



## Experimental study of the impacts of silver carp on plankton communities of eutrophic Villerest reservoir (France)

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### Abstract

We examined the impact of five silver carp biomass levels (0, 8, 16, 20, and 32 g m<sup>-3</sup>) on plankton communities and water quality of Villerest eutrophic reservoir (France). We realized the experiments using outdoor mesocosms. The presence of silver carp led to changes in zooplankton and phytoplankton assemblages. High fish biomass strongly reduced cladoceran abundance (through predation). Silver carp inefficiently grazed down particles < 20 µm. More importantly, however, the suppression of herbivorous cladocerans resulted in the increase of small size algae which were relieved from grazing and benefit from high nutrient concentrations.

In contrast, in mesocosms without fish, the dominance of cladocerans (mainly *Daphnia*) controlled small size algae and probably also larger size algae (colonial chlorophytes, cyanobacteria). Thus, the Secchi disc transparency increased markedly. Through cascade effects, the modification of grazers communities led to changes in the utilization patterns of the added nutrients by phytoplankton communities. In high fish biomass treatments, nutrients were more efficiently accumulated into particulate fractions compared with no-fish and low-fish biomass treatments that were characterized by higher dissolved nutrients concentrations. Zooplankton was an essential source of food for silver carp. The productivity of zooplankton sustained a moderate silver carp biomass (up to 16 g m<sup>-3</sup>). In the presence of the highest fish biomass, the productivity of zooplankton was not large enough and silver carps fed on additional phytoplankton. Although mesocosms with high fish biomass were characterized by a slight cyanobacteria development compared with other fish mesocosms, silver carp was not effective in reducing cyanobacteria dominance.

### Introduction

As confirmed by recent studies (Christoffersen et al., 1993; Vanni & Layne, 1997; Starling et al., in press), the cascading effects of fish on lower trophic levels continues to be a strong research focus in freshwater pelagic ecosystems. Of particular interest is the possible control of excessive phytoplankton through top down forces (Benndorf et al., 1984; Shapiro & Wright, 1984; Carpenter et al., 1985; Miura, 1990; Van Donk et al., 1990) i.e. biomanipulation (reviews in Benndorf, 1990 and Gophen, 1990). The classical view of top down control is the reduction of planktivorous fishes (through increased predation), which results in higher densities of herbivorous zooplankters

and consequently in lowered densities of algae due to zooplankton grazing. However, the ability of natural populations of zooplankton to control cyanobacterial blooms is still under discussion (see De Bernardi & Giussani, 1990). In the presence of a cyanobacterial bloom, the control of phytoplankton by zooplankton may not be effective (Bays & Crisman, 1983; Nilssen, 1984).

An alternative food web manipulation based on the direct control of undesirable net-phytoplankton by filter feeding phytoplanktivorous fish was investigated (Drenner et al., 1986; Starling, 1993). Several researchers have investigated the influence of pump filter feeding fishes, particularly silver carp (*Hypophthalmichthys molitrix*), on plankton community

structure and its potential use as a biomanipulation technique to reduce algal biomass (Kajak et al., 1977; Opuszynski, 1979; Burke et al., 1986; Drenner & Hambright, 1987; Leventer & Teltsch, 1990; Starling & Rocha, 1990; Laws & Weisburd, 1990; Vöros et al., 1997). However, the use of silver carp to control water quality in lakes and reservoirs is still controversial (Opuszynski, 1979, 1981; Smith, 1985, 1989; Burke et al., 1986; Milstein et al., 1988; Starling, 1993). The variety of biotic under which experiments were conducted, such as phytoplankton communities size and structure (Laws & Weisburd, 1990), efficiency of zooplankton grazing pressure on dominant algae (Arcifa et al., 1986), fish stocking rate and fish biomass (Lazzaro, 1992; Starling, 1993) explain these controversial results.

The purpose of our studies, therefore, was to evaluate the impact of silver carp on quality of eutrophic Villerest reservoir (France) characterized by summer cyanobacteria blooms (*Microcystis aeruginosa*). We conducted several experimental designs; here, we present the results of one of these mesocosm experiments in which we examine the impact of five silver carp biomass levels on plankton communities and water quality.

### Study area

The Villerest reservoir (Loire River, France) covers 700 ha and has a volume of about  $128 \times 10^6 \text{ m}^3$  (maximum depth 45 m, mean depth 18 m) (Desmolles, 1997). Since its construction (1983), the reservoir has been characterized by an accelerated eutrophication caused by human influences (urban sewage, public utilities, farmland). Aleya et al. (1994) showed that the reservoir receives high nutrient loading, chiefly of phosphorus and nitrogen, which are responsible for the strong eutrophication and the frequently observed blooms of *Microcystis aeruginosa*.

### Materials and methods

We conducted the experiment in white fiberglass mesocosms located on shore of the Villerest reservoir. The 28 mesocosms were 1.80 m in diameter and 2.20 m high, and contained 5500 l water per mesocosm. They were arranged in three rows and were sampled from a walkway between them. The mesocosms were filled with reservoir water using a

submerged pump. They were regularly mixed with an airlift mixer system to prevent stratification and to ensure a well-mixed environment (Drenner et al., 1986). The mesocosms were covered with a 0.5 cm mesh net to prevent fish from jumping out.

