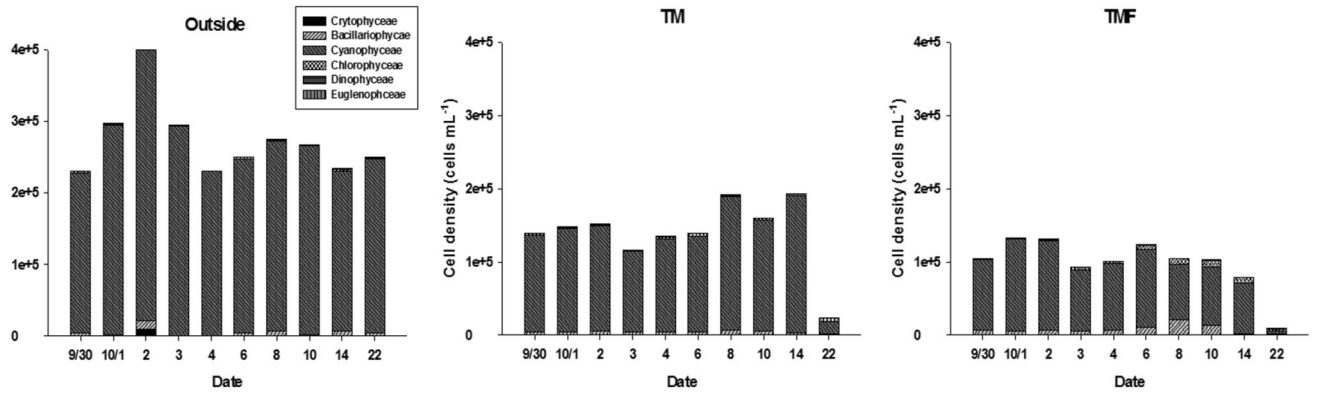

Fig. 3 Density of phytoplankton in each mesocosm (*C* control, *TM C. denticulata*, *TMF C. denticulata* + *P. fulvidraco*) during the experimental period. Values represent means

