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Experimental study of the impacts of planktivorous fishes on plankton community and eutrophication of a tropical Brazilian reservoir

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Abstract

We examined the impacts of three facultative planktivorous fishes, Congo tilapia (*Tilapia rendalli*), bluegill (*Lepomis macrochirus*) and tambaqui (*Colossoma macropomum*), and an obligate planktivorous fish, silver carp (*Hypophthalmichthys molitrix*) on plankton community and water quality of a tropical eutrophic reservoir, Paranoá Reservoir, Brasília, Brazil, conducting both laboratory selective grazing experiments and an enclosure experiment. The first two species inhabit this reservoir and the remaining two are recommended for introduction. The field experiment was performed in ten limnocorrals (2 m^3 each) and lasted five weeks. During the enclosure experiment, silver carp suppressed copepod nauplii, cladocerans and rotifers while the presence of tilapia and bluegill were associated with increased rotifers density. The dominant blue-green algae, *Cylindrospermopsis raciborskii* (98% of phytoplankton biomass) was enhanced in the presence of bluegill, tilapia and tambaqui, but reduced in the presence of silver carp. This impact on plankton is in agreement with the results of the laboratory feeding trials. The observed alterations in water quality parameters in fish limnocorrals are discussed in relation to plankton community and eutrophication of this ecosystem. It is suggested that the control of the undesirable algae *C. raciborskii* directly by silver carp grazing is a promising management tool.

Introduction

Since the early studies of Hrbácek (1962) and Brooks & Dodson (1965), considerable attention has focussed on the direct and indirect effects of planktivorous fish on plankton communities and eutrophication processes (see Hulbert & Mulla, 1981 and Lazzaro, 1987 for useful reviews). Most of these studies showed the enhancement of phytoplankton as the major negative indirect impact of large-bodied zooplankton suppression by visually-feeding planktivorous fishes. Consequently, biomanipulation approaches such as reduction of planktivorous populations were intensively investigated as a management tool to improve water quality (Benndorf *et al.*, 1984; Shapiro & Wright, 1984; Langeland *et al.*, 1987; Hosper, 1989).

Although differential impacts on plankton community is expected from particulate and filter-feeder planktivorous fish, only a few researchers have experimentally investigated the influence of pumping filter-feeding fishes on plankton community structure and their potential use as a biomanipulation technique to reduce algal biomass (Kajak *et al.*, 1977; Opuszynski, 1979;

Drenner *et al.*, 1987; Vinyard *et al.*, 1988). Despite the preliminary suggestions by Lazzaro (1987), informations on planktivorous impacts in tropical regions are still scarce (Arcifa *et al.*, 1986).

Our study was conducted to provide information about the effects of different types of planktivorous fishes on plankton community and water quality of a tropical eutrophic reservoir. We report in this paper on the potential use of filter-feeding silver carp for biological control of the dominant blue-green filamentous algae, *Cylindrospermopsis raciborskii*.

Study area

Paranoá Reservoir (maximum depth 38 m, mean depth 14 m) is located within the city limits of Brasília-Brazil (15° 48′ S and 47° 50′ N). It covers ca. 40 km^2 with a volume of about 560 10^6 m^3. In the last two decades, this reservoir has changed from an oligotrophic to a highly eutrophic water body due to sewage inflow, mainly from treatment plants (Bjork, 1979).

One of the most important symptoms of accelerated eutrophication in the reservoir is the high phytoplankton biomass, almost entirely composed of the filamentous blue-green algae *Cylindrospermopsis raciborskii*. Blooms of *Microcystis aeruginosa* in some reservoir areas, have also been reported and controlled by addition of copper sulphate (Mattos *et al.*, 1986). Zooplankton is dominated by rotifers, with more than 20 species. *Bosmina longirostris*, *B. hagmany* and *Diaphanosoma birgei* are the only cladocerans present and *Thermocyclops decipiens* the only copepod. The absence of large-bodied daphnids and the relatively small size of the abundant zooplankton limits the zooplankton's ability to consume *Cylindrospermopsis* filaments (Pinto-Coelho, 1983).

Since its construction in 1959, Paranoá Reservoir was stocked with some exotic fish species such as bluegill sunfish (*Lepomis macrochirus*) and Congo tilapia (*Tilapia rendalli*). In recent years, The Governmental Fisheries Agency (SUDEPE) has recommended the introduction of tambaqui (*Colossoma macropomum*) in the reservoir due to its high commercial value, and silver carp (*Hypophthalmichthys molitrix*) for biological control of phytoplankton biomass. We examined feeding and impacts of these four planktivore species before the introduction of silver carp and tambaqui into the reservoir.

