



Effects of co-cultured common carp on nutrients and food web dynamics in rohu aquaculture ponds

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ABSTRACT: Using the common carp *Cyprinus carpio* L. in polyculture ponds to increase both phyto- and zooplankton availability has become a popular practice for the cultivation of planktivorous fish, such as rohu *Labeo rohita* Hamilton. However, the dynamics of how common carp influences the environment and ecology in polyculture ponds are unclear. In the present study, the effects of various stocking densities (0, 0.5 and 1 m⁻²) of common carp on the dynamics of nutrients, phytoplankton, zooplankton and benthic macroinvertebrates were investigated every other week over a 137 d period in rohu (density: 1.5 m⁻²) ponds under fed and unfed conditions. All environmental parameters and all groups of phytoplankton, zooplankton and benthic macroinvertebrates significantly changed over time, although trends in these changes were inconsistent at different common carp densities. The correlation between phosphate-phosphorus (PO₄-P) and total phytoplankton biomass indicated that the phytoplankton biomass was limited by low PO₄-P concentrations in ponds without common carp. Common carp-driven resuspension increased N and P fluxes from the sediment to the water column and subsequently increased primary and secondary production. A stocking density of 0.5 common carp m⁻² had strong effects on nutrients and both phyto- and zooplankton availability, with an increasing trend over time. These effects were partially lost in ponds with 1 common carp m⁻², which can be considered as overstocking. This study suggests that an optimal density of common carp can be used as a management tool to manipulate the aquaculture environment for better growth and production of fish.

KEY WORDS: Polyculture · Fish yield · Stocking density · Resuspension · Nutrient flux · Water quality · Plankton · Benthos · Aquaculture environment

INTRODUCTION

Most of the nutrients in ponds are stored in bottom sediments in both organic and inorganic forms (Briggs & Funge-Smith 1994, Boyd 1995, Rahman et al. 2008). According to Biro (1995), sediment can store 100 to 1000 times more nutrients than water. Transference of nutrients back into the water column by the resuspension of sediment can have an important influence on the limnology of ponds (Zambrano & Hinojosa 1999, Rahman et al. 2010). Several fish species often resuspend sediment; the

best known is the common carp *Cyprinus carpio* (Costa-Pierce & Pullin 1989, Rahman et al. 2008). The common carp feeds on benthic organisms, and it often affects aerobic decomposition of organic matter and nutrient availability in the water column via bioturbation of benthic sediment (Breukelaar et al. 1994, Cline et al. 1994, Rahman et al. 2010). An increase in nutrient availability may enhance photosynthesis and the related phyto- and zooplankton production (Rahman & Verdegem 2007). Therefore, common carp is commonly used in polyculture ponds to increase both phyto- and zooplankton

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availability for planktivorous fish. Planktivorous fish reduce algal biomass and water turbidity, which in turn has an important impact on photosynthesis (Rahman 2006, Rahman & Verdegem 2007). Therefore, the combined effect of benthivorous and planktivorous fish on pond limnology is highly complex and has not been well quantified.

If resuspension of sediment by common carp is excessive, soluble phosphorus availability and water clarity typically decrease (Holdren & Armstrong 1980, Bostrom et al. 1988, Barton et al. 2000), thereby reducing photosynthesis and phytoplankton production. Therefore, the effect of common carp on pond limnology is largely dependent on its density. Considering both the positive and negative effects of common carp on nutrient and food web dynamics, stocking density of common carp is important for understanding pond ecology. Almost nothing is known about the effects of different densities of common carp on pond ecology in the presence of planktivorous fish.

In a prior study, the effects of different densities of common carp on pond environments, plankton and benthic macroinvertebrate availability, and fish production in rohu (*Labeo rohita*, a planktivorous fish) ponds were examined (Rahman et al. 2006). The prior study did not reveal the underlying mechanism affecting how the limnological condition of ponds changes over time. Such information is important to ensure adequate limnological conditions for the production of fish. Surplus natural food, along with good environmental conditions, lead to the stocking of an additional species or increasing the stocking density. Both activities further increase fish yield. In the current study, the effects of different densities of common carp on pond ecology with respect to the effects on nutrients, phytoplankton, zooplankton and benthic macroinvertebrate dynamics, and fish growth over time are described. The main objectives were: (1) to better understand the nature of nutrients, phytoplankton, zooplankton and benthic macroinvertebrate dynamics over time in rohu ponds with different densities of common carp and (2) to elucidate the possibility of further increasing fish production in these types of ponds.

MATERIALS AND METHODS

The trial was conducted in 18 earthen ponds (100 m² surface area, 1.2 m average depth) at the Fisheries Faculty Field Laboratory, Bangladesh Agricultural University, Bangladesh, for a period of 137 d

from March to July 2003. All ponds were individually filled with ground water from an adjacent deep tube-well. Each pond was stocked with rohu (1.5 rohu m⁻²). The experiment was designed as 3 × 2 factorial, with 3 levels of common carp density (0, 0.5 and 1 common carp m⁻²) and 2 levels of artificial feed (with and without feed). Each treatment was executed in triplicate. Rohu (average individual weight varied from 20.3 to 21.1 g) and common carp (20.6 to 21.4 g) were released into the ponds in the afternoon. The 30% protein diet containing fish meal (protein: 57.5%, inclusion in feed: 37%), rice bran (14%, 47%), mustard oil cake (14%, 15%), and vitamin premix (0%, 1%) was applied daily at 15 g kg^{-0.8} d⁻¹ from the day of releasing fingerlings until the end of the experiment. Total fish biomass was estimated monthly by weighing at least 20% of the fish stocked into each pond. Feeding rates were then adjusted for total fish biomass each month.