Silver carp that were obtained from a fish farm (Les Clouzioux, Brinon (18), France) were acclimated to reservoir plankton and water conditions in mesocosms during two weeks prior to the experiment. Mean ( $\pm$  SD) individual mass and length of silver carp were  $22.5 \pm 6.3 \text{ g}$  and  $11.9 \pm 1.2 \text{ cm}$ , respectively. On 23 July, fish were netted from the holding mesocosms, and stocked into the experimental mesocosms. Five levels of silver carp biomass (0, 8, 16, 20, 32  $\text{g m}^{-3}$ ) represented by the introduction of 0, 2, 4, 5, 7 silver carp per mesocosm, respectively) were tested. We used low (8  $\text{g m}^{-3}$ ; 180  $\text{kg ha}^{-1}$ ), medium (16, 20  $\text{g m}^{-3}$ ; 350, 450  $\text{kg ha}^{-1}$ ) and high (32  $\text{g m}^{-3}$ ; 700  $\text{kg ha}^{-1}$ ) fish biomass. Each treatment had three replicates that were randomly assigned among mesocosms.

Starting on day 0, 240  $\mu\text{gN l}^{-1}$  as  $\text{NH}_4\text{Cl}$  and  $\text{NaNO}_3$  and 30  $\mu\text{gP l}^{-1}$  as  $\text{KH}_2\text{PO}_4$  were added to each mesocosm three times a week to maintain high nutrient concentrations similar to those measured in reservoir. Beginning on 23 July (day 0), mesocosms were sampled at weekly intervals for 5 weeks (days 0, 7, 13, 20, 27). Zooplankton was sampled with vertical tows of a 60  $\mu\text{m}$  mesh plankton net and preserved in 5% sucrose formalin (Haney & Hall, 1973; Prepas, 1978) and counted under a binocular microscope (Wild M3Z) in a Dolfuss chamber. Phytoplankton samples were preserved with 1% Lugol's iodine and counted with an inverted microscope after sedimentation for 24 h (Utermöhl, 1958). In addition, each phytoplankton sample was subsampled for additional *Microcystis* countings. Cyanobacteria colonies were sonicated for 30 s (40 kHz) in Bioblock Vibra Cell 72434 disintegrator (Bioblock scientific, Illkirch, France) based on counting method of Humphries and Widjaja's (1979) and then directly counted with haemocytometer. Chlorophyll-a samples were collected on Whatman GF/C filters, and chlorophyll was extracted in 90% acetone for at least 6 h. The absorbance was measured at 665 nm and 750 nm before and after acidification (Lorenzen, 1967). One litre of water was sampled for chemical analysis of orthophosphate ( $\text{PO}_4\text{-P}$ ), total dissolved phosphorus (TDP), total particulate phosphorus (TPP), nitrates ( $\text{NO}_3\text{-N}$ ), ammonia ( $\text{NH}_4\text{-N}$ ), total dissolved nitrogen (TDN) and total particulate nitrogen (TPN) (APHA,

1992). The water temperature, pH, dissolved oxygen and transparency (Secchi disc depth) were also measured on each date.

On final date (August 19) fish were netted. After draining the mesocosms, periphyton was sampled by removing one  $5 \times 5$  cm area of periphyton (at 20 cm depth) with a blade and filtered using a Millipore Hawp Membrane filters (0.45  $\mu\text{m}$  pore size). Periphytic chlorophyll-*a* was extracted using the method as for phytoplankton.

Main effects of fish biomass were analyzed with a repeated measures ANOVA (5 fish biomass, and four sampling dates, days 7, 13, 20, 27). ANOVA on day 0 was tested to check that the initial values were similar in all enclosures. We chose a probability level  $\alpha < 0.10$  to reduce the chance of making the type error of failing to reject a false null hypothesis. Moreover, we applied Pearson correlation on biotic and abiotic parameters (days 7, 13, 20, 27).

## Results

On day 0 (pretreatment) there were no significant differences between mesocosms, except for *Ceriodaphnia* and copepod number and N/P ratio (respectively,  $p = 0.048$ ;  $p = 0.031$ ;  $p = 0.040$ ).

### Fish

Individual mass of silver carp slightly increased during the experiment in all the mesocosms, whereas length of fish was unchanged. The lowest individual gain in weight was observed in  $32 \text{ g m}^{-3}$  treatment, with mean ( $\pm$  SD) individual gain of only  $0.2 \pm 0.1$  g per fish for 27 days of experiment. In the other mesocosms, gain in weight was up to 6 times higher than in  $32 \text{ g m}^{-3}$  treatment.

### Zooplankton

Zooplankton was mainly represented by cladocerans, *Daphnia*, *Ceriodaphnia*, *Bosmina* and *Chydorus*; copepods, *Cyclops*, *Eudiaptomus*; and rotifers, *Keratella*, *Polyarthra* and *Asplanchna*. The daphnids (*D. longispina*) varied in length from 0.8 to 1.5 mm and were considered large when  $> 1$  mm (McQueen & Post, 1988). Microzooplankton, less efficient consumers of algae, were represented by *Bosmina longirostris* (0.2–0.6 mm) and *Chydorus sphaericus* (0.2–0.5 mm) and *Ceriodaphnia quadrangula* (0.4–0.8 mm). Zooplankton largely decreased with time in

all mesocosms. The decrease in zooplankton density was clearly a function of fish biomass ( $p = 0.000$ ; Figure 1).