Materials and methods

Laboratory selective grazing experiments

Silver carps and tambaquis were obtained from a fishfarm and bluegills and Congo tilapias were cast-netted from Paranoá Reservoir. Fishes used in feeding trials were fed reservoir plankton daily and acclimatized for 1 month in 120 l aquaria. Fish feeding rates on reservoir zooplankton and *Cylindrospermopsis raciborskii* filaments were determined by monitoring declines of their densities in 40 l aquaria containing 3–8 bluegills (65–95 mm SL), 2–3 silver carps (126–139 mm SL), 3–6 tambaquis (74–95 mm SL) and 3–5 tilapias (71–97 mm SL).

Six feeding trials were conducted for each fish species at 22–25 °C under fluorescent light. Before each experiment, clean aquaria were filled with concentrated reservoir water. The initial zooplankton densities ranged from 9098 to 15910 organisms l^{-1} and total *Cylindrospermopsis* filaments length from 316 to 4790 $\mu m\ l^{-1}$. Plankton was kept in suspension by aeration, fish movements and stirring the aquaria every 15 minutes. Triplicate water samples were collected from each well-mixed aquarium at 0 and 2 h of feeding by quickly lowering a plastic tube onto a randomly placed rubber stopper on the aquarium bottom (Drenner & McComas, 1980).

A known sample volume was strained through a 65 μm sieve to remove zooplankton which was preserved in 5% formalin while 50 ml of unfiltered water from the same sample were preserved in 1% lugol's solution for *Cylindrospermopsis* counts. The blue-green filaments were measured and enumerated in sedimentation chambers on

inverted microscope at 400×. Zooplankton organisms were counted in Sedgewick-Rafter cells using conventional light-microscope at 160×.

The feeding rate constant per gram of fish body weight (K/g) was calculated using the equation: $K/g = -ln(P_f/P_i)/XTg$, where P_i and P_f are initial and final plankton densities per litre, X is the density of fishes per litre, T is the experiment duration in hours and g is the mean biomass of individual fish (Dodson, 1975 modified by Drenner & McComas, 1980). The dimensions of K/g are litres per gram of fish per hour. Feeding rate constants were corrected for plankton loss from sources other than fish feeding, by monitoring simultaneously a control aquarium without fishes but containing an equal density of the same plankton.

Enclosure experiment

Prior to the enclosure experiment, silver carps and tambaquis obtained from a fishpond were acclimatized to reservoir plankton and water conditions for 2 month in 3 cylindrical net cages (1.2 m diameter; 1.2 m deep; 2 mm mesh). The outdoor experiment was conducted in March–April 1988 using a set of 10 cylindrical polyethylene enclosures (1.0 m diameter; 2.5 m deep; with plastic walls 0.2 mm thick) in a linear array. The limnocorrals completely isolated a 2 m^3 column of water and were open to the atmosphere but closed to sediment.

Each enclosure was filled with 0–3 m reservoir column water by 3 divers. Each folded limnocorral, vertically positioned, was taken by the divers down to a depth of 3.0 m where it was turned to a horizontal position and conducted to the surface, collecting the water column above. Immediately after reaching the surface, each enclosure was hung in individual floating collars and weights were attached to enclosure bottoms to insure a vertical position. Filling all enclosures took one hour. A fence made from the same polyethylene and covered by a 2 cm mesh net was erected around each limnocorral to prevent fish from jumping in or out and to avoid bird predation.

The enclosures were divided into 5 treatment groups with 2 replicates each. Two limnocorrals designated as control were kept fish free while each 2 of the remaining limnocorrals designated TQ, SC, TL and BG treatments were stocked respectively with 33 tambaquis (43–93 mm SL), 10 silver carps (85–135 mm SL), 12 Congo tilapias (56–110 mm SL) or 15 bluegills (70–113 mm SL). All fish enclosures received the same fish biomass (250 g). This high stocking level (3000 kg ha^{-1}) approximated the upper limit of *Tilapia rendalli* density in the shallow areas of Paranoá Reservoir estimated by cast netting.

During the 5 weeks of experiment, dissolved oxygen (Winkler method with azide modification), temperature and conductivity (YSI model 33 meter) were measured 3 times a week in each enclosure at 0 and 2 m depth. Transparency (Secchi disc) and pH (CELM meter) were also determined with this frequency. Integrated water samples (0–2.5 m) for chemical analyses and plankton countings were collected with a PVC tube sampler (3 m length; 5.5 cm diameter and 5 l volume). After well-mixed, 100 ml aliquot of each tube sample was preserved with 1% lugol for phytoplankton counting, 2 l were concentrated in a 45 μm sieve for zooplankton enumeration and 1 l was used for analysis of pH, total alkalinity (Gran titration in Talling, 1973), ammonia (Nessler method in APHA, 1985), nitrate, total dissolved phosphorus (Mackereth *et al.*, 1978), nitrite, orthophosphate and soluble reactive silicon (Golterman *et al.*, 1978).