Environmental parameters were measured every other week between 9:00 and 10:00 h, starting on the day of stocking. Dissolved oxygen (DO) was measured using the Winkler titration method (Stirling 1985), pH was measured with a pH meter (Jenway 3020), total ammonia nitrogen (TAN) and phosphate phosphorus (PO₄-P) were analysed spectrophotometrically (Stirling 1985), and nitrate nitrogen (NO₃-N), total phosphorus (TP), and total nitrogen (TN) were measured following APHA (1998).

Water samples for phyto- and zooplankton analysis were collected every other week by taking a 1 l sample at 10 different locations in each pond with a Niskin sampler. The composite 10 l samples were then passed through a 10 μm mesh plankton net. Each concentrated plankton sample was transferred to a plastic bottle and preserved with a 100 ml solution of 5% buffered formalin. Phyto- and zooplankton densities were estimated using a Sedgewick-Rafter (S-R) cell containing 1000 fields of 1 mm³. A 1 ml sample was put into the S-R cell and left for 10 min to allow plankton to settle. Phyto- and zooplankton in 10 randomly selected fields in the S-R cell were identified to genus and counted. Both phyto- and zooplankton were identified using the keys provided by Ward & Whipple (1959), Prescott (1962), Belcher & Swale (1976), and Bellinger (1992). Phyto- and zooplankton densities were calculated using the formula:

$$N = (P \times 10000) / L \quad (1)$$

where N is the number of phyto- and zooplankton per litre pond water, P is the number of phyto- and zooplankton counted in 10 fields, L is the volume of the pond water sample (10 l).

Benthic macroinvertebrate samples were collected every other week with an Ekman dredge. Bottom samples from 3 randomly selected sites were collected and washed through a 250 μm mesh sieve. Benthic macroinvertebrates remaining on the sieve were preserved in a plastic vial containing a 10% buffered formalin solution. Identification keys used for benthic macroinvertebrates were according to Brinkhurst (1971) and Pinder & Reiss (1983). Benthic macroinvertebrate density was calculated using the formula:

$$N = Y \times 10000/3A \quad (2)$$

where N is the number of benthic macroinvertebrates (m^{-2}), Y is the total number of benthic macroinvertebrates counted in 3 samples, A is the area of the Ekman dredge (cm^2). Biovolumes of phytoplankton and zooplankton and benthic macroinvertebrates were calculated using literature values described by Rahman et al. (2006).

Sedimentation and resuspension were assessed by traps, which were made using plastic boxes (area: 96 cm^2) of 15 cm height with a metal net (mesh: 1 cm) tightly placed on the top of each box to avoid disturbance of materials by fish. To stabilize each box on the bottom of the pond, inside each box a heavy stone was placed in the center. Three boxes were randomly placed on the bottom of each pond and retrieved after 7 to 14 d, depending on the material accumulation rate in the box. The total solid weight of trapped particulate matter was determined following drying at 60°C to constant weight. Finally, the sum of sedimentation and resuspension was calculated as grams per square metre per day.

All data were checked for normality and analysed using a repeated-measures 2-way analysis of variance (ANOVA). Common carp density and artificial feeding were considered main factors, and time was treated as a sub-factor. If a factor or interaction was significant, differences between the means were analysed by Tukey test for unplanned multiple comparisons of means ($\alpha = 0.05$). The factors common carp density and artificial feeding are discussed in a separate article (Rahman et al. 2006). The interaction of time and artificial feed was not significant ($p > 0.05$); therefore, this interaction will not be discussed. The present paper discusses the effects of time and its interaction with common carp density. Correlations between $\text{PO}_4\text{-P}$ and total phytoplankton in ponds with and without common carp were tested for significance using SPSS (Version 16.0).

RESULTS

The effects of time and its interaction with common carp density on environmental parameters, and the abundance of different groups of phytoplankton, zooplankton and benthic macroinvertebrates are presented in Tables 1 & 2, respectively. $\text{PO}_4\text{-P}$ and TP concentrations in the water and benthic macroinvertebrate availability in bottom sediment increased with increasing time. This trend was not observed in the other variables, which (except for Cladocera and Copepoda) significantly changed over time ($p < 0.01$), showing peaks at different sampling days (Tables 1 & 2). These results are different depending on common carp stocking densities (except temperature and Bacillariophyceae) (Figs. 1–3). After the first 2 sampling days, DO concentrations decreased with increasing common carp density (Fig. 1). Time effects on the $\text{PO}_4\text{-P}$ and TP increase were more pronounced in the presence of 0.5 common carp m^{-2} , followed by 1 common carp m^{-2} , and then without common carp. $\text{NO}_3\text{-N}$, TAN and TN concentrations were higher in ponds with common carp (either 0.5 or 1 m^{-2}) than in ponds without common carp throughout the experimental period.