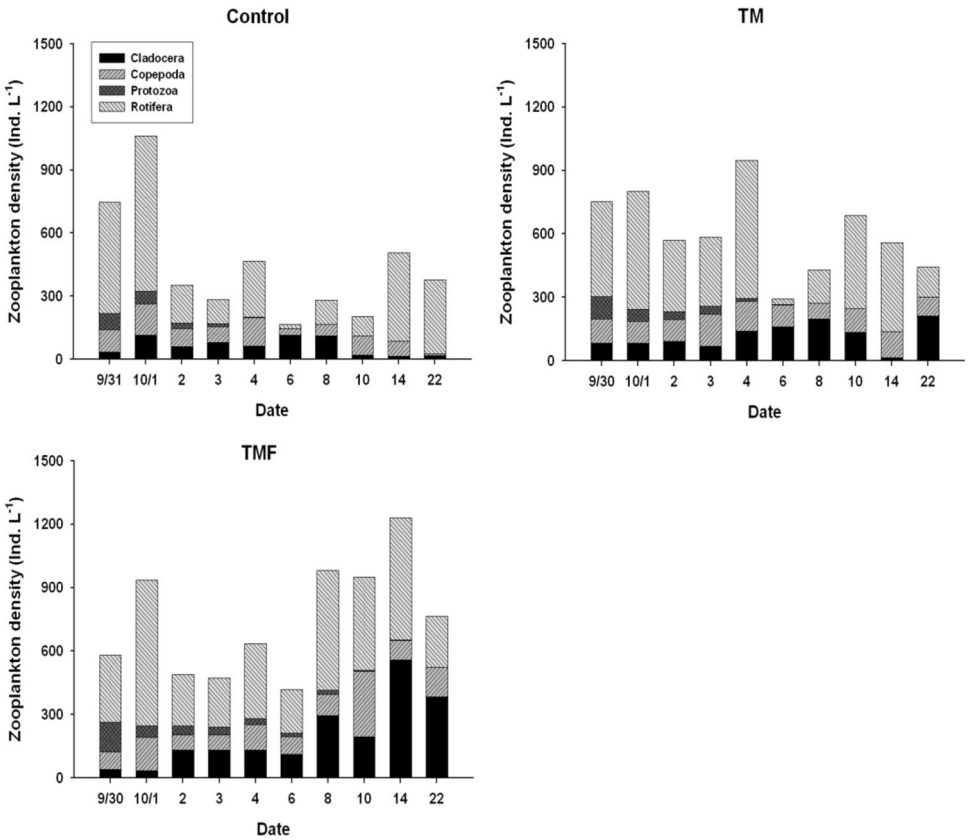

Fig. 4 Density of zooplankton in each mesocosm (*C* control, *TM C. denticulata*, *TMF C. denticulata* + *P. fulvidraco*) during the experimental period. Values represent means

ration was 1.08 ~ 1.55 at.% and 0.36 ~ 3.91 at.% for ^{13}C and ^{15}N respectively, in the TMF mesocosm (Fig. 7).

Temporal variation of microcystin concentration in the mesocosms

The particulate microcystin concentrations (MC-RR, YR, LR) in water slightly decreased from October 6, and were highest on October 3 in all mesocosms (Fig. 8). Microcystin concentration in the combined treatment with *C. denticulata and P. fulvidraco* mesocosm (TMF) was normally lower than that in the control and TM mesocosm, and might be related with the abundance of phytoplankton cells.

Discussion

Biocontrol of *M. aeruginosa* bloom with *C. denticulata* and *P. fulvidraco*

In this study, statistical tests of means for environmental variables such as pH, turbidity, and Chl-*a* and total