Total rotifer densities decreased markedly with time (Figure 1), especially during the first week of experiment in all mesocosms. Treatment levels did not significantly differ ( $p = 0.124$ ). Total copepods densities also decreased with time and a significant impact of silver carp biomass was noted for total copepods ( $p = 0.000$ ) and nauplii ( $p = 0.000$ ) (Figure 1). Copepods (mainly nauplii) initially accounted for more than 75% of total zooplankton, but decreased with time in all mesocosms except in  $32 \text{ g m}^{-3}$  fish biomass treatment in which they represented near 80% of total zooplankton on final day. Cladoceran densities also decreased with time and a clear impact of fish biomass was observed ( $p = 0.000$ ; Figure 1). *Ceriodaphnia* and *Bosmina* densities showed the same pattern of change, decreasing in all mesocosms during the experiment indicating a significant impact of silver carp biomass ( $p = 0.011$  and  $p = 0.000$ , respectively; Figure 1). Impact of fish biomass on *Daphnia* and *Chydorus* densities was also significant ( $p = 0.000$  and  $p = 0.002$ , respectively), but the responses of these two populations differed both at low or high-fish biomass. In low silver carp biomass treatment or in no fish treatment *Daphnia* densities tended to increase but in other mesocosms they were clearly reduced (Figure 1). *Chydorus* density responded similarly, increasing in low fish biomass and no fish treatments. On day 0, *Daphnia* density represented less than 4% of total zooplankton. During the experiment changes in zooplankton structure were important: on the final day, *Daphnia* represented from 22 to 72% of total zooplankton in low fish biomass treatments (0, 8,  $16 \text{ g m}^{-3}$ ) whereas in the highest fish biomass treatments ( $32 \text{ g m}^{-3}$ ) it represented about 1%.

Thus, the highest silver carp biomass ( $32 \text{ g m}^{-3}$  treatment) had a pronounced, negative impact on *Daphnia* but a less marked impact on copepods. In no-fish mesocosms, *Daphnia* appeared to be more competitive and the general decrease of copepods and rotifers led to an increase in *Daphnia* densities. In no fish mesocosms, cladocerans largely dominated zooplankton on day 27, representing 70.9% of total zooplankton against 21.9% on day 0 in the same treatment levels.

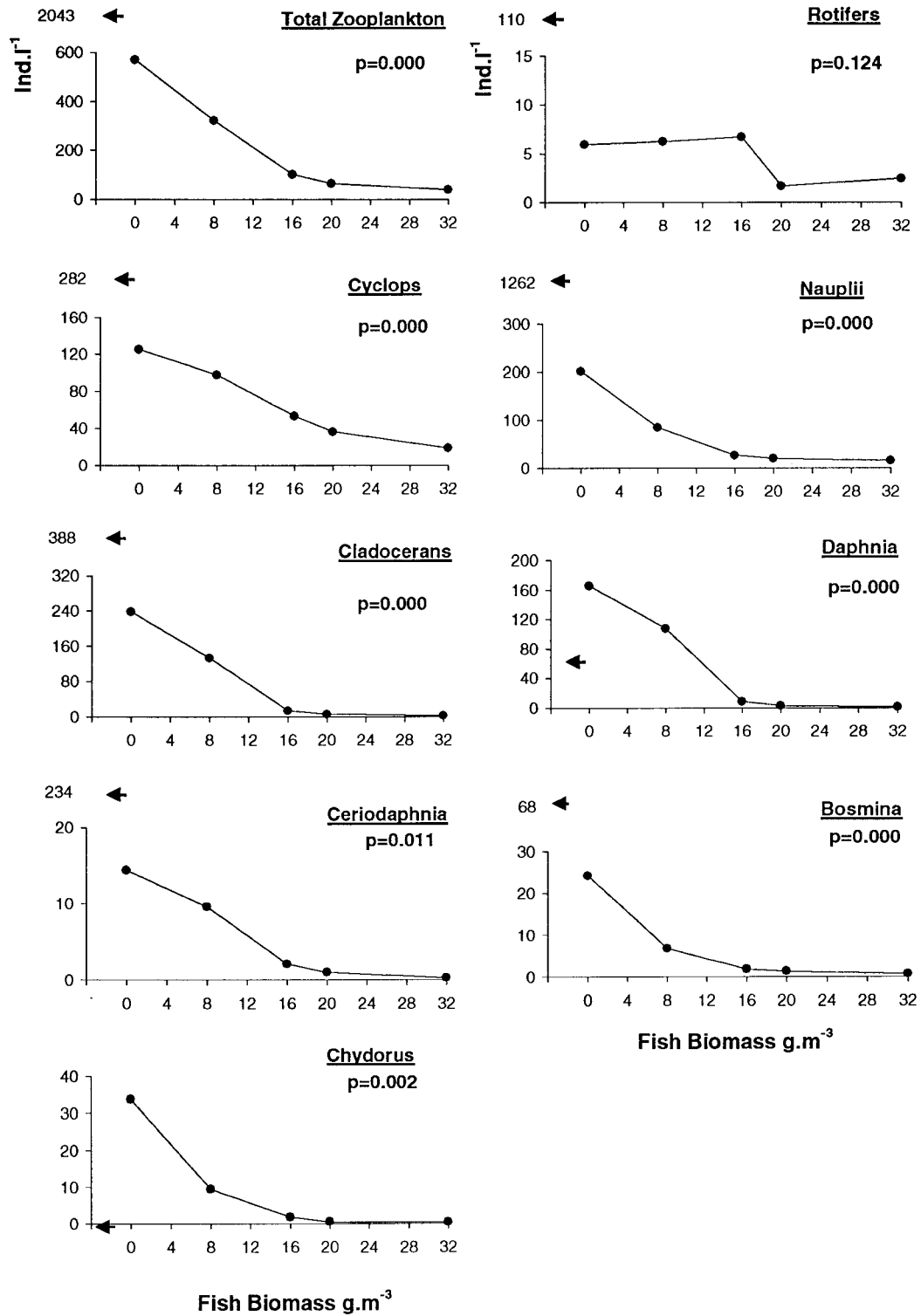


Figure 1. Mean responses of zooplankton (ind l<sup>-1</sup>) on four sampling dates (days 7, 13, 20, 27) after fish introduction. Probability values from repeated-measures ANOVA of fish biomass main effects are indicated on each graph. ◀: pre-fish conditions (mean value on day 0).