The average daily sum of sedimentation and resuspension increased with higher carp density (Fig. 4A), and in all treatments, over time (Fig. 4B). It was almost doubled in the ponds with 1 common carp m^{-2} (352 g solid $\text{m}^{-2} \text{d}^{-1}$) compared to the ponds with 0.5 common carp m^{-2} (199 g solid $\text{m}^{-2} \text{d}^{-1}$). Time effects on the average daily sum of sedimentation and resuspension were also more pronounced in the presence of 1 common carp m^{-2} , followed by 0.5 common carp m^{-2} , and then without common carp.

The overall phytoplankton and zooplankton abundances were higher in ponds with 0.5 common carp m^{-2} , followed by 1 common carp m^{-2} , and without common carp (Fig. 2). Total phytoplankton and zooplankton abundances increased with increasing time only in ponds with 0.5 common carp m^{-2} , while in ponds with 1 common carp m^{-2} , they changed negligibly after the initial 2 samplings. A significant correlation between $\text{PO}_4\text{-P}$ and total phytoplankton biomass was observed; this correlation was stronger in ponds without common carp ($r = 0.64$, $p < 0.01$) than in ponds with common carp ($r = 0.50$, $p < 0.01$) (Fig. 5). The abundance of benthic macroinvertebrates strongly increased with increasing time in ponds without common carp, slightly increased in ponds with 0.5 common carp m^{-2} , and in ponds with 1 common carp m^{-2} even decreased towards the end of the experiment (Fig. 3). Rohu biomass increased

Table 1. Effects of time on environmental parameters in ponds based on a 2-way repeated-measures ANOVA. Time × CC: interaction of time and common carp (CC) density; Time × Feed: interaction of time and artificial feed. Mean values in the same row with no superscript in common differ significantly ($p < 0.05$). If the effects are significant, ANOVA was followed by Tukey test. * $p \leq 0.05$; ** $p < 0.01$; NS: not significant. DO: dissolved oxygen; TAN: total ammonia nitrogen; TN: total nitrogen; TP: total phosphorus

Variable	Tukey test													
	Time	Time × CC	Time × Feed	14 Mar	28 Mar	11 Apr	25 Apr	9 May	23 May	6 Jun	20 Jun	4 Jul	19 Jul	30 Jul
Temp.(°C)	**	NS	NS	24.9 ^g	27.4 ^d	26.1 ^f	27.0 ^e	27.0 ^e	27.9 ^c	29.1 ^b	27.2 ^{de}	19.1 ^b	27.9 ^c	29.7 ^a
DO (mg l ⁻¹)	**	**	*	7.12 ^a	7.10 ^a	6.22 ^e	6.24 ^e	6.74 ^b	6.57 ^{bc}	6.47 ^d	6.53 ^{bcd}	6.47 ^d	6.26 ^e	6.25 ^e
pH range	-	-	-	7.4–8.3	7.5–8.1	7.5–8.3	6.8–8.0	7.2–8.4	7.1–7.9	6.9–7.7	6.5–7.8	6.7–7.9	6.5–7.8	7.1–7.6
NO ₃ -N (mg l ⁻¹)	**	**	*	0.54 ^d	0.58 ^{bcd}	0.63 ^{bcd}	0.69 ^{bc}	0.85 ^b	1.15 ^a	1.15 ^a	1.04 ^{ab}	1.06 ^{ab}	1.05 ^{ab}	1.15 ^a
TAN (mg l ⁻¹)	**	*	NS	0.22 ^d	0.24 ^{cd}	0.29 ^{abc}	0.32 ^{ab}	0.35 ^a	0.33 ^{ab}	0.33 ^{ab}	0.31 ^{abc}	0.30 ^{abc}	0.28 ^{bc}	0.26 ^{bc}
TN (mg l ⁻¹)	**	*	NS	1.17 ^d	1.16 ^d	1.52 ^c	1.84 ^b	1.77 ^{bc}	2.29 ^a	2.16 ^{ab}	1.88 ^b	1.88 ^b	1.79 ^{bc}	1.86 ^b
PO ₄ -P (mg l ⁻¹)	**	**	**	0.63 ^f	0.68 ^{ef}	0.72 ^{de}	0.81 ^{bcd}	0.89 ^{bc}	0.95 ^{bc}	1.07 ^b	1.08 ^b	1.09 ^b	1.14 ^{ab}	1.26 ^a
TP (mg l ⁻¹)	**	*	NS	1.26 ^f	1.29 ^f	1.34 ^{ef}	1.37 ^{cde}	1.35 ^{ef}	1.48 ^{cd}	1.61 ^{bc}	1.56 ^c	1.66 ^b	1.86 ^a	1.88 ^a

Table 2. Effects of time on the abundance (based on total volume) of different groups of plankton (mm³ l⁻¹) and benthic macroinvertebrates (cm³ m⁻²) abundance in ponds based on a 2-way repeated-measures ANOVA. Time × CC: interaction of time and common carp density; Time × Feed: interaction of time and artificial feed. Mean values in the same row with no superscript in common differ significantly ($p < 0.05$). If the effects are significant, ANOVA was followed by Tukey test. * $p \leq 0.05$; ** $p < 0.01$; NS: not significant

