



Direct and indirect effects of carp (*Cyprinus carpio* L.) on macrophyte and benthic communities in experimental shallow ponds in central Mexico

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Abstract

An experiment was conducted for 11 months in five controlled small ponds (≈ 0.05 ha) to determine the effects of common carp on water turbidity, and macrophyte and benthic communities in subtropical shallow systems. By using exclosures in ponds, we also looked for carp direct effects (by predation disturbance) and indirect effects (by increasing turbidity, and decreasing refuge sites) on rooted macrophyte and benthic communities. Results showed that at densities equal or higher than 0.8 ind. m^{-2} carp suffers from intraspecific competition. At the same densities, carp produces an increment of water turbidity, but the relation is non-linear, suggesting a switch effect, from a clear-water-system to a turbid-water-system. We also found that a direct effect of carp on macrophytes depends on the susceptibility of each species. Carp affects benthic abundance directly by predation, but its indirect effects on it remain unknown.

Introduction

Effects of benthivorous fish, such as common carp (*Cyprinus carpio* L.) on temperate shallow lakes are related to a disruption of the bottom caused by its feeding habits (Tatrai et al., 1994). These fish feed by sucking the sediment with the mouth, selecting food by filtering it with the gills and rejecting the rest to the water column (Lammens, 1991). This feeding mechanism produces changes in macrophyte and benthic communities. Benthivorous fish have direct effects over populations of particular species of rooted macrophytes by predating on their tissues and roots (Ten Winkel & Meulemans, 1984). Also by predation, these fish have a direct effect on reducing the abundance and diversity of benthic community (Zur, 1979; Riera et al., 1991; Tatrai et al., 1994).

Indirect effects caused by carp on macrophytes are related to changes in the turbidity of the water column. The constant removal of sediments while looking for food results in a relocation of solids and nutrients, particularly phosphorous, from the bottom to the water column (Meijer et al., 1990; Cline et al., 1994; Tatrai et al., 1996; Shormann & Cotner, 1997). The final result is a decrease in water transparency by ways

of an increment of concentration of suspended solids throughout the water column and a swelling of algae population through a 'bottom-up' effects (Tatrai et al., 1990; Breukelaar et al., 1994; Carvalho & Moss, 1995; Roberts et al., 1995; Jayaweera & Asaeda, 1996). An increment of turbidity may produce a decrease in coverage of plants in a lake (Spence, 1982; Crowder & Painter, 1991; Lauridsen et al., 1994), that creates a positive loop feedback in water turbidity. The lack of a submerged plants-barrier between bottom lake and water column introduces the possibility of a sediment re-suspension by wind-induced wave action (Hosper, 1994). Also, macrophytes serve as refuge for zooplankton against predation (Jeppesen et al., 1997; Stansfield et al., 1997). In the absence of these plants, zooplankton abundance decreases (Schriver et al., 1995) breaking the possibility of a 'top-down' control. Therefore, high abundance of benthivorous fish in temperate shallow lakes could result in a loose macrophyte stabiliser of a clear-water state (Hosper & Meijer, 1993) and produces a high stable turbid-water state in the system (Hosper, 1994).

Because the spatial heterogeneity assembled by plants provides habitats for benthic organisms (Gilinsky, 1984; Van Donk et al., 1990; Hildrew & Giller,

1995; Tatrai et al., 1996), this community is affected indirectly by benthivorous presence through macrophyte cover depletion in the lake (Crowder & Painter, 1991).

Consequently, rooted macrophytes and benthos may be directly affected by the introduction of carp via direct predation and indirectly by an increase on turbidity of the water in the former case and a decrease on macrophytes coverage in the latter. However, not all carp densities may produce an effect on the system. In lower densities, carp may not produce changes as big as those produced by higher densities of this cyprinid.