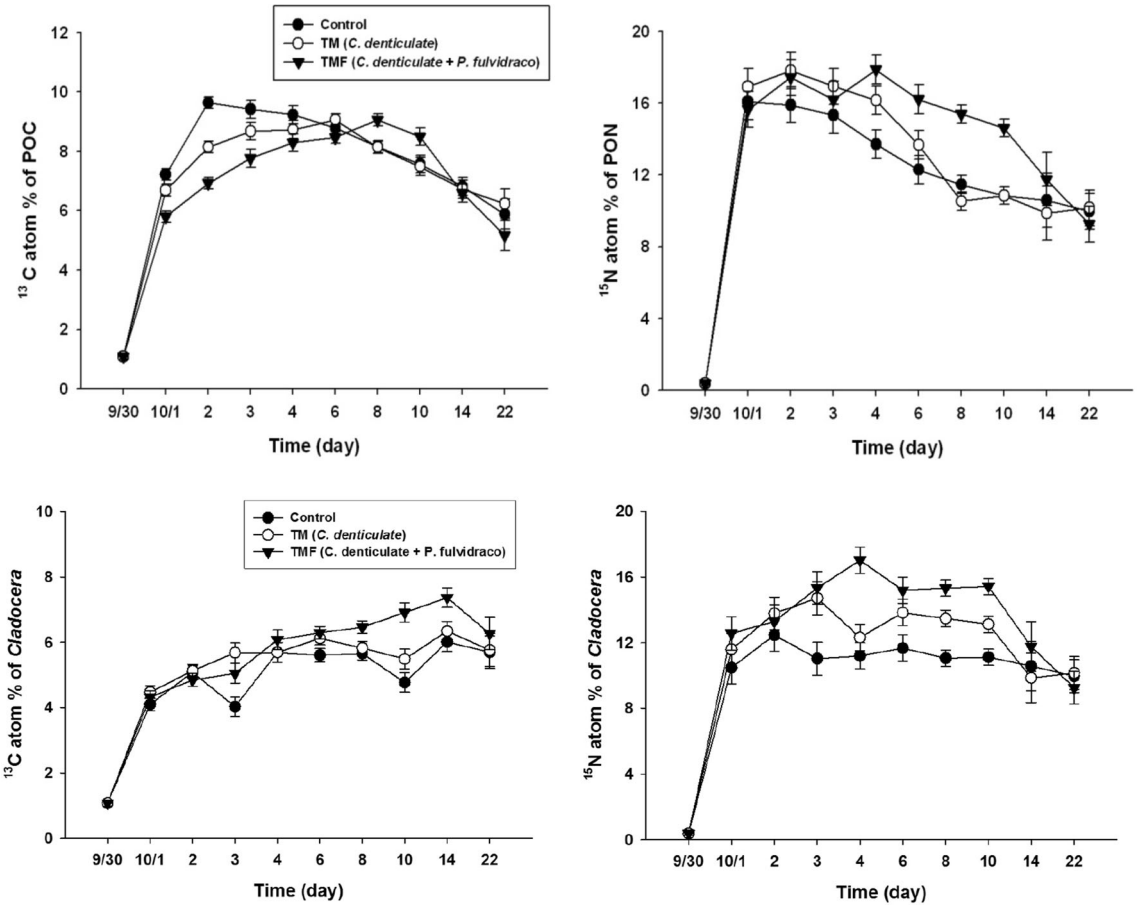

Fig. 5 ^{13}C and ^{15}N at.% of particulate organic matter (POC and PON) and zooplankton (Cladocera) in each mesocosm during the experimental period. Values represent mean ± SE

inorganic nitrogen concentrations showed that there were significant differences between the outside water and both treatment mesocosms (Table 2). Chl-*a* concentration and turbidity were less in both treatment mesocosms compared with those in the control mesocosm. This suggests that *C. denticulata* preyed on *M. aeruginosa*, which resulted in greater water clarity. However, reduced Chl-*a* concentration and turbidity may not be direct evidence of *C. denticulata* assimilation of *M. aeruginosa* because *C. denticulata* may expel toxic cyanobacteria without digesting them in the form of feces or pseudofeces that is released into the water column or sink to the bottom. Therefore, the grazing efficiency of *C. denticulata* was evaluated according to the ^{13}C and ^{15}N at.% incorporated into the biota. In this study, mesocosm size and wall type may have affected the feeding behavior of the *C. denticulata*. However, Gorokhova and Hansson (1997) showed that container size has a rather limited effect on the food consumption of opossum shrimp *Mysis mixta,* which feeds the same way as *C. denticulata*. Hansson et al. (2001) also demonstrated that similar consumption rates were obtained for different types of containers. Thus, it is not necessary to consider mesocosm size and wall type in our discussion.

The ^{13}C and ^{15}N at.% in *C. denticulata* showed continuously increasing trends for the TM and TMF mesocosms, exhibiting a close coupling with temporal variation in Chl-*a* concentration in the corresponding mesocosms throughout the entire study period (Figs. 1, 7). These results indicate that *C. denticulata* fed on *M. aeruginosa* directly. If *C. denticulata* had released *M. aeruginosa* into the water column as an undigested food, a slightly enriched ^{13}C and ^{15}N at.% would have been detected in digestive gland tissue but not in muscle tissue because of little energy transfer from the digestive gland to the muscle tissue. However, the ^{13}C and ^{15}N at.% of both digestive gland and muscle tissue in *C. denticulata* were clearly enriched and increased continuously until the end of the experiment (Fig. 6), indicating that *C. denticulata* assimilated *M. aeruginosa* into its body through feeding and digestion. Therefore, our results suggest that *C. denticulata* should be a keystone taxon for removing toxic cyanobacteria such as *M. aeruginosa*.