Phytoplankton cell counts were performed following Utermohl's procedure on an inverted microscope at 400×. The biomass of the most abundant algal species was estimated using approximated geometrical models and assuming a specific gravity of 1 mg mm^{-3}. For zooplankton, 3 subsamples in Sedgewick-Rafter cells were completely searched at 160× in a conventional microscope. Fish mortality in the enclosures was monitored at each sampling date (1–2 days interval), and any dead fish was removed and replaced by a live one of approximately the same biomass.

A two-way ANOVA, with treatment and time being the two factors simultaneosly tested, was performed for each logtransformed variable from the enclosure experiment. The logarithmic transformation ($X' = lnX + 1$) was applied to make the variance independent of the mean (Sokal & Rohlf, 1981). The Duncan multiple range test was used to test significance of differences among treatment means at Alpha = 0.05. All computations were done with The Statistical Analysis System (SAS).

Results

Laboratory selective grazing experiments

The general pattern of feeding rate constant for different prey sizes was not similar among fish species (Fig. 1). Bluegills, which were always observed to feed as particulate feeders, had feeding rates increasing with particle size, with maximum values on *Thermocyclops decipiens* (copepodites + adults). This fish did not consume rotifers and *T. decipiens* nauplius.

In contrast, all other fish species were observed to feed as filter-feeders only. Feeding rates of tambaqui and silver carp tended to decrease with particle size while feeding rates of tilapia reached a maximum in an intermediate size zooplankton (mainly *Bosmina spp.*). Tilapias were frequently observed collecting prey on the surface and near the bottom rather than filter-feeding in midwater. On the other hand, silver carps and tambaquis were always observed pump filter-feeding in midwater.

All filter-feeding species showed low feeding rates on the most evasive zooplankton, *T. decipiens* (copepodites + adults). Silver carp had higher feeding rates than tambaqui and tilapia