Most theories on benthivorous effects are restricted to temperate zones, leaving changes of the dynamics of tropical and subtropical systems due to this type of fish poorly understood. In a preliminary study of carp effects on subtropical systems of Central Mexico, we found a relation between *C. carpio* abundance and water turbidity, suspended solids, macrophytes and epibenthic abundance (Zambrano et al., in press). However, factors such as nutrient release or algal bloom did not seem to behave as in temperate zones. The lack of results on these last parameters suggests possible differences in mechanisms of carp effects between temperate and subtropical systems.

Stocking of benthivorous common carp (*C. carpio*) is prevalent in subtropical ponds of rural zones from the Mexican Volcanic Belt, partly as a result of its high capacity to survive and grow in poor quality waters (Maitland & Campbell, 1992). The risk of carp introduction that affects these subtropical systems, identified as being of conservation value because of their high density of endemic species, moved us to understand what interactions were prevalent between this introduced species and its host system. The aim of this study was to determine the effect of different densities of carp on water turbidity in experimental ponds in Central Mexico, and to understand both direct and indirect mechanisms by which this cyprinid affects benthic and macrophyte communities.

Methods

On March of 1997 on El Cerrillo station (19° 20' W and 99° 40' N, altitude 2600 m, mean annual temperature 13 °C and mean annual precipitation 768.5 mm), five experimental ponds (area 500 m²) were filled with well water up to a 1 m depth. Refilling the ponds every two months prevented a decrease in water level due to evaporation. In four ponds, juvenile carp

(mean total length, $T_L = 5.3$ cm) were introduced at densities of A = 0.3, B = 0.5, C = 1.7 and D = 3.8 ind. m⁻²; whereas none was introduced in a fifth pond (E). Densities used at ponds B and D are the standard populations densities usually recommended by local fisheries authorities for carp aquaculture. Accidentally, in the fourth week of the experiment, some carp from pond D invaded control pond E. From that moment, this last pond was used also to evaluate changes in the system with carp introduction. Final densities and fish total length were measured on each pond after 11 months, on February of 1998. Analysis of gut contents was undertaken on 100 carp randomly selected at different sizes from all ponds. For each pond at least 15 carp gut contents were analyzed.

As an estimation of water turbidity, Secchi depth measurements were taken daily over a 35 week period. After this period, turbidity did not change on the ponds. Also, in the last day of the experiment a pooled sample (of two subsamples taken randomly) of 1 l of water was collected to obtain concentration (mg l⁻¹) of total suspended solids.

Before the experiment started, twenty eight round exclosures with 1.5 m of diameter were built with 1 mm nylon mesh based on metal polls on three ponds: ten exclosures, were in the pond with the highest carp density (pond D), ten in the pond with the middle carp density (pond B) and eight in the pond that was carp-free at the beginning (pond E). To avoid exclosure effects, such as changes in light penetration, wave action, stabilising sediments and presence of substrate for invertebrates, half of them (five on each pond) were not completely closed; the middle lower part of the mesh was cut-off in order for carp to swim freely inside. In July, three pots were placed on each exclosure with four previously weighted and measured species of rooted plants: the first pot contained *Elatine americana* and *Eleocharis palustris*; the second pot contained *Sagittaria mexicana*, and the third pot contained *Elodea canadensis*. Plant length (cm) was measured monthly, and at the end of the experiment, in January, all of them were measured and weighted.

In order to analyse benthos abundance, 43 samples of 1 l of mud were collected on January of 1998 with an Eckman grab. Mud samples were collected from the inside of each exclosure and from five random points outside of the exclosures from each one of ponds B, D and E. Organisms were separated from the mud in the field by 3 sieves (4 mm, 2 mm and 0.4 mm mesh size) and identified and counted in the laboratory.

Carp survival rate at different densities was obtained from the proportion between the initial and final numbers of individuals on each pond. Because some fish passed from pond D to E, remaining individuals and total area were added from both ponds to get the surviving rate. A linear regression was used to test changes in the carp length after 11 months at different pond densities. Also, from carp final total length A coefficient of dispersion (CD) was obtained for each pond in order to consider the variance of carp growth at different densities. Carp biomass was calculated from the size of each carp by using the following relationship, estimated from a previous study in the zone: $\ln(\text{gr.}) = -3.54 + [2.94 \ln(\text{cm})]$.