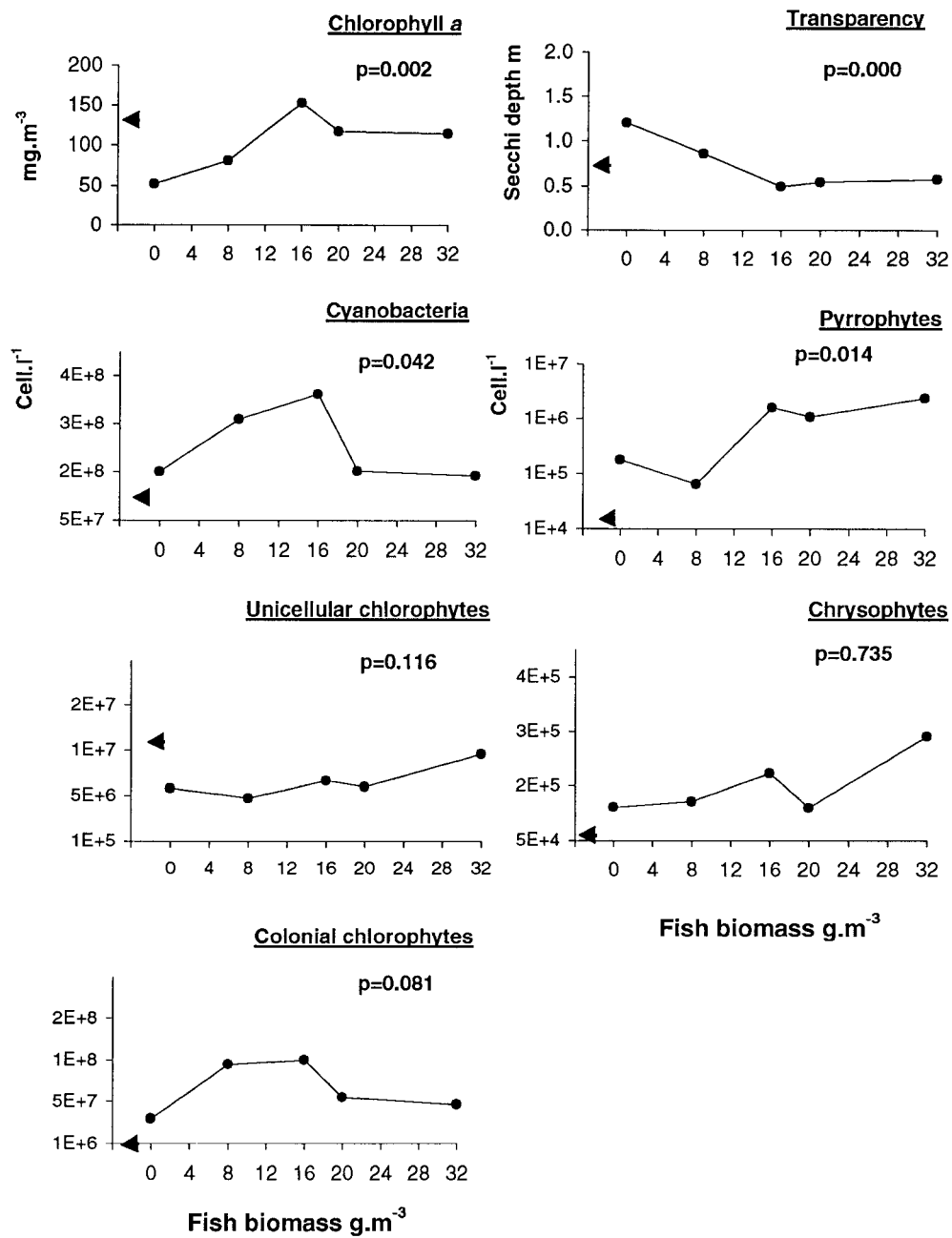


Figure 2. Mean responses of chlorophyll-*a* (mg m<sup>-3</sup>), transparency (Secchi depth m), phytoplankton (cell l<sup>-1</sup>) on four sampling dates (days 7, 13, 20, 27) after fish introduction. Probability values from repeated-measures ANOVA of fish biomass main effects are indicated on each graph. ◀: pre-fish conditions (mean value on day 0).

### Phytoplankton

Chlorophyll-*a* concentration was significantly affected differently by fish biomass ( $p = 0.002$ ; Figure 2): a decrease in chlorophyll-*a* concentrations in 0 and 8 g m<sup>-3</sup> fish biomass mesocosms, but an increase in higher fish biomass treatments (16, 20 and 32 g m<sup>-3</sup>). Chlorophyll-*a* concentrations were negatively correlated with total zooplankton, cladocerans, and *Daphnia* densities ( $r = -0.450$ ,  $r = -0.508$ ,  $r = -0.575$ , respectively;  $\alpha = 0.05$ ) but positively correlated with *Cryptomonas* densities ( $r = +0.311$ ;  $\alpha = 0.05$ ).

Total phytoplankton densities increased with time in all treatment levels, exhibiting a significant impact of fish biomass ( $p = 0.054$ ). The chlorophyll-*a* increase was highest in 8 and 16 g m<sup>-3</sup> fish biomass mesocosms, none in no fish mesocosms and only slight in high fish biomass treatments. On day 0, cyanobacteria density, mainly represented by *Microcystis aeruginosa*, accounted on average for 79.1%  $\pm$  5.7 of total phytoplankton density in all enclosures. On the final date, cyanobacteria densities had increased in all treatment levels, exhibiting a significant impact of fish biomass ( $p = 0.054$ ). The largest increase was observed in mesocosms containing 8, 16 g m<sup>-3</sup> fish biomass (Figure 2) but lowest increase in the 32 g m<sup>-3</sup> treatments. On day 27, cyanobacteria comprised 85.4% of total phytoplankton density in 32 g m<sup>-3</sup> fish-biomass mesocosms and >95.5% in all other treatment levels.