Variable	Tukey test													
	Time	Time × CC	Time × Feed	14 Mar	28 Mar	11 Apr	25 Apr	9 May	23 May	6 Jun	20 Jun	4 Jul	19 Jul	30 Jul
Bacillariophyceae	**	NS	NS	0.036 ^{bc}	0.044 ^a	0.045 ^a	0.033 ^c	0.038 ^{abc}	0.040 ^{abc}	0.039 ^{abc}	0.040 ^{abc}	0.045 ^a	0.042 ^{ab}	0.042 ^{ab}
Chlorophyceae	**	**	NS	0.131 ^{bcd}	0.127 ^{cd}	0.127 ^{cd}	0.120 ^d	0.137 ^{bc}	0.124 ^c	0.130 ^{bcd}	0.141 ^b	0.135 ^{b^{bc}}	0.143 ^b	0.153 ^a
Cyanophyceae	**	**	NS	0.095 ^{ab}	0.104 ^a	0.078 ^c	0.076 ^c	0.089 ^{ab}	0.077 ^c	0.081 ^{bc}	0.075 ^c	0.096 ^{ab}	0.082 ^{bc}	0.094 ^{ab}
Euglenophyceae	**	**	NS	0.027 ^c	0.035 ^{bc}	0.042 ^b	0.036 ^{bc}	0.042 ^b	0.041 ^b	0.038 ^{bc}	0.042 ^b	0.047 ^{ab}	0.050 ^a	0.052 ^a
Total phytoplankton	**	**	NS	0.295 ^{bcd}	0.317 ^{abc}	0.292 ^{bcd}	0.258 ^d	0.309 ^{abc}	0.278 ^{cd}	0.277 ^{cd}	0.301 ^{abc}	0.321 ^{ab}	0.323 ^{ab}	0.344 ^a
Rotifera	**	**	*	0.026 ^b	0.026 ^b	0.032 ^{ab}	0.032 ^{ab}	0.033 ^{ab}	0.032 ^{ab}	0.032 ^{ab}	0.034 ^{ab}	0.036 ^a	0.037 ^a	0.037 ^a
Cladocera	NS	**	NS	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.011	0.011	0.012
Copepoda	NS	**	NS	0.011	0.012	0.012	0.010	0.013	0.012	0.012	0.013	0.014	0.013	0.014
Total zooplankton	**	**	*	0.047 ^d	0.048 ^d	0.054 ^{abcd}	0.052 ^{bcd}	0.056 ^{abc}	0.056 ^{abc}	0.056 ^{abc}	0.057 ^{abc}	0.059 ^{ab}	0.060 ^{ab}	0.062 ^a
Macroinvertebrates	**	**	NS	2.52 ^g	3.45 ^f	3.72 ^{ef}	3.99 ^{def}	4.21 ^{cde}	4.69 ^{bcd}	4.57 ^{bcd}	5.15 ^{abc}	5.04 ^{abc}	5.43 ^{ab}	5.60 ^a