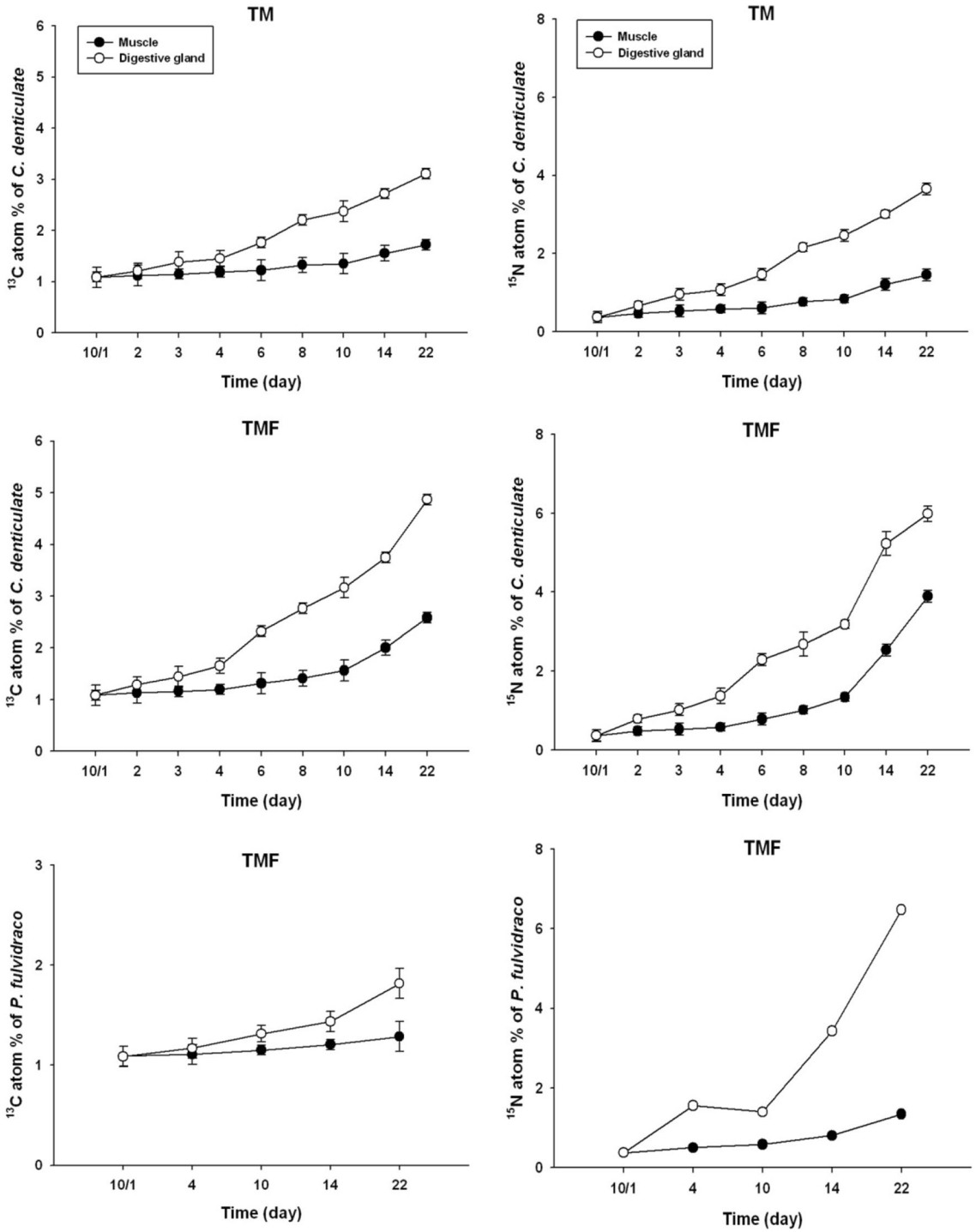

Fig. 6 ^{13}C and ^{15}N at.% in different tissues of *C. denticulata* and *P. fulvidraco* in treatment mesocosms (TM and TMF) during the experimental period. Values represent mean ± SE