A cumulative macrophyte biomass index was obtained from the ratio between the final and the initial macrophyte weight. A similar ratio was used to obtain a macrophyte height index for *E. canadensis*. For the other plants, November height data were used as final height because plant mortality increased in December in all pots. For the three species, the November data had the highest difference in height for all plants from the initial size. To assess statistical differences in cumulative macrophyte biomass index and in macrophyte height index for each plant, nested ANOVAs were used to prove effects on ponds and exclosures (nested in ponds) on variables using data from complete exclosures (C) and incomplete exclosures (I). Data were transformed with log function in the models to get a normal error. ANOVAs were run using the statistical GLIM 3.77 package.

In a similar way, to assess differences in benthic abundance a nested ANOVA was used to prove effects on ponds and exclosures (again, nested in ponds) on variables using data from complete exclosures (C), incomplete exclosures (I) and from the five random outside points (O). Poisson error and log-link were used for variables. To avoid over-dispersion problems, scaled analysis was carried as indicated in Crawley (1993). The model was run using the same package as the one used for estimating differences in macrophyte growth index.

Results

Carp densities changed at the end of the experiment with respect to their initial densities. Carp survival rate in ponds were A = 0.83, B = 0.8, C = 0.47 and D + E = 0.55. Final densities were A = 0.25, B = 0.4, C = 0.8 m^{-2} , D = 1.1 and E = 1.0 ind. m^{-2} . There is a significant in-

verse correlation between the final mean T_L of the fish and pond density (Figure 1a). Carp abundance affected its growth rate; thus, at low densities, the fish size is nearly one third longer than at densities around 1 ind. m^{-2} . Also, carp class size structure seemed to depend on individual density. At densities near to or lower than 0.4 ind. m^{-2} carp, the class size structure had a smaller variance and a normal distribution, but the coefficient of dispersion increased and the distribution of class sizes are skewed to the right at higher densities (Figure 1c). In consequence, total carp biomass did not increase in a linear relation with its abundance, there is a decrement of the total carp yield rate at higher densities (Figure 1b).

Composition of carp diet did not vary from other studies (Chapman & Fernando, 1994). Detritus appeared in 60% of the gut contents, algae in 41%, seeds and tissue plants in 31% for each one, and animal remains such as chironomids and oligochaeta in 23% of the cases.

In ponds with the lowest carp densities (A and B), turbidity did not increase enough to avoid the Secchi disc to be seen in the pond bottom, but it did so with higher carp abundance (C and D), with effects apparent as early as six weeks after the beginning of the experiment (Figure 2). Pond E remained clear until carp invaded it, and then it took only about two weeks for water to become turbid. Turbidity did not increase proportionally to carp abundance; once the water column started to be turbid, Secchi depth arrived to a rank between 50 and 60 cm (Figure 2). Suspended solids concentration varied on each pond, being higher in carp with densities equal and higher to 0.8 ind. m^{-2} : A = 8, B = 3, C = 447, D = 398 and E = 991 mg l^{-1} .

None of the four experimental plant species on pots had height ratio differences between complete and incomplete exclosures (Table 1). *S. mexicana* had a higher height trend in complete exclosures, while *E. palustris* had the opposite (Figure 3). In the cumulative biomass index, *S. mexicana* had significantly more biomass in complete exclosures than in incomplete exclosures (Table 2; Figure 4). On the contrary, the weight of *E. canadensis* was significantly smaller in complete exclosures than in incomplete ones (Table 2; Figure 4). The other two macrophyte species did not have any difference between exclosures on both biomass and height rates (Figures 3 & 4). None of the tests showed a pond effect on the data (Tables 1 & 2).

