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Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil)

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SUMMARY

1. Exotic invasive species modify natural food webs in a way frequently hard to predict. In several aquatic environments in Brazil the introduction of *Oreochromis niloticus* (tilapia) was followed by changes in water quality. Yet, because of its rapid and easy growth, this fish has been used in many aquaculture programmes around the country.
2. To measure the effects of tilapia on the phytoplankton community and on water conditions of a large tropical reservoir in south-eastern Brazil (Furnas Reservoir), we performed two *in situ* experiments using three controls (no fish) and three tilapia enclosures (high fish density). Abiotic and biotic parameters were measured at 4 day intervals for 28 days.
3. Fish presence increased nitrogen (N) and phosphorus (P) availability (ammonium 260 and 70% mean increase – first and second experiment; and total phosphorus 540 and 270% mean increase) via excretion. Nutrient recycling by fish can thus be significant in the nutrient dynamics of the reservoir. The higher chlorophyll *a* concentration in the experimental fish tanks (86 and 34 $\mu g\ L^{-1}$, first and second experiment, respectively) was the result of a positive bottom-up effect on the phytoplankton community (approximately 2 $\mu g\ L^{-1}$ in the reservoir and control tank).
4. Because tilapia feed selectively on large algae (mainly cyanobacteria and diatoms), several small-sized or mucilaginous colonial chlorophyceans proliferated at the end of the experiments. Thus, the trophic cascade revealed strong influences on algal composition as well as on biomass.
5. Tilapia can contribute to the eutrophication of a waterbody by both top-down and bottom-up forces. In particular, by supplying considerable amount of nutrients it promotes the increase of fast growing algae. Tilapia must be used cautiously in aquaculture to avoid unexpected environmental degradation.

Keywords: eutrophication, *Oreochromis*, phytoplankton, selective feeding, tilapia, trophic cascade

Introduction

The trophic state of aquatic systems is controlled not only by external nutrient load, but also by the structure of the food web (Tátrai *et al*., 1990b; Tüzün & Mason, 1996; Starling, 1998). Based on this assertion, different studies have shown the potential of trophic chain biomanipulation as a strategy to improve water quality in lentic ecosystems (Tüzün & Mason, 1996; Starling, 1998). The trophic cascade concept as proposed by Carpenter, Kitchell & Hodgson (1985) motivated many of these studies, which demonstrated the existence of interactions among

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distant trophic levels. The cascade idea encouraged the search for keystone species or species groups, which can have a strong influence on the structure of an aquatic community. In this way, most of the work on biomanipulation has been developed to understand two key links: the size-selective zooplanktivorous fishes, and the large cladocerans. In theory, a decrease in the density of zooplanktivorous fishes should lead to an increase in cladoceran populations, resulting in the reduction of algal biomass and an increase in water quality. Although these tendencies have been observed in some experimental studies (Søndergaard *et al.*, 1990), trophic interactions are not so simple in natural environments (Lazzaro *et al.*, 2003). As shown by Carpenter *et al.* (1985), many natural systems consist of complex food webs that include trophic levels with a high number of species in the same guild, each species responding in a different way to the same environmental pressure (Lövgren & Persson, 2002) and having very different trophic effects in the food web.

The complexity of natural systems and the lack of a clear pattern in the results obtained from different studies led to doubts about the potential to improve water quality by biomanipulation (Matveev, Matveeva & Jones, 2000; Radke & Kahl, 2002). Although studies on biomanipulation have been rare in tropical systems, food web structure has generally been found to be distinct from that observed in temperate regions (Starling, 1993, 1998). In tropical regions, for instance, the zooplankton does not seem able to control algal biomass, a role that is played instead mainly by omnivorous, filter-feeding fishes (Komárková, 1998).

Many omnivorous filter-feeding tropical fishes are commercially important, both for sports-fishing and aquaculture, and they have been widely introduced into tropical aquatic systems. Often, exotic filtering fishes can modify water quality more strongly than native species of the same guild (Parkos, Santucci & Wahl, 2003). Because of the potentially negative effects of aquaculture on natural systems (Alongi *et al.*, 2003) and the potentially positive power of biomanipulation (Starling, 1998), it is critical to obtain a sound understanding of the interactions between fishes and the plankton community, in order to improve fish production and preserve water quality. Nevertheless, few studies have emphasised the effect of filtering fishes on water quality (Parkos *et al.*, 2003).

The Nile tilapia, *Oreochromis niloticus* Linnaeus, is an African omnivorous filtering fish, which is largely phytoplanktivorous. It is a globally common cichlid species, which has been introduced to tropical lakes and reservoirs and is important in aquaculture. Tilapia species are considered a problem in some Brazilian reservoirs, and the exclusion or control of their populations to improve water quality has been suggested by some researchers (Starling, 1998; Starling *et al.*, 2002; Lazzaro *et al.*, 2003). The cultivation of *O. niloticus* in net cages is increasing in Brazil, frequently without any control to assure preservation of water conditions. The reservoir of the hydroelectric power plant of Furnas is a system exposed to uncontrolled expansion of net cage aquaculture. This widespread activity is an important source of pollution of the reservoir and its consequences for water quality are just starting to be studied (Rocha, 2001). As lentic systems are more vulnerable to aquaculture than rivers (Alongi *et al.*, 2003) its potential effects need to be investigated. The main objective of our study was to measure the influence of high densities of *O. niloticus* on water quality and phytoplankton community composition in Furnas reservoir, so as to better understand the food web dynamics of the reservoir.