In the present study, *C. denticulate* seemed to be quite tolerant of microcystins, depurating these cyanotoxins efficiently. When *C. denticulate* was fed toxic *M. aeruginosa* for 3 weeks, the organic matter derived from *M. aeruginosa* was continuously assimilated into the body despite apparent toxicity. This means that *C. denticulate* can enzymatically produce a conjugate of the hepatotoxin to detoxify cyanobacterial toxicity (Pflugmacher et al. 1998). These toxic inhibition enzymes are still unclear in the atyid shrimp, whereas detoxification has been studied in various aquatic organisms such as macrophytes, invertebrates, and fishes (Pflugmacher et al. 1998; Wiegand

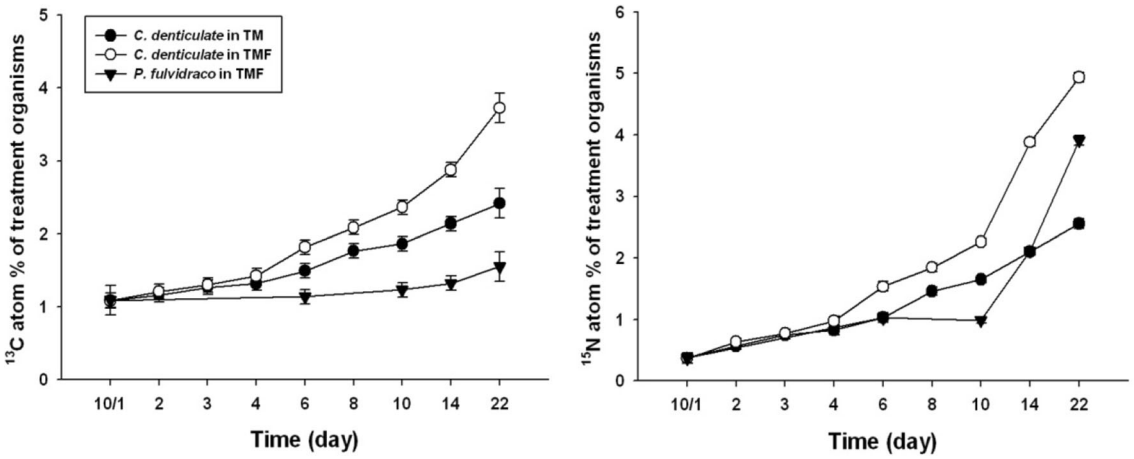

Fig. 7 ^{13}C and ^{15}N at.% of *C. denticulata* and *P. fulvidraco* in treatment mesocosms (TM and TMF) during the experimental period. Values represent mean ± SE