Abundance of benthic organisms was significantly different depending on the treatment that was followed (Table 3). Ponds D and E had greater abundance of

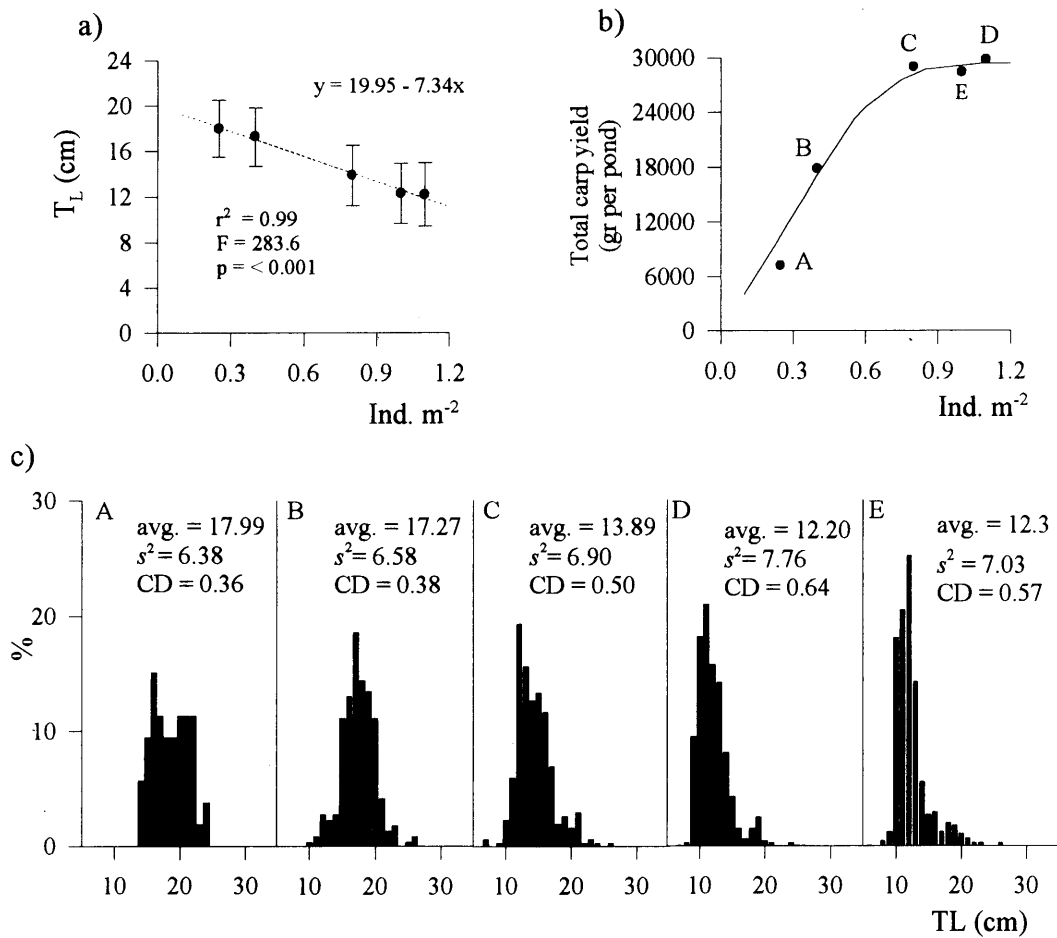


Figure 1. Final carp size and weight in experimental ponds. (a) Relation between carp density and mean final total length. (b) Total yield carp in each pond, the line represents an hypothetical relationship between carp total yield and its final density. (c) Proportion of different carp class size, note changes in the bars distribution are skewed to the right in ponds with higher carp densities. Capital letters represents each studied pond.