On day 0, pyrophytes and chrysophytes represented less than 1% of total phytoplankton density. Chrysophytes were mainly represented by diatoms. Chrysophyte density was increased in all mesocosms (Figure 2) and no significant difference was noted between treatment levels ( $p = 0.735$ ). Also pyrophyte densities (mainly *Cryptomonas*) increased with time in all mesocosms. This increase was clearly a function of silver carp biomass ( $p = 0.014$ ; Figure 2). Moreover, *Cryptomonas* density was negatively correlated with total zooplankton and *Daphnia* densities ( $r = -0.327$  and  $r = -0.320$ , respectively;  $\alpha = 0.05$ ). Chlorophytes densities were reduced by the final day in 0 in low-fish biomass mesocosms, but not in other mesocosms. Impact of fish biomass on total chlorophytes was not significant ( $p = 0.101$ ), but was significant for colonial chlorophytes ( $p = 0.084$ ). The increase in colonial chlorophytes was particularly clear for low and medium silver carp biomass, but slight in other treatment levels (0, 20, 32 g m<sup>-3</sup>) (Figure 2). Unicellular chlorophytes, mainly <20  $\mu$ m,

slightly decreased in all mesocosms. Although the highest densities of unicellular chlorophytes were observed in high fish biomass treatments, effect of fish biomass was not significant ( $p = 0.116$ ). These algae were negatively correlated with *Daphnia* densities ( $r = -0.327$ ,  $\alpha = 0.05$ ).

### Periphyton

Mean periphytic chlorophyll-*a* concentration at the end of experiment was  $3.96 \pm 1.84 \mu\text{g cm}^{-2}$ ; treatments levels did not differ significantly ( $p = 0.101$ ).

### Abiotic parameters

Mean temperature during the experiment ( $20.9 \pm 1.3^\circ\text{C}$ ) did not differ between treatment levels ( $p = 0.255$ ). Transparency was clearly an indirect function of fish biomass ( $p = 0.000$ ; Figure 3), Secchi-disc transparency increased with time in no fish- and low-fish biomass mesocosms but reverse was true in medium and high-fish biomass mesocosms. On day 27, transparency minima (Secchi depth < 0.45 m) were noted in 16, 20 and 32 g m<sup>-3</sup> fish biomass mesocosms, but maxima (Secchi depth > 0.90 m) in 0 and 8 g m<sup>-3</sup> fish biomass mesocosms. Transparency was positively correlated with total zooplankton, total cladocerans, and *Daphnia* densities ( $r = +0.562$ ,  $r = +0.810$ ,  $r = +0.733$ , respectively;  $\alpha = 0.05$ ).

Silver carp biomass had significant impact on TPN concentrations which increased with fish biomass ( $p = 0.092$ ), whereas in no fish mesocosms TPN tended to decrease (Figure 3). We also observed a significant impact of fish biomass on TPP ( $p = 0.023$ ; Figure 3). Concentrations of TPP decreased during the experiment in 0 and 8 g m<sup>-3</sup> treatments but in higher fish biomass mesocosms TPP concentrations were maintained. TPN and TPP were positively correlated with small size algae *Cryptomonas* ( $r = +0.400$  and  $r = +0.272$ , respectively;  $\alpha = 0.05$ ), but negatively with total zooplankton ( $r = -0.572$  and  $r = -0.225$ , respectively;  $\alpha = 0.05$ ).

The dissolved nutrient concentrations (TDP, PO<sub>4</sub>-P, TDN, NO<sub>3</sub>-N, NH<sub>4</sub>-N) increased with time (Figure 3); a significant impact of silver carp biomass was noted for these parameters (TDN:  $p = 0.002$ , PO<sub>4</sub>:  $p = 0.000$ , NO<sub>3</sub>:  $p = 0.000$ , NH<sub>4</sub>:  $p = 0.002$ ), except for TDP. The increase of these concentrations was significantly higher in no fish mesocosms and low-fish biomass treatments. TDN, NO<sub>3</sub><sup>-</sup>, and NH<sub>4</sub><sup>+</sup> concentrations were positively correlated with *Daphnia*