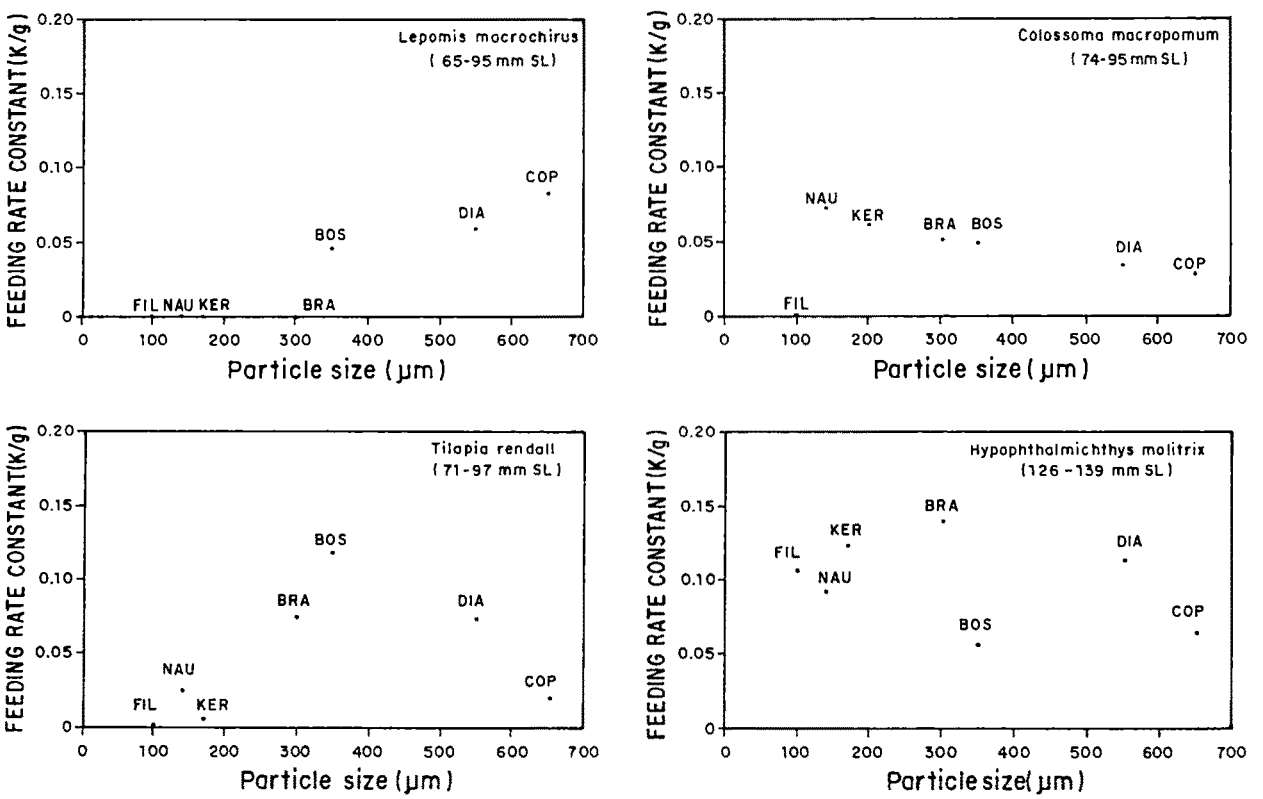


Fig. 1. Feeding rate constants (K/g) of different fish species ($l^{-1}\ g^{-1}$ fish hr^{-1}) on *Cylindrospermopsis* filaments (FIL), *Thermocyclops* nauplius (NAU), *Keratella* (KER), *Brachionus* (BRA), *Bosmina* (BOS), *Diaphanosoma* (DIA) and *Thermocyclops* copepodites + adults (COP) (n = 4). The size range of fish is also given.

Table 1. Mean values of physical and chemical parameters in each treatment for enclosure experiment (n = 28). Two-way ANOVA probability values for treatment effect and interaction (treatment × time) are given.

	Treatments mean values					Probability	
	CTL	BG	TQ	TL	SC	Treat	Inter.
Temperature (°C)	25.9	25.7	25.8	25.8	25.8	0.83	0.73
Oxygen (mg l^{-1})	7.3	7.1	7.4	7.3	7.2	0.71	0.11
Conductivity (μS cm^{-1})	47.8	50.3	48.6	53.0	50.7	0.16	0.01
pH	9.1	9.5	9.3	9.7	9.4	0.22	0.02
Transparency (cm)	45	39	40	38	42	0.15	<0.01

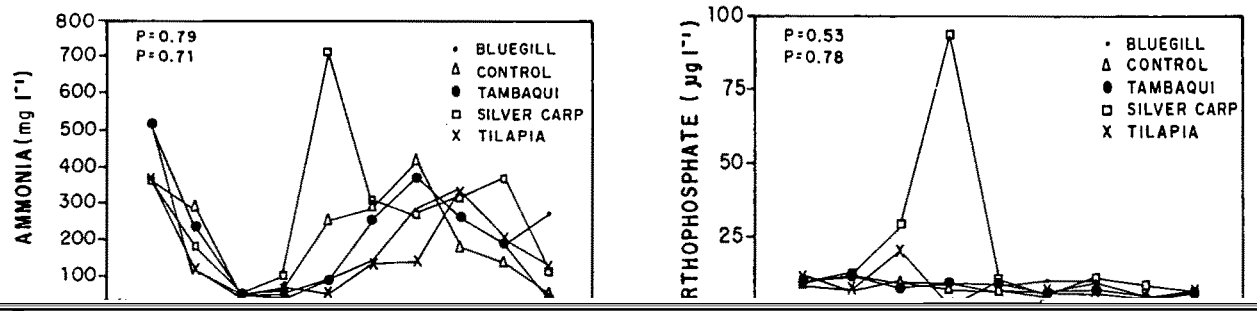
Table 2. Average pH, conductivity and transparency values for each treatment during 'in situ' experiment. Means with the same letter are not significantly different (Duncan's Multiple Range Test; Alpha = 0.05).