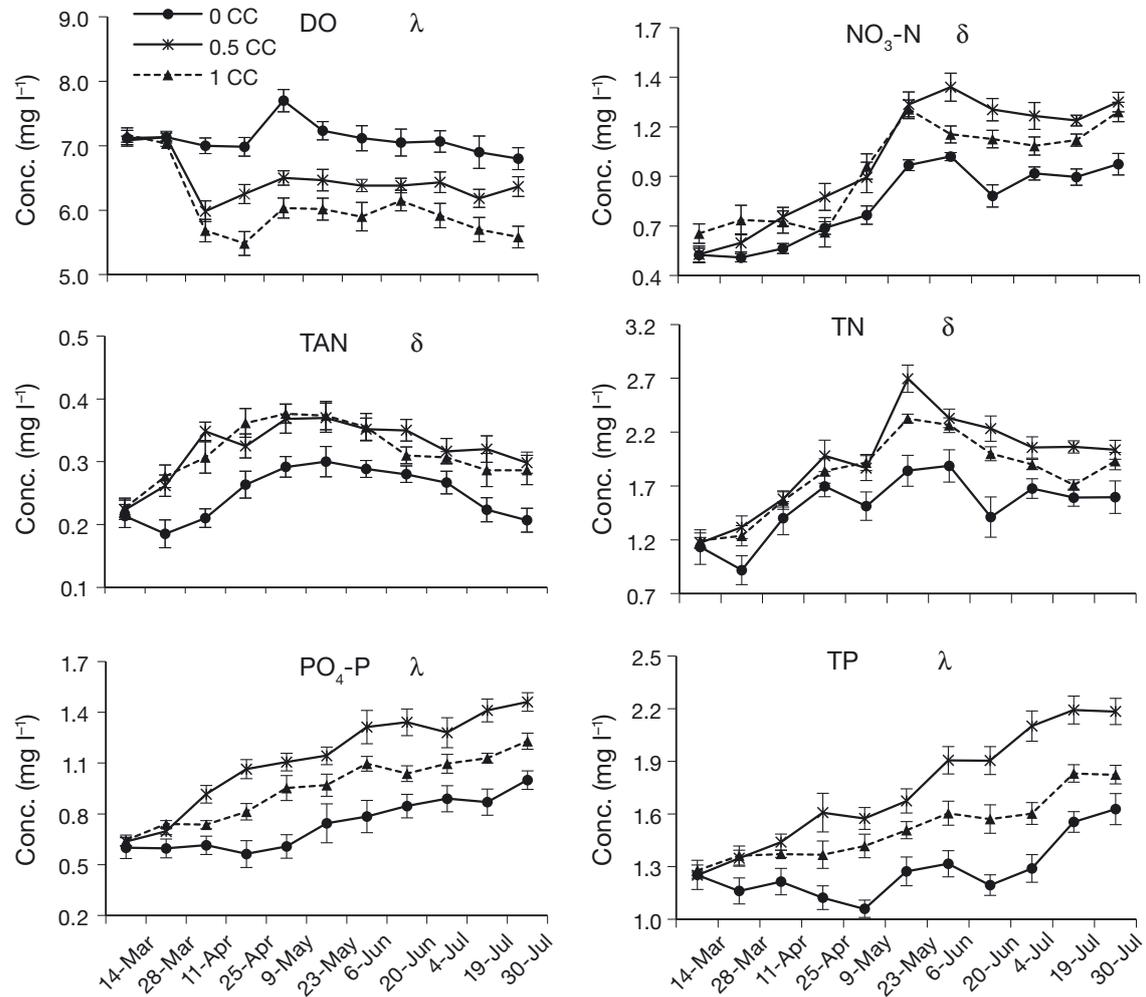


Fig. 1. Interaction between time and common carp (CC; *Cyprinus carpio*) density on the changes in different environmental parameters. Data are means (\pm SE). 0 CC, 0.5 CC and 1 CC indicate the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} , respectively. δ indicates the significant difference ($p < 0.01$) between the ponds with common carp and without common carp. λ indicates that the ponds without common carp, ponds with 0.5 common carp m^{-2} , and the ponds with 1 common carp m^{-2} are significantly different from each other ($p < 0.05$). See Table 1 for abbreviations

with time in all treatments, more pronounced in the presence of 0.5 common carp m^{-2} than in the presence of 1 common carp m^{-2} , or in its absence (Fig. 6). No significant difference was observed between the ponds with 1 common carp m^{-2} and without common carp on rohu biomass. Temporal increase of total fish biomass was most pronounced in ponds with 0.5 common carp m^{-2} , followed by 1 and 0 common carp m^{-2} .

DISCUSSION

The water-quality parameters of all ponds remained within ranges allowing high fish growth rates. The main primary factors influencing the abi-

otic and biotic properties of the pond water were time and sediment resuspension by common carp. The effect of time on water quality, and the abundance of phytoplankton, zooplankton and benthic macroinvertebrates in ponds with different densities of common carp are clearly shown in this study. Decreasing DO concentrations with increasing common carp density reflects additional respiration by common carp and higher aerobic decomposition rates caused by common carp sediment resuspension during grazing on benthic macroinvertebrates (Andersson et al. 1988, Beristain 2005). Higher aerobic decomposition can be supported by higher sediment resuspension, which was greater in ponds with 1 common carp m^{-2} , followed by 1 common carp m^{-2} , and without common carp.