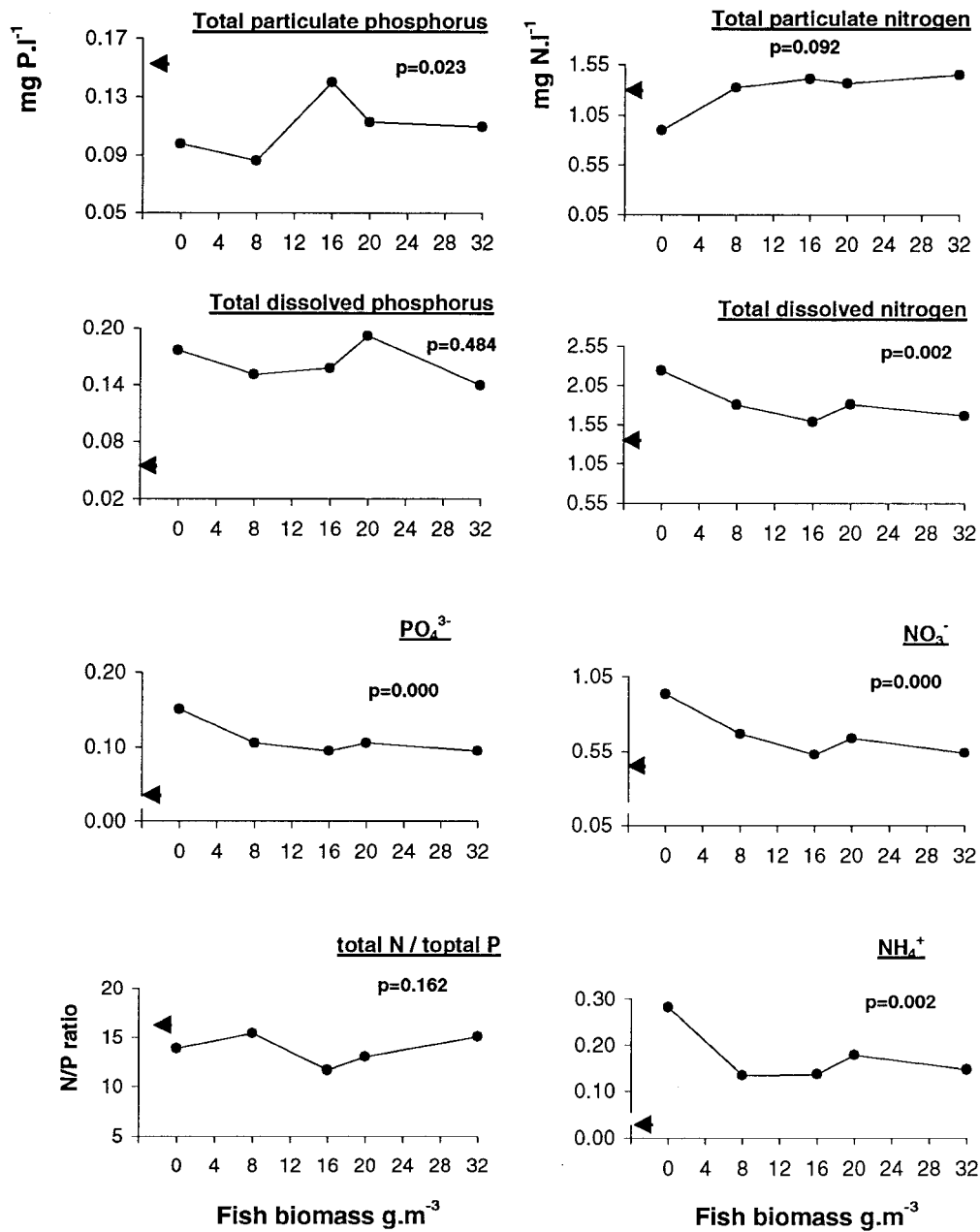


Figure 3. Mean responses of total particulate phosphorus, total dissolved phosphorus, orthophosphates ( $\text{mgP l}^{-1}$ ), total particulate nitrogen, total dissolved nitrogen, nitrates, ammonia ( $\text{mgN l}^{-1}$ ) and total nitrogen /total phosphorus (mass ratio) on four sampling dates (days 7, 13, 20, 27) after fish introduction. Probability values from repeated-measures ANOVA of fish biomass main effects are indicated on each graph.  $\blacktriangle$ : pre-fish conditions (mean value on day 0).

densities ( $r = +0.552$ ,  $r = +0.581$ ,  $r = +0.334$ ; respectively;  $\alpha = 0.05$ ) and transparency ( $r = +0.571$ ,  $r = +0.658$ ,  $r = +0.653$ , respectively;  $\alpha = 0.05$ ). In contrast, TDN and nitrates were negatively correlated with *Cryptomonas* ( $r = -0.490$ ,  $r = -0.411$ , respectively;  $\alpha = 0.05$ ). On day 0, the initial mean TN/TP (mass ratio) for all treatments was 16.67, but decreased during the experiment and all values on final day were  $< 9.1$ . No significant difference were found between treatment levels ( $p = 0.162$ ) (Figure 3).

## Discussion

Although we observed a general decrease in total zooplankton density in all treatment levels, our results clearly highlighted the negative impact of the high silver carp biomasses (20, 32  $\text{g m}^{-3}$ ) on zooplankton abundance. The experimental conditions probably accentuated the decrease in zooplankton density because of the confinement of zooplankton and of predators and prey (in fish treatments) in a relatively small water volume. However, the decrease observed in copepod and cladoceran numbers was clearly a function of fish biomass. These observations are consistent with several earlier work using silver carp (e.g., Milstein et al., 1988; Barthelmes, 1989; Burke et al., 1986) and gizzard shad (Lazzaro, 1992), which demonstrate that zooplankton suppression was a direct function of filter-feeding fish biomass. Although a general decrease in copepod numbers was noted through time, copepods were the predominant zooplankters in the highest fish biomass treatments. In contrast, large cladocerans dominated in the no fish or low fish biomass mesocosms.