Parameter	Treat	Time-days													
		01	03	05	08	10	12	15	17	19	22	24	26	29	31
pH	CTL	7.95 (A)	9.70 (A)	9.85 (A)	10.05 (A)	9.30 (A)	8.80 (B)	8.80 (B)	8.55 (B)	8.80 (B)	8.85 (B)	9.00 (AB)	9.10 (A)	9.25 (A)	9.35 (A)
	BG	7.60 (A)	9.55 (A)	9.45 (A)	9.80 (A)	9.80 (A)	9.90 (A)	10.10 (A)	10.30 (A)	10.40 (A)	9.60 (AB)	8.60 (B)	9.20 (A)	9.35 (A)	9.30 (A)
	TQ	7.65 (A)	9.20 (A)	9.45 (A)	9.70 (A)	9.65 (A)	9.80 (A)	9.95 (A)	9.60 (A)	9.50 (B)	8.85 (B)	8.85 (AB)	9.05 (A)	9.45 (A)	9.75 (A)
	SC	7.80 (A)	9.60 (A)	9.85 (A)	10.10 (A)	9.95 (A)	9.70 (A)	9.60 (A)	9.70 (A)	9.10 (B)	9.40 (AB)	9.00 (AB)	8.95 (A)	9.05 (A)	9.30 (A)
	TL	7.60 (A)	9.60 (A)	9.70 (A)	10.10 (A)	10.05 (A)	10.20 (A)	10.30 (A)	10.35 (A)	10.45 (A)	9.80 (A)	9.60 (A)	8.85 (A)	9.40 (A)	9.50 (A)
Conduct. (μS cm^{-1})	CTL	50.0 (A)	50.0 (A)	50.0 (A)	53.4 (A)	41.0 (B)	45.0 (C)	41.5 (C)	49.0 (C)	47.4 (C)	50.0 (A)	50.0 (A)	50.0 (A)	43.4 (AB)	49.0 (A)
	BG	50.0 (A)	50.0 (A)	46.4 (A)	51.8 (AB)	52.0 (A)	52.0 (AB)	48.5 (B)	58.3 (AB)	56.1 (AB)	53.4 (A)	50.0 (A)	48.5 (A)	40.0 (B)	47.4 (A)
	TQ	50.0 (A)	50.0 (A)	47.0 (A)	44.7 (B)	44.7 (AB)	47.4 (BC)	50.0 (AB)	50.8 (BC)	52.0 (AB)	50.0 (A)	50.0 (A)	50.0 (A)	45.0 (AB)	49.0 (A)
	SC	50.0 (A)	50.0 (A)	50.0 (A)	50.0 (A)	50.0 (AB)	52.4 (A)	54.8 (AB)	53.8 (AB)	50.0 (BC)	50.0 (BC)	50.0 (A)	50.0 (A)	50.0 (A)	48.5 (A)
	TL	50.0 (A)	50.0 (A)	50.0 (A)	50.0 (AB)	51.0 (A)	59.0 (A)	57.0 (A)	60.0 (A)	60.0 (A)	54.8 (A)	53.9 (A)	51.0 (A)	45.0 (AB)	50.0 (A)
Transpar. (cm)	CTL	52 (A)	42 (A)	47 (A)	47 (A)	44 (A)	41 (A)	44 (A)	41 (A)	46 (A)	44 (A)	41 (A)	48 (A)	41 (A)	45 (A)
	BG	52 (AB)	45 (AB)	47 (A)	41 (A)	42 (A)	36 (A)	32 (B)	26 (C)	28 (B)	41 (A)	43 (A)	40 (B)	37 (A)	39 (AB)
	TQ	52 (A)	47 (A)	47 (A)	42 (A)	41 (A)	39 (A)	34 (B)	34 (AB)	32 (B)	40 (A)	38 (AB)	38 (AB)	38 (A)	35 (B)
	SC	51 (A)	45 (A)	45 (A)	43 (A)	41 (A)	39 (A)	33 (B)	31 (C)	41 (A)	41 (A)	38 (B)	43 (AB)	44 (A)	48 (A)
	TL	51 (A)	45 (A)	47 (A)	44 (A)	40 (A)	36 (A)	32 (B)	29 (C)	29 (B)	27 (B)	32 (B)	37 (B)	40 (A)	41 (B)

on small prey such as rotifers and *T. decipiens* nauplius. Only silver carp efficiently grazed *Cylindrospermopsis* filaments (Fig. 1).

Enclosure experiment

There were no significant differences in water temperature and dissolved oxygen among treatments (Table 1). Transparency in fish enclosures was significantly lower than control (fishless) after the middle of incubation (Table 2). Among fish treatments, silver carp generally showed higher transparency level. It might be a consequence of *Cylindrospermopsis* reduction in silver carp enclosures in comparison to other fish treatments. Almost all fish enclosures had higher conductivity than the control on 5 sampling dates