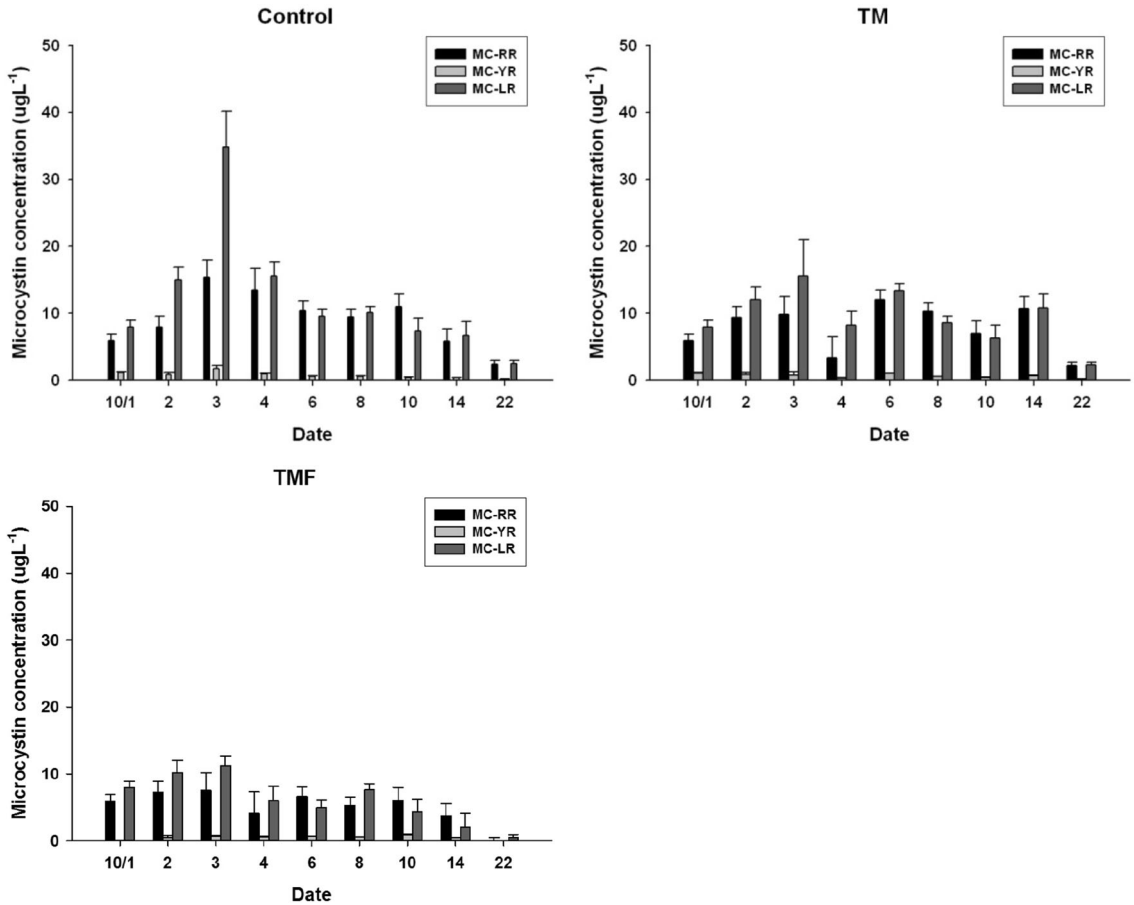

Fig. 8 Microcystin concentration of particulate organic matter in each mesocosm during the experimental period. Values represent mean ± SE

et al. 1999). Some kinds of freshwater shrimps can be sustained under highly toxic cyanobacteria bloom conditions. For example, mysid shrimps (*Mysis relicta*) showed high survival in the presence of toxic cyanobacteria in a laboratory experiment (Engstrom et al. 2002) and the mortality of *M. mixta* did not increase during an experiment period where mysids were exposed to high concentrations of toxic *Nodularia spumigena,* which suggests that they should be tolerant against cyanobacterial toxins (Engstrom et al. 2001). Furthermore, Piola et al. (2008)

reported that cyanobacterial assimilation of *P. australiensis* may contribute up to 69% of its carbon and nitrogen requirements, possibly biosynthesizing cyanobacteria hepatotoxins or related compounds. Therefore, some kinds of freshwater shrimp have been considered as candidate organisms to control toxic cyanobacteria bloom through feeding activity. On the other hand, some grazers avoid harmful algae by selective feeding or vertical migration because of algal toxicity. In fact, only a few filaments of cyanobacteria were found in the stomach of *M. mixta* when cyanobacteria blooms occurred (Viherluoto et al. 2000).

However, in the present study, *C. denticulata* did not select or avoid its prey and had to assimilate toxic *M. aeruginosa* into its digestive gland and muscle tissue because *M. aeruginosa* comprised 97% of the total phytoplankton biomass during the entire mesocosm experiment. As a result, *C. denticulata* continuously assimilated toxic *M. aeruginosa* through its depuration ability. The depuration mechanism may be closely related to the production and degradation cycles of a protein phosphatase–MCYST adduct (Vasconcelos et al. 2001). Beattie et al. (2003) reported that toxic compounds in brine shrimp (*Artemia salina*) were conjugated to glutathione via GST as an initial step in microcystin and nodularin detoxication. Therefore, the depuration enzyme of *C. denticulata* may be activated when it is exposed to a toxic *M. aeruginosa* bloom.