Cladocerans densities highly varied in the different treatment levels, especially in the abundance of large *Daphnia*, which were clearly affected by fish predation pressure. At high fish treatment these daphnids became rare, and other cladocerans densities (*Ceriodaphnia*, *Bosmina*, *Chydorus*) were markedly reduced as well. In contrast, in no fish mesocosms and 8  $\text{g m}^{-3}$  treatments, *Daphnia* free from silver carp predation increased and largely dominated total zooplankton on the final date. Literature on feeding of the planktivorous carps is extensive but contradictory due to a variety of physical and biological conditions under which investigations were conducted. However, it is possible to see some general patterns in silver carp feeding habits. Silver carp is an obligate, filter-feeding planktivore (Itawa, 1977). Laboratory feeding experiments

demonstrated that silver carp efficiently consume large nanoplankton, net phytoplankton and zooplankton, but not algae  $< 10\mu\text{m}$  (Cremer & Smitherman, 1980; Burke et al., 1986; Smith, 1989; Domaizon, 1999). Moreover, several authors report the importance of detritus in silver carp diet (Spataru, 1977; Opuszynski, 1979, 1981). Silver carp should be considered omnivores (Bitterlich & Gnaiger, 1984) with a predation efficiency highly a function of the filtering apparatus. The silver carp fine mesh gill raker (8  $\mu\text{m}$ , Cremer & Smitherman, 1980; 12 to 26  $\mu\text{m}$ , Hampl et al., 1983; 30 to 40  $\mu\text{m}$ , Spataru & Gophen, 1985) allows to retain all rotifers, copepods and cladocerans present in Villerest reservoir. So, the possible selectivity of silver carp on zooplankton is governed by prey escape ability. Drenner et al. (1987) and Drenner & McComas (1980) estimating the direct escape response of different zooplankton species, concluded that cladocerans are more vulnerable than copepods to capture mechanisms of filter feeding planktivores. Our results are consistent with these observations, since cladocerans and particularly *Daphnia* densities were largely affected by the presence of high fish biomass whereas in these mesocosms copepods were dominant. However, copepods which were primarily represented by nauplii were also significantly affected by fish biomass. We suggest that silver carp predation is highly efficient on nauplii because of their low escape ability. This hypothesis is consistent with the observations of Starling & Rocha (1990) who reported high feeding rates on *Thermocyclops* nauplius which were strongly suppressed by silver carp during a limnocorral experiment. In contrast, adult cyclopoid copepods can avoid capture by filter feeding silver carp (Kajak et al., 1977; Domaizon 1999). Our general observations on the effect of silver carp on zooplankton corroborate the literature observations (Burke et al., 1986; Laws & Weisburd, 1990; Miura, 1990; Lazzaro, 1992; Lieberman, 1996), which report that planktivorous silver carp can have a profound effect on the composition and structure of the zooplankton as a function of fish biomass.

The differences in zooplankton species and size composition (especially in cladocerans) between high and low silver carp biomass treatments explain the changes in phytoplankton and transparency. The general pattern was an increase in total phytoplankton, particularly at low fish biomass treatments (8, 16  $\text{g m}^{-3}$ ). However, the phytoplankton communities developed differently as a function of fish biomass. The dramatic reduction of zooplankton by silver carp



in high fish biomass treatments, particularly *Daphnia*, results in a decrease in zooplankton grazing on nanoplankton causing an increase in the production of small algae. Similar observations have already been reported (Opuszynski, 1979; Milstein et al., 1988; Laws & Weisburd, 1990). During our experiments, small algae ( $< 20 \mu\text{m}$ ) were mainly represented by unicellular flagellates *Cryptomonas ovata* ( $18 \mu\text{m}$  in largest diameter), unicellular chlorophytes ( $< 20 \mu\text{m}$ , e.g., *Chlorella*) and pennate diatoms ( $< 20 \mu\text{m}$  in smallest dimension). *Daphnia* is an efficient filter feeder for a large spectrum of particles sizes (Brooks & Dodson, 1965; Schoenberg & Carlson, 1984) and can exert a significant grazing pressure on all components of microbial food webs including pico-, nano- and microplankton (Jürgens, 1994). Moreover it is established that silver carp does not efficiently consume phytoplankton  $< 20 \mu\text{m}$  (Cremer & Smitherman, 1980; Smith, 1985, 1989; Miura, 1990). Consequently, silver carp can remove large cladocerans *Daphnia*, so that zooplankton grazing on the phytoplankton community is reduced, allowing the increase in small algae abundance, leading to a decrease in transparency. According to Lathrop et al (1996) the bloom of species with large colonial size leads to a greater transparency than bloom dominated by smaller species. Similarly, we observed the highest Secchi-disc value in low fish biomass treatments characterized by the highest cyanobacteria and colonial chlorophytes densities. In contrast,  $32 \text{ g m}^{-3}$  fish treatments were characterized by the highest densities of small algae and the lowest transparency, although total phytoplankton density was lower. For similar cell densities, the association of cells in colonies leads to a greater penetration of light compared to single cells which are well dispatched. This explains the possibility of no decline in algal biomass but increase in water clarity when phytoplankton is dominated by colonial species (Lathrop et al., 1996).

Contrary to several authors who reported a decrease in cyanobacteria abundance in the presence of silver carp (Kajak et al., 1975; Miura, 1990; Starling & Rocha, 1990; Starling et al., in press), we did not observe any significant reduction in *Microcystis* abundance. However, we noted that a lower increase was observed in  $32 \text{ g m}^{-3}$  treatments. Densities of colonial chlorophyte followed the same trends. Although cyanobacteria are generally considered as poorly grazed by zooplankton and cladocerans in particular, due to their low nutritional value, inconvenient size and shape and possible toxicity (Lampert, 1977,

1981; Gliwicz, 1977, 1990; Briand & McCauley, 1978), a large number of experiments (DeBernardi & Giussani, 1978; DeBernardi et al., 1982; Thomson et al., 1982; Holm et al., 1983; Schoenberg & Carlson, 1984; Christoffersen et al., 1993) showed that *Daphnia* may feed on algal colonies and more precisely on small *Microcystis* colonies. We considered that, during our experiment, the strong decrease in cladocerans was partly responsible for the increase of cyanobacteria and colonial chlorophytes abundance. The second parameter involved in cyanobacteria development was the silver carp grazing pressure which increased with fish biomass.