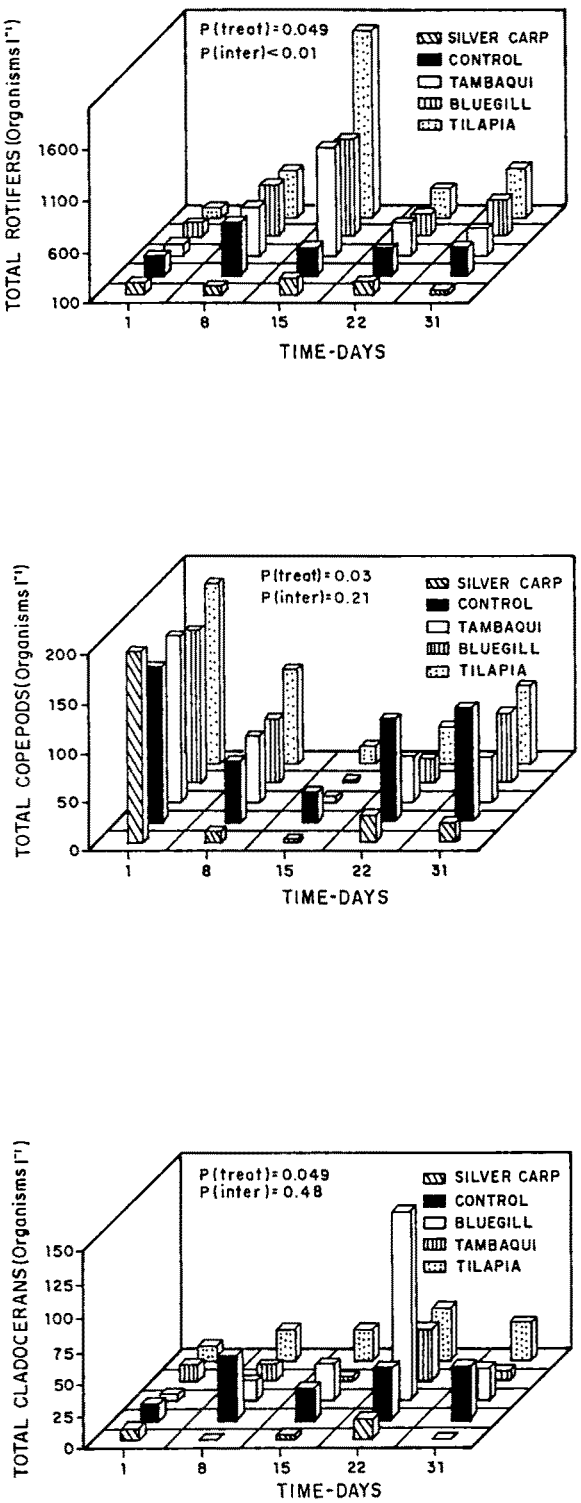


Fig. 3. Density of major zooplankton groups in each treatment during enclosure experiment. ANOVA probability values for treatment and interaction are given to the left of each histogram.

between 10 and 19 days of experiment. The pH was also higher in fish enclosures by the middle of incubation period (days 12, 15 and 17).

There was a great short-term increase in ammonia, total dissolved phosphorus and orthophosphate at 15 days in SC treatment due to partial decomposition of some dead fish before they were removed. But there were no differences in nutrients among treatments (Fig. 2).

In the enclosure experiment, where zooplankton community was numerically dominated by rotifers, there were significant differences among treatments for main zooplankton groups (Fig. 3). Copepods were significantly suppressed by silver carp in relation to TQ, TL and control treatments. Copepod reduction by silver carp was mainly a result of the suppression of nauplius rather than that of copepodites and adults, whose abundance was low during the experiment. Cladocerans, mainly *Diaphanosoma*, were also significantly suppressed by silver carp, as compared with BG, TL and control treatments. Total rotifer density did not vary significantly among treatments, probably due to short-term increases of *Brachionus calicyflorus* and *Rotaria sp.* reported for specific enclosures. However, total rotifer density excluding these two species (designated total rotifers*) varied significantly among treatments (Fig. 3). In accordance to laboratory selective grazing experiments, silver carp suppressed rotifers* while the presence of bluegill and tilapia was associated with increased rotifers density.

In the enclosure experiment, where phytoplankton was almost completely composed of *Cylindrospermopsis raciborskii*, the presence of fish did not significantly affect *Chlorella vulgaris*, *Cryptomonas sp.* and *Oscillatoria sp.* biomass (Fig. 4). As in selective grazing experiments, silver carp significantly suppressed *Cylindrospermopsis* biomass as compared with other fish species (Fig. 4).

Discussion

In the present study, no significant impacts of different planktivorous fish on nutrients were