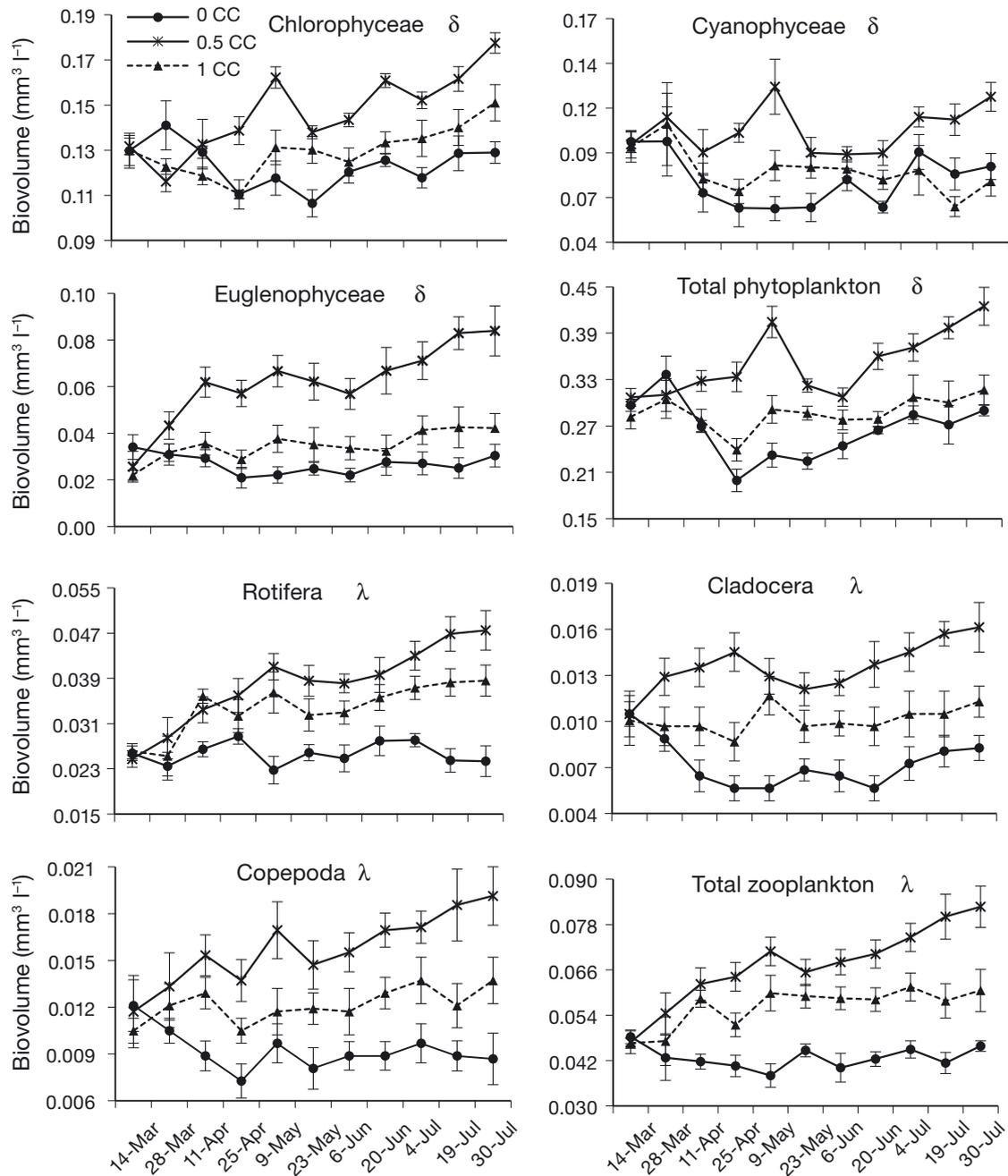


Fig. 2. Interaction between time and common carp (CC; *Cyprinus carpio*) density on the changes in different groups of plankton biovolumes in the pond sediment. Data are means (\pm SE). 0 CC, 0.5 CC and 1 CC indicate the ponds without common carp, with 0.5 common carp m⁻², and with 1 common carp m⁻², respectively. δ indicates that the ponds with 0.5 common carp m⁻² are significantly different ($p < 0.05$) from the ponds with 1 common carp m⁻², and the ponds without common carp. λ indicates that the ponds without common carp, with 0.5 common carp m⁻², and with 1 common carp m⁻² are significantly different from each other ($p < 0.05$)

Generally, diffusion of nutrients from the bottom sediment to the water is very slow (Avnimelech et al. 1999, Ritvo et al. 2004), but common carp activity increases the rate of diffusion of nutrients across the sediment–water interface (Hohener & Gachter 1994). Among various benthic macroinvertebrates, chirono-

mid larvae are a very important benthic food source for common carp. Chironomid larvae normally live up to several centimetres deep in the sediment. Common carp increases the diffusion of nutrients across the sediment–water interface during browsing for chironomid larvae. Decomposition of higher organic

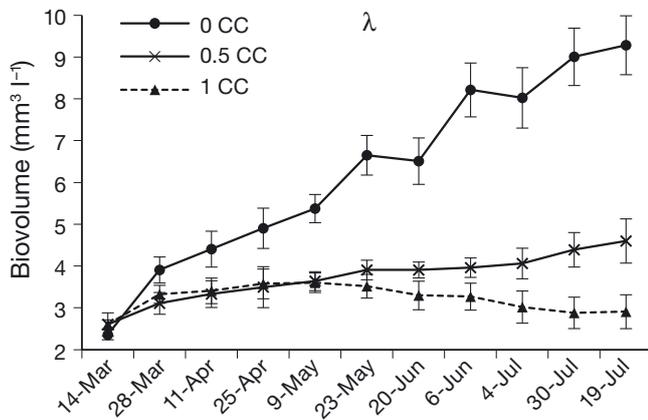


Fig. 3. Interaction between time and common carp (CC; *Cyprinus carpio*) density on the changes of benthic macroinvertebrate biovolumes in the pond sediment. Data are means (\pm SE). 0 CC, 0.5 CC and 1 CC indicate the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} , respectively. λ indicates that the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} are significantly different from each other ($p < 0.05$)

matter and nutrient diffusion mediated by common carp enhanced N and P fluxes between the sediment and water column (Hargreaves 1998), resulting in higher N and P concentrations over time in ponds with common carp compared to those without common carp. Higher nutrient availability stimulated photosynthesis, thereby increasing phytoplankton and zooplankton biomass through time in ponds with common carp compared to those without common carp (Milstein 1992, Rahman & Verdegem 2007).

The decrease in benthic macroinvertebrates with increasing common carp density indicates that common carp feed on benthic macroinvertebrates (Tatrai et al. 1994, Zambrano & Hinojosa 1999). The increase in sediment resuspension with increasing common carp density indicates increased bottom disturbance by more common carp. Increased sediment resuspension increases turbidity which reduces photosynthesis and, subsequently, phytoplankton and zooplankton production (Hosseini & Oerdoeg 1988). Common carp is an omnivorous fish, primarily feeding on zooplankton and benthic macroinvertebrates (Rahman & Meyer 2009, Rahman et al. 2009, Rahman & Verdegem 2010). It is likely that a tipping-point exists, whereby additional common carp increase the grazing pressure on zooplankton and benthic macroinvertebrates, leading to overgrazing of zooplankton and benthic macroinvertebrates to the point where their recovery is not possible (Steffens 1990). These 2 effects (i.e. increased water turbidity, overgrazing) likely resulted in lower zooplankton and benthic