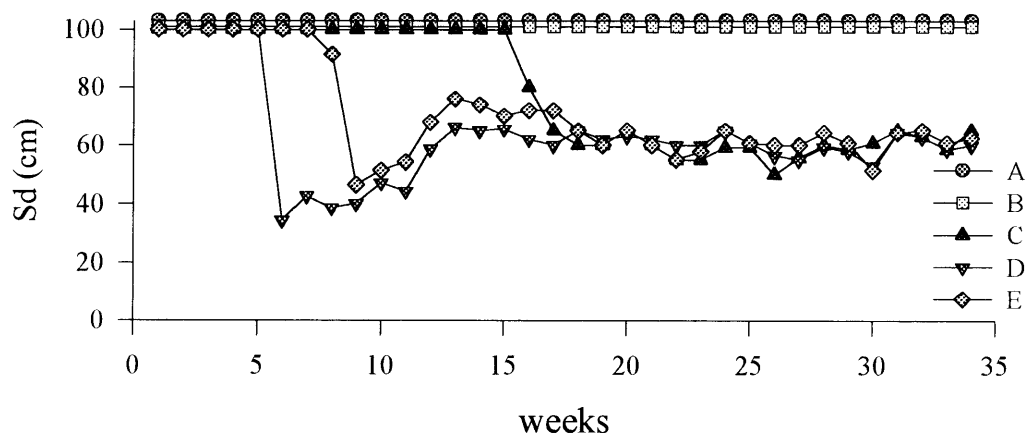


Figure 2. Temporal variation of water turbidity in five experimental ponds. Sd – Secchi depth. Capital letters represents each studied pond.

Table 1. Nested ANOVAs for macrophytes height index: based on final and initial height ratio (see text). C – complete exclosures and I – incomplete exclosures

Factor	s.s.	d.f.	MS	F	p
<i>Sagittaria mexicana</i>					
Ponds	0.16	2	0.080	2.2	ns
C-I within Pond	0.11	3	0.036	0.9	ns
Residual	0.93	24	0.039		
Total	1.20	29			
<i>Elatine americana</i>					
Ponds	0.25	2	0.123	4.1	ns
C-I within pond	0.09	3	0.030	1.3	ns
Residual	0.54	24	0.023		
Total	0.88	29			
<i>Elodea canadensis</i>					
Ponds	0.55	2	0.275	3.8	ns
C-I within pond	0.22	3	0.073	1.1	ns
Residual	1.06	24	0.067		
Total	1.83	29			
<i>Eleocharis palustris</i>					
Ponds	0.07	2	0.037	0.9	ns
C-I within pond	0.12	3	0.041	2.1	ns
Residual	0.47	24	0.020		
Total	0.67	29			

Table 2. Nested ANOVAs for macrophytes based on cumulative biomass index (see text). C – complete exclosures and I – incomplete exclosures

Factor	s.s.	d.f.	MS	F	p
<i>Sagittaria mexicana</i>					
Ponds	0.08	2	0.041	0.8	ns
C-I within Pond	0.16	3	0.054	5.8	<0.05
Residual	0.22	24	0.009		
Total	0.47	29			
<i>Elatine americana</i>					
Ponds	0.21	2	0.106	0.9	ns
C-I within pond	0.34	3	0.114	1.2	ns
Residual	2.30	24	0.096		
Total	2.85	29			
<i>Elodea canadensis</i>					
Ponds	1.46	2	0.732	5	ns
C-I within pond	0.44	3	0.148	4.8	<0.05
Residual	0.73	24	0.031		
Total	2.64	29			
<i>Eleocharis palustris</i>					
Ponds	0.87	2	0.433	8.5	ns
C-I within pond	0.15	3	0.051	0.4	ns
Residual	3.00	24	0.125		
Total	4.01	29			

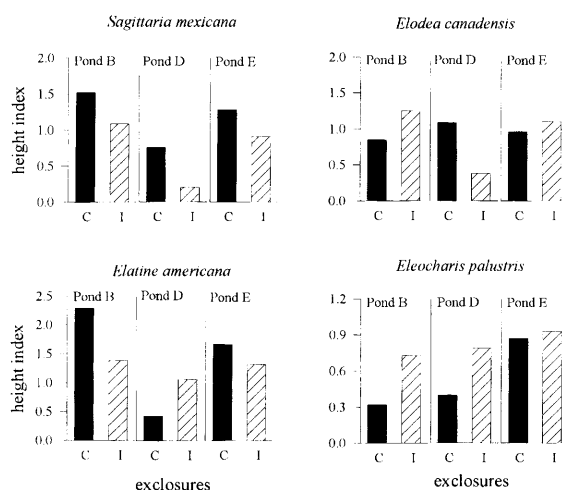


Figure 3. Differences macrophytes height ratio calculated from final and initial height in experimental ponds and treatments (see text). C – complete exclosures (black column) and I – incomplete exclosure (dashed column).