Methods

In situ experiments were performed in the Furnas reservoir in the province of Minas Gerais–Brazil. This hydroelectric reservoir has been in operation since 1963 and is one of the largest in the country, with a surface area of 1459 km^2, a volume of 22 950 km^3, mean depth of 16 m and a maximum depth of 90 m. The reservoir system is mostly oligo- to mesotrophic, but its dendritic morphology fosters eutrophic conditions in several small bays (Sá, 1994).

Two experiments of 28 days each (experiment 1: beginning of the rainy season, from 7 October to 4 November 1998, and experiment 2: beginning of the dry season, from 13 May to 10 June 1999) were run in a bay near the dam, where depth was about 60 m. All physical and chemical water variables were measured at 4 day intervals.

Each experiment was performed in six cylindrical enclosures of clear polyethylene, 0.9 m in diameter and 2.7 m in depth. They had a capacity of 2200 L, were closed at the bottom and open to the atmosphere at the top. A special support system was built to maintain the structure 30 cm above the water surface in order to avoid entry of lake water into the enclosure. The enclosures were covered with a net of 2.0 cm mesh size to keep predatory birds away and to prevent fish from escaping. We filled the enclosures with surface water by submersing them.

There were two treatments, each established in triplicate. Control enclosures (C) contained no fishes, whereas experimental tilapia enclosures (T) each received 10 tilapia of standard length about 13 cm. Mean fish biomass was 430 and 420 g m^{-3} in each tank, in the first and second experiments, respectively. Overall fish density in the reservoir is lower, but this high biomass is actually used in local fish farming net-cages and was necessary to estimate potential fish impacts. Before fishes were stocked in the experimental enclosures, they were kept for 24 h in 100-L containers where they received no food, allowing their intestines to be at least partially empty. All fishes were measured and weighed immediately before and after the experiments. The tilapia received no food during the experiment except for plankton naturally available in the water. All experimental fishes were supplied by the Hydrobiology and Pisciculture Station at Furnas (Furnas Centrais Elétricas S.A., Brazil).

For quantification of phytoplankton and analyses of physico-chemical variables, water samples were collected with a Van Dorn water sampler at 1.7 m depth in each enclosure and in the reservoir itself. Variables measured were temperature, pH (pH-meter Micronal B375), conductivity (standardised to 25 °C, Digimed DM31), transparency (Secchi disk) [when the Secchi depth was greater than the enclosure depth (2.4 m) we used total enclosure depth as a measure of transparency] and dissolved oxygen (by Winkler method on triplicate subsamples). Nutrients were measured by spectrophotometric methods on triplicate subsamples, and for dissolved nutrients water was prefiltered on a glass fibre filter (S&S GFA, pore size 1.2 μm; Schleicher & Schuell, Dassel, Germany). Samples were frozen until analysed following procedures described in American Public Health Association (1995). Precision level of the methods was 3 μg L^{-1} for soluble reactive phosphorus (SRP), 10 μg L^{-1} for total phosphorus (TP), 20 μg L^{-1} for ammonium, 5 μg L^{-1} for nitrate and 2 μg L^{-1} for nitrite. Chlorophyll concentration was determined by filtration onto 47 mm S&S GFA filters, and extraction and measurement followed Lorenzen (1967). Phytoplankton samples were preserved with Lugol's iodine. Counts were carried out under an inverted microscope by the Utermöhl technique. Algae were enumerated until at least 100 individuals per dominant species were recorded, giving a precision of ±20% within 95% confidence limits.

Climatic data (total rainfall and daily air temperature – minimum and maximum) were obtained from a meteorological station located about 500 m from the experimental site and provided by the company Furnas Centrais Elétricas S.A.

We compared changes in fish weight at the beginning and end of each experiment by paired *t*-test. The *t*-test was also used to compare climatic conditions between experiments. Within each experiment, differences between treatments T, C and R (reservoir) in physico-chemical and plankton biomass variables were tested using repeated-measures ANOVA (RMA) for the eight sampling days. Specific differences between treatments were identified by planned contrasts. We compared: (i) fish enclosures versus other treatments – 'fishless' and 'reservoir' – to identify the effect of tilapia on water quality variables, and (ii) enclosures without fish versus reservoir, to look for differences between the two controls.

Results

Climatic conditions, physico-chemical water properties, phytoplankton abundance and fish survival

In keeping with the neotropical savanna climate, total rainfall differed between the wet and dry seasons (*t*-test, $P = 0.01$) but maximum air temperature showed no significant seasonal change (*t*-test, $P = 0.18$). Water temperature was significantly different between the two experiments, although it was not affected by treatment (fish or no fish) (Tables 1 and 2).