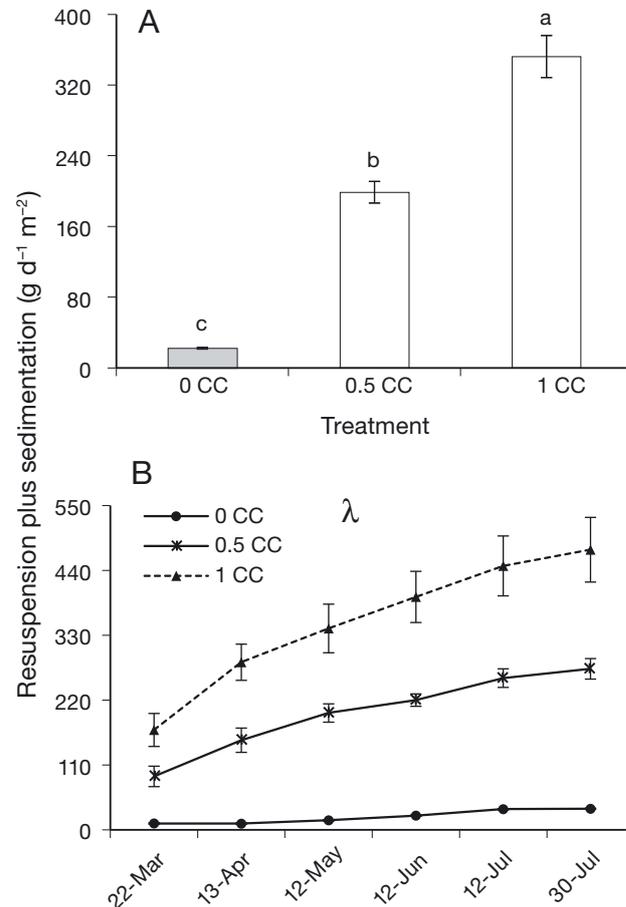


Fig. 4. (A) Mean resuspension and sedimentation at different stocking densities of common carp (CC; *Cyprinus carpio*) and (B) the interaction between time and common carp density on resuspension and sedimentation. Data are means (\pm SE). 0 CC, 0.5 CC and 1 CC indicate the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} , respectively. All treatments differ significantly ($p < 0.01$), as indicated by different superscript letters. λ indicates that the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} are significantly different from each other ($p < 0.05$)

macroinvertebrate availability in ponds with 1 common carp m^{-2} compared to those with 0.5 common carp m^{-2} .

Higher sediment resuspension in ponds with 1 common carp m^{-2} than in ponds with 0.5 common carp m^{-2} might also be explained by PO_4 -P availability in the water. Excessive resuspension of sediment may increase the redox potential. An increased redox potential would have a positive effect on the precipitation of soluble phosphorus (PO_4 -P) through the formation of phosphate-rich inorganic particles (e.g. with iron as iron [III] phosphate; Holdren & Armstrong 1980, Bostrom et al. 1988, Boyd 1995). This precipitation might have been higher in ponds with 1 common carp

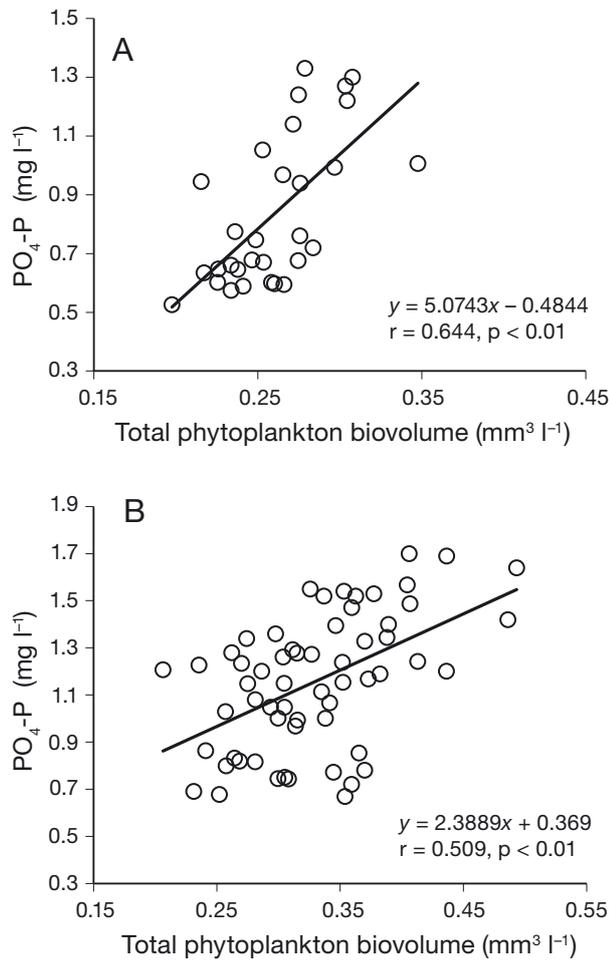


Fig. 5. Relationship between $\text{PO}_4\text{-P}$ concentration and total phytoplankton biovolume in ponds (A) without and (B) with common carp (*Cyprinus carpio*)

m^{-2} than in ponds with 0.5 common carp m^{-2} , because sediment resuspension increased with increasing common carp density. This might have resulted in the lower $\text{PO}_4\text{-P}$ concentration observed in ponds with 1 common carp m^{-2} compared to ponds with 0.5 common carp m^{-2} .