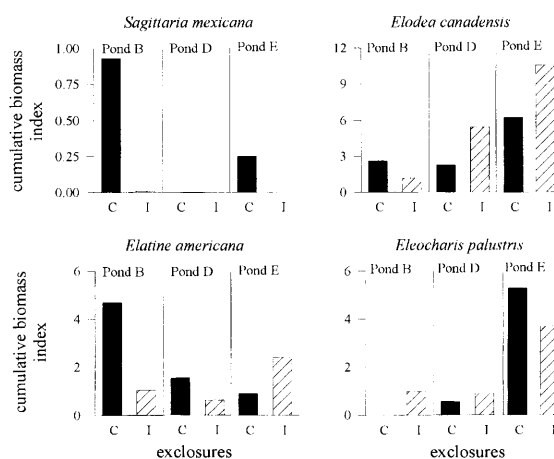


Figure 4. Differences in macrophyte cumulative ratio calculated from final and initial height in experimental ponds and treatments (see text). C – complete exclosures (black column) and I – incomplete exclosure (dashed column).

Table 3. Nested ANOVA for benthic abundance C – completes and I – Incomplete exclosures

Factor	s.s.	d.f.	MS	F	p
Ponds	10.90	2	5.450	1.2	ns
C-I within Pond	26.77	6	4.462	4.7	<0.01
Residual	34.46	36	0.957		
Total	72.14	44			

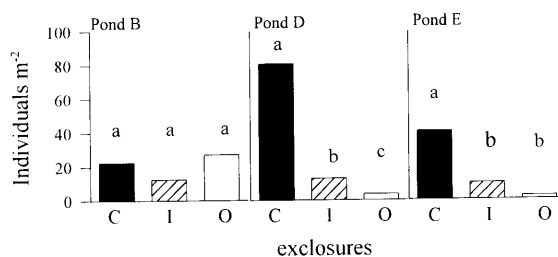


Figure 5. Abundance of benthic organisms in experimental ponds and treatments. Different letters (a, b and c) represent significant differences between each exclosure, while same letters represent none differences between them. C – complete exclosure (black column), I – incomplete exclosure (dashed column) and O – outside of exclosure (white column).

benthic organisms in complete exclosures than in incomplete exclosures and outside samples, while pond B did not have any significant difference between treatments (Figure 5). There was no pond effect on the benthic abundance (Table 3).

Discussion

At the end of the experiment densities from all ponds were always smaller than the number of individuals introduced at the beginning. These changes could be due, at least in part, to the activity of poachers; however, the proportion of mortality increases with carp pond density suggesting that this species suffers from intraspecific competition when resources become scarce (Begon et al., 1996). The similar reduction of carp size in denser ponds supports this idea because its individual growth rate decreases at low food availability (Lam & Shephard, 1988). The relationship between total carp biomass on each pond and its density is similar with crop studies suggesting that no matter how many individuals there are in a system, the final yield cannot pass from a maximum limited by resources (Kays & Harper, 1974); although most of this theory has been created for plants, results of

carp growth may be explained by the law of constant final yield (Kira et al., 1953 in Begon et al., 1996). The law proposes that, at high densities, there is a constant relationship between individual numbers per area and the total sum of their weight because there is a limitation in nutrient resources that avoids a higher biomass accumulation per individual by intraspecific competition.