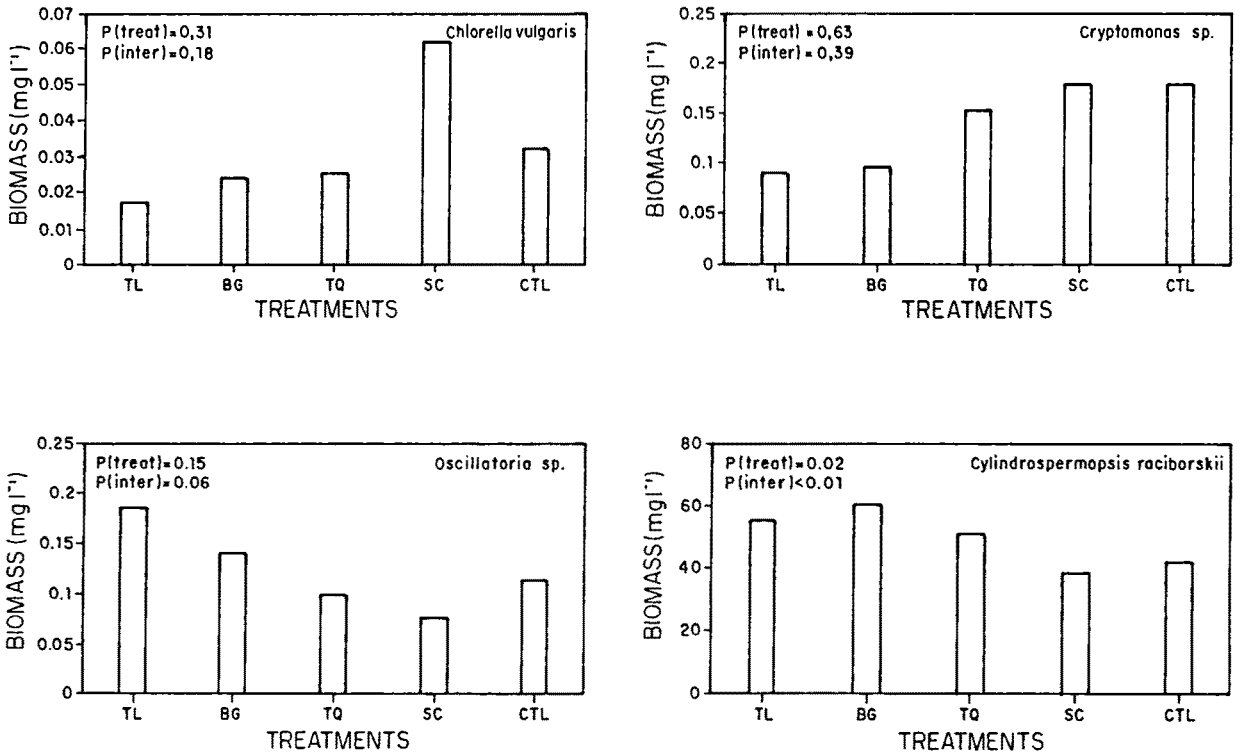


Fig. 4. Phytoplankton biomass in tilapia (TL), bluegill (BG), tambaqui (TQ), silver carp (SC) and control (CTL) treatments for enclosure experiment (n = 10 for *Chlorella*, *Cryptomonas* and *Oscillatoria* and n = 20 for *Cylindrospermopsis*). ANOVA probability values for treatment and interaction are given to the left of each histogram.

detected even in cases in which there was fish death and decomposition. Fish mortality is often associated with manipulations of planktivorous fish (Threlkeld, 1987). We found a high mortality of silver carp probably caused by the predation of birds on surface swimming fishes, as 3 herons (*Butorides striatus*) were captured by the net covering silver carp enclosure's fence. This high silver carp mortality in the limnocorrals produced high short-term increases of some nutrient concentrations (Fig. 2) that may have influenced other parameters like transparency and phytoplankton biomass. Short-term increases of nutrient concentrations and also changes in some water quality parameters such as phytoplankton counts, turbidity and Secchi depth are consequences of fish death and decomposition (Kushlan, 1974; Threlkeld, 1987). This could explain the significantly lower transparency level on two sampling dates of SC treatment relative to control, even though phytoplankton biomass was not different. In contrast, the other fish treatments, especially bluegill that was almost not affected by fish mortality, presented decreases in transparency indirectly by enhancing *Cylindrospermopsis* biomass in relation to control. Several studies (Arcifa *et al.*, 1986; Langeland *et al.*, 1987; McQueen & Post, 1988) also showed a reduction in transparency because of increased phytoplankton biomass in the presence of size-selective zooplanktivorous fish.

Another impact of this type of planktivore is an increase in small-bodied zooplankton, mainly rotifers (Hulbert & Mulla, 1981; Arcifa *et al.*, 1986; Langeland *et al.*, 1987). In our study, we observed an enhancement of rotifers in bluegill (particulate feeder) and tilapia enclosures. Although tilapias were not observed visually selecting prey in laboratory experiments, most of the time they displayed the unusual behaviour of collecting surface-floating prey (mainly *Bosmina*) rather than filter-feeding in the midwater. For this

reason, tilapia presented higher feeding rate constant for intermediate size zooplankton and lower for smaller prey such as rotifers (Fig. 1).

On the other hand, filter-feeding silver carp, as shown by feeding rate constant, strongly suppressed rotifers and also cladocerans and copepod nauplius. Drenner & McComas (1980) emphasized that zooplankton selection by omnivorous filter-feeding gizzard shad, *Dorosoma cepedianum*, is mainly a function of prey escape ability instead of filter apparatus properties. Although we did not measure the distance between gill rakers of experimental fishes, the silver carp fine mesh gill raker (8 μm according to Cremer & Smitherman, 1980;, 20 μm according to Boruckij, 1973 and 30–40 μm according to Spataru & Gophen, 1985) allows all reservoir rotifers, cladocerans and copepods to be retained by its filtering apparatus. In this situation, the selectivity of silver carp on zooplankton is governed by prey escape ability.

Kajak *et al.* (1977) suggested that copepod cyclopoid can avoid capture by filter-feeding silver carp. It is in accordance with our laboratory results, where silver carp had lower feeding rates on the cyclopoid *Thermocyclops decipiens* (in the stages of copepodites and adults), the most evasive large-bodied reservoir zooplankton. However, silver carp had high feeding rates on *Thermocyclops* nauplius and they were strongly suppressed in limnocorrals.