However, in our experiments, nutrient concentrations changed. It is therefore a legitimate question if the changes in phytoplankton populations resulted primarily from grazing by herbivores or from changes in nutrients levels and in N/P ratios. Additions of nutrients ( $\text{NH}_4$ ,  $\text{NO}_3$ ,  $\text{PO}_4$  at N/P mass ratio:8:1) increased the concentration of N and P, especially P, in enclosures and could partly explain the decrease of N/P mass ratio during the experiment. Several literature data show an optimal development of this non heterocystous cyanobacteria for N/P ratio not exceeding 5 compared with a ratio of 10 for most phytoplankton species (Schindler, 1977; Downing & McCauley, 1992; Aleya et al., 1994). So, the general decrease in this ratio may have promoted cyanobacteria development, cyanobacteria being highly competitive at very low values of N/P ratio (Aleya et al., 1994). However, the TN/TP did not significantly differ between treatment levels, so, this parameter alone cannot explain the observed differences in cyanobacteria development.

We noted a significant impact of silver carp biomass on N and P concentrations. The dynamic of N and P loadings was influenced by contrasting conditions of zooplankton grazers. When large grazers such as *Daphnia* are removed by silver carp (through predation) an important fraction of added nutrients is transformed into particulate pool (phytoplanktonic biomass). On the other hand, when *Daphnia* are abundant, a greater fraction of the added nutrient concentrations (N and P) accumulates in the dissolved pool. The same nutrient loading produced a greater increase in small algal abundance and chlorophyll-a concentrations when *Daphnia* are lacking. In high fish biomass mesocosms, small size algae seemed to be the principal respondents to increased availability of nutrients, and the large size phytoplankton species developed to a limited extent being grazed by fish

and affected by competition with small size algae. These small size algae are known for a greater affinity and faster specific uptake rates for both nitrates and ammonia (Sherr et al., 1982; Hein et al., 1995). Our results demonstrated that by modifying grazer communities through the introduction of high silver carp biomass (maximum  $32 \text{ g m}^{-3}$ ,  $700 \text{ kg ha}^{-1}$ ) we observed changes in the utilization patterns of the added nutrients by phytoplankton communities. Also, several studies have shown that grazers can modify the relationships between nutrients and algal biomass (Mazumder et al., 1988; Sarnelle, 1992; Mazumder & Lean, 1994).

The very low gain in weight for silver carp in the highest fish treatment suggested food limitation i.e. zooplankton which was an essential food source for silver carp, but was virtually eliminated in these treatments. The productivity of the zooplankton is apparently not large enough to sustain a biomass  $> 16 \text{ g m}^{-3}$ . At high fish treatment levels, silver carp switched more on feeding on colonial phytoplanktonic species.

## Conclusion

Our experimental study highlights the effects of silver carp biomass on plankton communities and water quality of the temperate eutrophic Villerest reservoir. We distinguished between direct and indirect effects of silver carp on zooplankton. First, zooplankton density and structure were modified as a function of silver carp biomass. Cladocerans were strongly affected by the presence of medium and high fish biomass, with a threshold fish biomass ( $8 \text{ g m}^{-3}$ ) above which cladocerans are largely eliminated.

Second, indirect effects of silver carp relate to zooplankton-phytoplankton interactions and dynamic of nutrients. Through trophic cascades, the elimination of cladocerans, in treatments 20 and  $32 \text{ g m}^{-3}$ , led to a strong development of small-sized algae ( $< 20 \mu\text{m}$ ) and a modification in the utilization of dissolved nutrients. Three different cases were observed depending on fish biomass: (a) in no-fish mesocosms, the dominance of cladocerans permitted the control of phytoplankton development, particularly the small-sized species. Although nutrient concentrations were high, the predation pressure of zooplankton led to only a moderate phytoplankton development; (b) in low fish biomass treatments, the low reduction in zooplankton density had no major impact on small size algae

development. In these mesocosms the productivity of zooplankton succeeded in sustaining a moderate silver carp biomasses; (c) in medium and high fish biomass treatments, zooplankton could not sustain silver carp biomasses, and the drastic decrease in cladoceran densities led to a strong increase in small size algae and, therefore, a reduction in transparency. In these mesocosms, nutrients were more efficiently accumulated into particulate fractions, especially in small size algae.

Directs effects of silver carp on cyanobacteria include a decrease in N/P ratio values probably which lead to a general increase in cyanobacteria density. However? the grazing pressure of zooplankton and silver carp played a major role in cyanobacteria development: (a) in no fish mesocosms, the presence of high cladoceran densities led to a moderated development of cyanobacteria; (b) in low fish biomass treatments, cyanobacteria densities increased due to a reduced zooplankton grazing pressure and an insufficient silver carp grazing pressure; (c) high fish biomass treatments were characterized by a limited cyanobacteria development due to a more efficient silver carp grazing pressure and to competition with small size algae. The predation pressure of silver carp on colonial algae increased due to the inability of zooplankton to sustain the highest fish biomasses. The gain in weight for silver carp in these treatments was very low suggesting the importance of zooplankton as food source for this fish. Zooplankton represents for fish a food that is rich in protein and fatty acids and cyanobacteria have a lower nutritional quality (Giraud et al., 1996).

It was clear, at the end of this experiment, that, below  $12 \text{ g m}^{-3}$  ( $260 \text{ kg ha}^{-1}$ ) of stocking fish biomass, indirect effects due to zooplankton elimination would be minimized but silver carp grazing would not be strong enough to control cyanobacteria development. Above this stocking biomass threshold, the undesirable effects like nanoplankton development and reduction in water transparency could be more important than the beneficial effects on cyanobacteria.

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