The limiting food resource for the common carp is the benthic community. Exclosure results suggest that the abundance of the latter is reduced by carp predation. Thus, if density is high, carp may deplete their resources faster than they become replenished. With a depletion of benthic abundance the foraging activity should increase, and consequently, also the amount of suspended solids in water, a factor that is clearly related to water turbidity (Scheffer, 1998). The fact that an increment of suspended solids and turbidity was produced at the same fish density at which a carp overpopulation reaction appears to support this explanation.

At the beginning of the experiment, it was expected that water turbidity would increase proportionally to carp density throughout the entire density range as it happened in other studies (Breukelaar et al., 1994). However, Secchi disc values indicating a turbid or a pristine condition were virtually constant for all ponds throughout the experiment, as the periods of change in turbidity were very short. This phenomenon suggests the existence of a switching mechanism in the system between two stable points: clear and turbid (Scheffer et al., 1993). The time elapsed before the switch effect seemed to be the variable that changed with the density of carp; the lowest cyprinid density that produced an increment in turbidity in the water column (Pond C) delayed about 10 weeks with respect to the onset of the change at the pond with the highest density (D). Although this study did not provide a definite answer to the question as to why there is a switch mechanism, one possibility is that carp-dredging activity by pumping sediments to the surface is not the unique force. Benthic foraging also rather disturbs the process of sediment consolidation (Delgado et al., 1991) creating a softer sediment which is easier to raise through the water column by wave and current actions (Scheffer, 1998). This double effect may be the cause of switch from pristine to turbid water points, particularly in windy zones such as is the case of the one studied.

Carp direct effects seem to be differential on macrophytes species. *E. americana* and *Eleocharis palustris* did not suffer by carp presence. Only *S. mexicana*

is directly affected by common carp presence, possibly by predation because this plant has soft tissues and roots. On the contrary, *E. canadensis* is more resistant and accumulated more biomass inside of incomplete enclosures, suggesting an enclosure effect on this plant.

Despite the consistent results of the effect of higher carp densities on turbidity, which should produce a negative indirect effect on the plant community, the null pond effect (two turbids and one pristine) on plant growth suggests that changes in light penetration did not affect, as we expected, the macrophyte performance. Turbidity may not be a killing factor for macrophytes when ponds are shallow enough to allow light to penetrate close to the bottom as in the case of the experimental ponds used here. Macrophytes can survive in shallower zones in turbid lakes (Crowder & Painter, 1991), and some of them could suffer from an elongation phenomenon resulting from the lack of light (Taiz & Zeiger, 1991). However, it is necessary to perform more studies to get a conclusive result from this trend.

Although benthic intraspecific competition is not frequent in patchy aquatic habitats (Tokeshi, 1995), direct predation of carp on benthic community may alter the competitive relationships between them (Abrams, 1983; Diehl, 1995), particularly in ponds without high macrophyte coverage. The presence of plants increases the resilience of the benthic community to disturbances (Hildrew & Giller, 1995) and decreases the efficiency of predation pressure (Dahl & Greenberg, 1998). This may produce a benthic community aggregation (Flecker & Allan, 1984) in safer spatial heterogeneous areas such as enclosures were. This hypothesis could explain the highest benthic abundance inside of enclosures in densest carp ponds.

The results of this study show that at high densities, common carp suffers from intraspecific competition increasing its mortality rate and reducing its individual growth rate. At the same high densities, effects of carp on turbidity in the water (by increasing the concentration of suspended solids) become apparent. Both changes suggest a link between the water transparency depletion and carp intraspecific competition through the increment of carp foraging intensity (pumping more sediment from the bottom) at low resources abundance. Once carp creates an effect on the system, a switch mechanism seems to appear instead of a proportional interaction between carp density and water turbidity. Direct effects of carp on macrophyte communities appear to depend on the susceptibility

of the species. Despite of the change due to carp on water turbidity, the indirect effects that carp produces on this macrophyte community through this way is not known. Carp affects benthic abundance directly. Indirect effects of carp on benthic communities remain unknown.

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