In the present study, where rotifers made up more than 50% of zooplankton density, a higher impact of filter-feeding fish on zooplankton in comparison with particulate feeder was expected from laboratory results (Fig. 1). In fact, among fish treatments, silver carp suppressed zooplankton the most (Fig. 3). Similar impact of silver carp on zooplankton was reported by Opuszynski (1979), Burke *et al.* (1986) and Vinyard *et al.* (in prep.).

Since reservoir zooplankton is generally considered unable to consume *Cylindrospermopsis* (Pinto-Coelho, 1983), the drastic suppression of all zooplankton groups by silver carp did not interfere directly by reducing zooplankton grazing pressure on this blue-green algae. However, the indirect effect resulting from the decrease of zooplankton grazing on nanophytoplankton may enhance production of small algae. We found an increase in *Chlorella vulgaris* (9 μm) and *Cryptomonas sp.* (15 μm) biomass in silver carp enclosures, even though statistically not significant (Fig. 4). However, it should be mentioned that some smaller nanoplankton and picoplankton organisms were not analyzed.

Despite the controversy on the lower level of particle size selected by silver carp gill racker mesh (8, 20 or 30 μm), we have evidence (gut content analysis, unpubl. material) indicating that *Chlorella vulgaris* and *Cryptomonas sp.* were very little consumed by silver carp. We expected a greater enhancement of *Chlorella* and *Cryptomonas* but this might have been prevented by unsuitable abiotic conditions in enclosures stocked with silver carp. All fish enclosures had high pH values during the experiment which except in silver carp enclosures, could be attributed to higher CO_2 removal because of increased phytoplankton production. In SC treatment where fish mortality influenced some chemical parameters, it is difficult to explain the mechanisms involved in the maintenance of high pH values in spite of an expected tendency of pH lowering from phytoplankton suppression by silver carp.

According to Moss (1972), the low CO_2 concentration resulting from high pH favours some algae species which are able to utilize CO_2 in very low concentrations or bicarbonate directly as a carbon source. Shapiro (1984) indicated a dominance of blue-green species in such situation and also showed, from experimental studies, a shift toward green algae when pH was artificially lowered. In our study, multiple regression analysis (unpubl. material) suggested a strong direct relation between pH and *Cylindrospermopsis* biomass.

Thus, the high pH values in silver carp enclosures may have influenced phytoplankton by favouring *Cylindrospermopsis* maintenance and preventing *Chlorella* and *Cryptomonas* enhancement. Opuszynski (1979) presented the same explanation for an unexpected reduction of nano-

phytoplankton in ponds stocked with silver carp.

In fact, we expected a greater suppression of *Cylindrospermopsis* biomass from high silver carp feeding rate on this blue-green algae. According to Lazzaro (1987), large elongated organisms such as long blue-green filaments become more vulnerable to retention on the branchial apparatus of filtering fishes. However, Kajak *et al.* (1977) found that although *Oscillatoria agardhii* trichomes (300–600 μm length and 6 μm diameter) and *Aphanizomenon flos-aquae* were highly ingested by silver carp, they were not digested. Unfortunately we did not investigate the digestibility of *Cylindrospermopsis* filaments by silver carp. If the ingested filaments were not well digested, they may have returned to the environment as additional nutrients to the remaining population. This might be another explanation for the absence of significative contrast between silver carp and control enclosures in *Cylindrospermopsis* biomass.

In addition to the pH effect, additional nutrient release from dead fish is another factor that might have prevented a greater suppression of this algae by silver carp. Drenner *et al.* (1986) also hypothetised that the phytoplankton enhancement in the presence of omnivorous, filter-feeding *Dorosoma* was probably due to additional nutrient supply by nutrient regeneration of living fish or by decomposition of fish that died during their experiment. Threlkeld (1988) concluded that intended addition of dead fish in enclosures on decomposition promoted increase in phytoplankton biomass. From our data, we cannot reject these hypotheses.

In summary, we consider that the final biomass of *Cylindrospermopsis* in silver carp limnocorrals might have resulted from a counteracting factors. The direct grazing by silver carp and also increased competition with nanophytoplankton by zooplankton removal might have been offset by additional supply of nutrients from dead fish and favorable chemical conditions (pH). We have also to consider the possible influence of the digestibility of ingested *Cylindrospermopsis* filaments which we did not investigate.

Although our study shows that silver carp might be able to control this algae biomass, information on other presupposed effects such as drastic nanophytoplankton enhancement as a consequence of zooplankton suppression and a better knowledge of fish relations in the food web of Paranoá Reservoir are required before its introduction in this ecosystem.

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