In this study, the feeding ability of *C. denticulata* was evaluated in the absence and presence of a predator that is widely distributed in freshwater ecosystems. The incorporated at.% of *C. denticulata* in the TMF mesocosm was higher than that in the TM mesocosm (Fig. 7), demonstrating that digestion and assimilation of prey is more frequent than ingestion of undigested foods in the TM mesocosm. This means that *C. denticulata* should assimilate *M. aeruginosa* effectively into its body under the grazing pressure of *P. fulvidraco*. Moreover, the removal rate of *M. aeruginosa* by *C. denticulata* should be associated with predation pressure (Figs. 2, 7). This can be described by biomass ratio-dependent functional responses, i.e., the relationship between food density and the ingestion rate at which an individual consumes its food (Holling 1959). There are many reports showing that predator presence has a dramatic effect on the behavior of its prey (e.g., Sih et al. 1985). Arditi and Ginzburg (1991a) suggested that prey and predator abundances should be considered as ratio-dependent functional responses. In our study, the biomass of *C. denticulata* may have been reduced by the grazing pressure of the predator *P. fulvidraco* in the TMF mesocosm. However, ^{13}C and ^{15}N at.% (enhanced by prey assimilation rate) in individual *C. denticulata* increased with a decrease in the density of *C. denticulata*. These results are supported by previous reports showing that the feeding efficiency of the mysid shrimp (*M. mixta*) decreases when their abundance increases (Hansson et al. 2001), due to heterogeneity in the distribution of predators and prey, including spatial refuges for the prey (Arditi et al. 1991b; Abrams and Walters 1996). A change in predator–prey population dynamics resulted from ratio-dependent functional responses with changing predator density (Arditi et al. 1991b; Abrams and Walters 1996). Therefore, the removal efficiency of *M. aeruginosa* by *C. denticulata* seems to be dependent upon the number of *C. denticulata* present. As a result, the feeding rate of *C. denticulata* in the TMF mesocosm was higher than that in the TM mesocosm throughout the experiment. This result corresponded with an apparently lower Chl-*a* concentration and a higher removal rate of Chl-*a* in the TMF mesocosm than in the TM mesocosm (Figs. 1, 2).

Biocontrol effect of *C. denticulata* and *P. fulvidraco* on zooplankton

The number of zooplankton decreased from 746 to 379 cells L^{-1} in the control mesocosm and from 751 to 444 cells L^{-1} in the TM mesocosm, and increased from 580 to 763 cells L^{-1} in the TMF mesocosm, especially 1230 cells L^{-1} on September 14 (Fig. 4). Zooplankton is a primary consumer of phytoplankton in lake ecosystems (Dodson 1974) and is recognized as the most significant aquatic organism to impact upon phytoplankton bloom (Matveev et al. 1994; Sarnelle 2005). However, in this study, the grazing pressure of zooplankton seems to have been weak in the TM mesocosm as well as in the control mesocosm, and the reason for the decrease in the number of individual zooplankton might have been the toxicity of *M. aeruginosa* (Lampert 1981; DeMott and Moxter 1991). Whereas the abundances of individual zooplankton apparently increased in the TMF mesocosm during the experimental period, the ^{13}C and ^{15}N at.% of zooplankton, cladoceran species, showed higher values in the TMF mesocosm than in the control and TM mesocosms (Fig. 5). The dietary assimilation rate and abundances of individual zooplankton in both treatment mesocosms were higher, compared with the control mesocosm under toxic cyanobacterial bloom conditions. The feeding ability of *C. denticulata* probably influenced zooplankton grazing by reducing the toxic algal biomass as a prey in the treatment mesocosms; this effect was stronger in the TMF mesocosm than in the TM mesocosm. It can be assumed that *C. denticulata* may break large colonies of cyanobacteria species through the feeding process, enabling subsequent consumption by zooplankton species because each zooplankton species has a different selective feeding pattern, depending mainly on prey size (e.g., Pagano et al. 1999).