Higher phosphorus concentration can also be explained by the higher biomass of fish, zooplankton and benthic macroinvertebrates in treatments with 0.5 common carp m^{-2} compared to those with 1 common carp m^{-2} (Figs. 2–4), all of which release phosphorus (Gallepp 1979, Brabrand et al. 1990, Lupatsch & Kissil 1998). Higher $\text{PO}_4\text{-P}$ concentration resulted in higher phytoplankton densities (also reported by Yusoff & McNabb 1997) in ponds with 0.5 common carp m^{-2} than in ponds with 1 common carp m^{-2} . In the present study, soluble phosphorus seems to be the most important factor responsible for phytoplankton dynamics. The relationships between $\text{PO}_4\text{-P}$

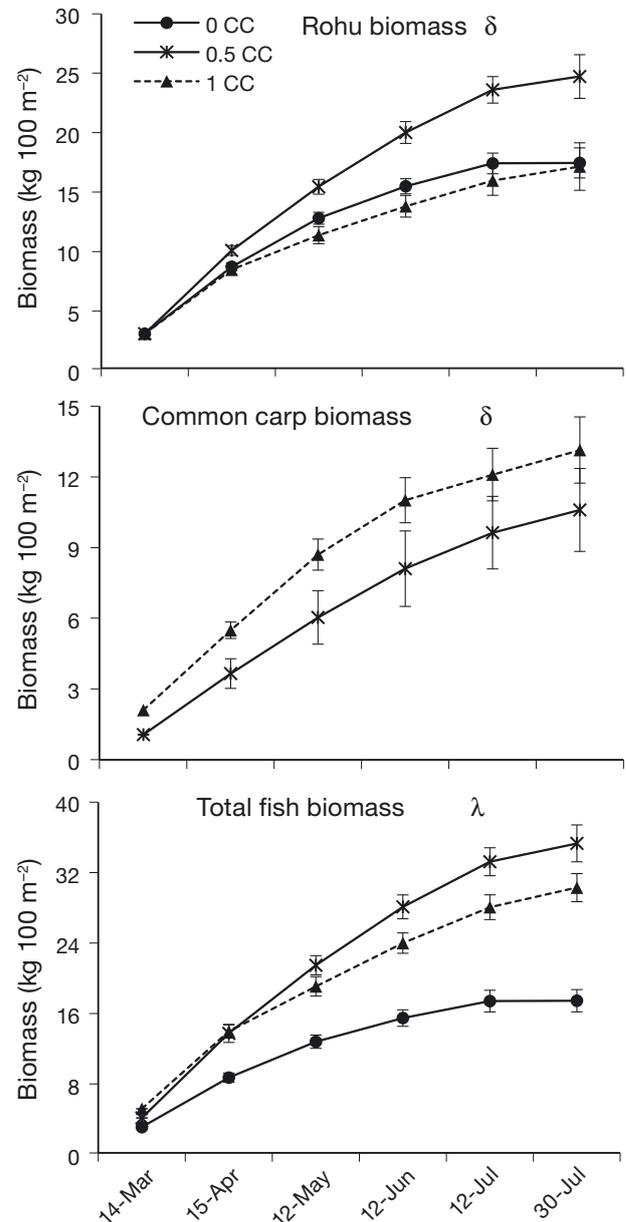


Fig. 6. Changes of fish biomass in ponds with different common carp (CC; *Cyprinus carpio*) densities. Data are means (\pm SE). 0 CC, 0.5 CC and 1 CC indicate the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} , respectively. δ indicates that the ponds with 0.5 common carp m^{-2} are significantly different from the ponds with 1 common carp m^{-2} and the ponds without common carp. λ indicates that the ponds without common carp, with 0.5 common carp m^{-2} , and with 1 common carp m^{-2} are significantly different from each other ($p < 0.05$)

P and total phytoplankton indicate that phytoplankton biomass was limited by soluble phosphorus concentrations in ponds without common carp. This is in agreement with Schindler (1988), Elser et al. (1990) and Diana et al. (1997), who reported that phospho-

rus is an important limiting nutrient in most freshwater ecosystems. Smith (1985) showed that phytoplankton production at optimum light intensity was highly dependent on phosphorus concentration.

In conclusion, common carp enhanced phytoplankton production and accelerated nutrient fluxes to higher trophic levels by releasing nutrients from the sediment. Stocking 0.5 common carp m^{-2} had stronger effects than 1 common carp m^{-2} on nutrient, phytoplankton and zooplankton availability over time. At this intermediate common carp stocking density, growth and production of fish were also the highest. The effects were partially lost in ponds with 1 common carp m^{-2} . Phyto- and zooplankton availability increased through time in ponds with 0.5 common carp m^{-2} . This suggests that the net availability of phyto- and zooplankton and their utilization by fish increased with time. Thus, there might be an opportunity to stock an additional planktivorous species at lower density with 1.5 rohu and 0.5 common carp m^{-2} . If this were to occur, a proper evaluation of stocking densities of new species is recommended to optimise nutrient, phytoplankton and zooplankton and benthic macroinvertebrate availability. In the present experimental design, the stocking of 1 common carp m^{-2} can be considered as overstocking, a conclusion which was also supported by the changes in phytoplankton, zooplankton and benthic macroinvertebrate availability over time. This study has found that an optimal stocking density of common carp can be used as a management tool to manipulate limnological processes for the better growth and production of fish.

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