The cyanobacteria aggregates are inedible prey (large colonial size) for most zooplankton species, and only small colonies or dispersed cells of cyanobacteria can be ingested (Jarvis et al. 1987). Therefore, there is a possibility of breakage of colonial *M. aeruginosa* by *C. denticulata* in the present mesocosm experiment, indicating that inedible *M. aeruginosa* colonies may be grazed efficiently as small and edible particles by zooplankton species (e.g., small cladocerans and copepods).

In this study, the species abundances and composition of zooplankton were changed in the treatment mesocosms (Fig. 4). In the TMF mesocosm, total zooplankton abundance apparently increased through an increase in cladoceran species (30.0% on October 8, 45.4% on October 14, 50.3% on October 22) since the middle of the experimental period (Fig. 4). Some large-size cladocerans such as *Daphnia* sp. could consume cyanobacteria (Kirk and Gilbert 1992), but *Daphnia* was not found in our study. Zooplankters were usually rotifers, calanoid copepods, and small cladoceran (e.g., *Bosmina*). It has not yet been established whether these small zooplanktons are all effective consumers of cyanobacteria, even though there is no doubt that zooplankton can consume toxic cyanobacteria (Burns et al. 1989). The increase in small cladoceran species (e.g., *Bosmina coregoni* and *Bosmina longispina*) in the TMF mesocosm might be related to prey size and ingestion rate. The feeding behavior of *C. denticulata* can change from larger colonial *M. aeruginosa* aggregates to shortened breakage cells, and small cyanobacteria particles would have been better food for smaller cladocerans compared with actively growing or colonial cyanobacteria. Usually, smaller cyanobacteria species are more readily ingested by daphnids than larger colonies (Bernardi and Giussani 1990), and *Bosmina longirostris* readily ingest *Anabaena* spp. and *M. aeruginosa* (Fulton and Paerl 1987). Furthermore, Henning et al. (1991) showed that *B. coregoni* ingested, at high rates, toxic *M. aeruginosa* that was avoided by *Daphnia magna*. Therefore, in this study, smaller cladoceran species, which were dominated by *B. longirostris* and *B. coregoni*, increased in density with an apparent change in zooplankton community composition.

Our study revealed that the atyid shrimp *C. denticulata* is a useful organism for controlling a cyanobacterial bloom in eutrophic waters, especially in agricultural reservoirs where nutrient loading could not be reduced sufficiently and where grazing by zooplankton cannot control phytoplankton biomass effectively. In addition, the present results demonstrate that biomanipulation of the atyid shrimp (*C. denticulata*) and bagrid catfish (*P. fulvidraco*) increased zooplankton assimilation of toxic *M. aeruginosa* and enhanced the zooplankton community biomass with the appearance of smaller cladoceran species. This is the first in situ experimental study to clarify the biocontrol effects of an atyid shrimp (*C. denticulata*) and bagrid catfish (*P. fulvidraco*) on a toxic cyanobacterium (*M. aeruginosa)* bloom in a eutrophic agricultural reservoir.

Conclusions

The ability of atyid shrimp (*C. denticulata*) and bagrid catfish (*P. fulvidraco*) to control a massive bloom of *M. aeruginosa* was tested in in situ mesocosm experiments in a eutrophic agricultural reservoir. *C. denticulata* actively assimilated toxic *M. aeruginosa,* resulting in increased density of small cladoceran zooplankton and positive effects on their feeding ability. Indeed, the incorporation efficiency of *M. aeruginosa* by *C. denticulata* was affected by the grazing pressure of *P. fulvidraco* and was ratio dependent on the prey and predator biomasses. Our research highlights new findings for controlling a massive bloom of toxic *M. aeruginosa* by combination treatment with *C. denticulata* and *P. fulvidraco* as a key predator organism. This had notable impacts on zooplankton density and species composition, which were possibly due to changes in the shape of *M. aeruginosa* cells from a large colony to small edible particles induced by the feeding activity of *C. denticulata*. This is the first evaluation of the effects of biocontrol on a toxic cyanobacteria (*M. aeruginosa*) bloom using an in situ mesocosm experiment and dual stable isotope tracers (^{13}C and ^{15}N).

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