Treatments had different effects on nitrogen (N) and phosphorus (P) concentrations. Ammonium in the control enclosures had values similar to those in the lake (Tables 1 and 2). However, a significant increase in both experiments (RMA, $P = 0.001$and 0.01, respectively for the first and second experiments) was observed in the tilapia enclosures over the first 2 weeks, followed by a gradual decline to the end of the experiment (Fig. 1a,b). The mean increases in ammonium in the first and second experiments were 260 and 70%, respectively.

Table 1 *F*-ratios, *P*-values and planned comparisons (contrast analysis) for repeated measures ANOVAS of experiment 1 data

	$F_{2,4}$	*P*-value	Planned comparisons (contrasts)
Water temperature	6.89	0.06	
PH	28.34	0.004*	T < (C, R); R = C
Secchi transparency	1858.8	<0.001*	T < (C, R); R > C
Dissolved oxygen	119.1	<0.001*	T < (C, R); R = C
Ammonium	59.75	0.001*	T > (C, R); R = C
Nitrite	2.93	0.16	
Nitrate	29.83	0.004*	T = (C, R); R > C
SRP	1.84	0.27	
Total-P	41.05	0.002*	T > (C, R); R = C
Chlorophyll *a*	73.24	<0.001*	T > (C, R); R = C

*Significant differences ($P < 0.05$) between treatments.
C, control enclosures; T, tilapia enclosures; R, reservoir.

Table 2 *F*-ratios, *P*-values and planned comparisons (contrast analysis) for repeated measures ANOVAS of experiment 2 data

	F_2,4	*P*-value	Planned comparisons (contrasts)
Water temperature	1.41	0.34	
pH	14.8	0.01*	T < (C, R); R < C
Secchi transparency	276.01	<0.001*	T < (C, R); R > C
Dissolved oxygen	29.8	0.004*	T < (C, R); R = C
Ammonium	16.87	0.01*	T > (C, R); R = C
Nitrite	7.66	0.04*	T > (C, R); R < C
Nitrate	40.18	0.002*	T > (C, R); R > C
SRP	1.51	0.32	
Total-P	9.21	0.032*	T > (C, R); R = C
Chlorophyll *a*	7.50	0.044*	T > (C, R); R = C

*Significant differences ($P < 0.05$) between treatments.
C, control enclosures; T, tilapia enclosures; R, reservoir.

The main form of N in Furnas reservoir was nitrate, but no differences were observed between the tilapia enclosures and the reservoir in relation to this variable (Fig. 1c,d; Tables 1 and 2). The control enclosures showed a gradual fall in nitrate concentration over time and very low levels at the end of the experiments (RMA, $P = 0.004$ and 0.002, for the first and the second experiments, respectively).

Concentrations of SRP were always low and were not affected by treatments (Tables 1 and 2). Concentrations of TP (Fig. 1e,f) remained approximately constant in the control tanks, but they increased significantly in the fish tanks (RMA, $P = 0.002$ and 0.032, for the first and second experiment, respectively).

Similar changes in TN : TP ratios were found in the tilapia enclosures in both experiments. We observed an increase in ratio in the middle of the experimental period and a sharp reduction in the final days (Fig. 1g,h). TN : TP in control enclosures was very similar to that in the reservoir throughout most of the study period, and at the end of both experiments the controls exhibited very low TN : TP ratios (Fig. 1g,h).

Chlorophyll *a* concentration did not change significantly in the control tanks (Tables 1 and 2). However, it was considerably enhanced by the presence of tilapia (Fig. 2a,b; Tables 1 and 2), reaching values as high as 86 and 34 $\mu g\ L^{-1}$ in the first and second experiments, respectively.

Water transparency (Fig. 2c,d) was also affected significantly by the presence of tilapia, showing a strong reduction ($P < 0.001$) in both experiments (Tables 1 and 2). Although oxygen concentration did not change in the control enclosures in relation to the reservoir, it was significantly different in the tilapia enclosures (Tables 1 and 2). In the latter DO fell significantly at the beginning of the experiments but then increased so that the initial oxygen conditions were re-established (Fig. 2e,f).

A significant difference in pH between the control enclosures and the reservoir was observed in the second experiment only (RMA, $P = 0.01$; Table 2). However, differences were very small and were the result of a pH decrease in the reservoir and not an increase in the control tanks (Fig. 2g,h). In the tilapia enclosures (Fig. 2g,h) the general pattern was for an initial decrease followed by a gradual increase until the end of each experimental period (RMA, $P = 0.004$ and 0.01, for the first and second experiments, respectively).

Tilapia survival during the experiments was 100%. Fish biomass decreased by between 5 and 10% in both experiments (*t*-test, $P < 0.05$). Replicates were quite uniform for most of the measured parameters both among treatments and between the first and second experiments.

Phytoplankton community structure

The phytoplankton community of Furnas reservoir differed in composition during the two experiments, consonant with normal changes between wet and dry seasons. The first experiment (Fig. 3) started with a Cyanobacteria-dominated community (60% of indi-

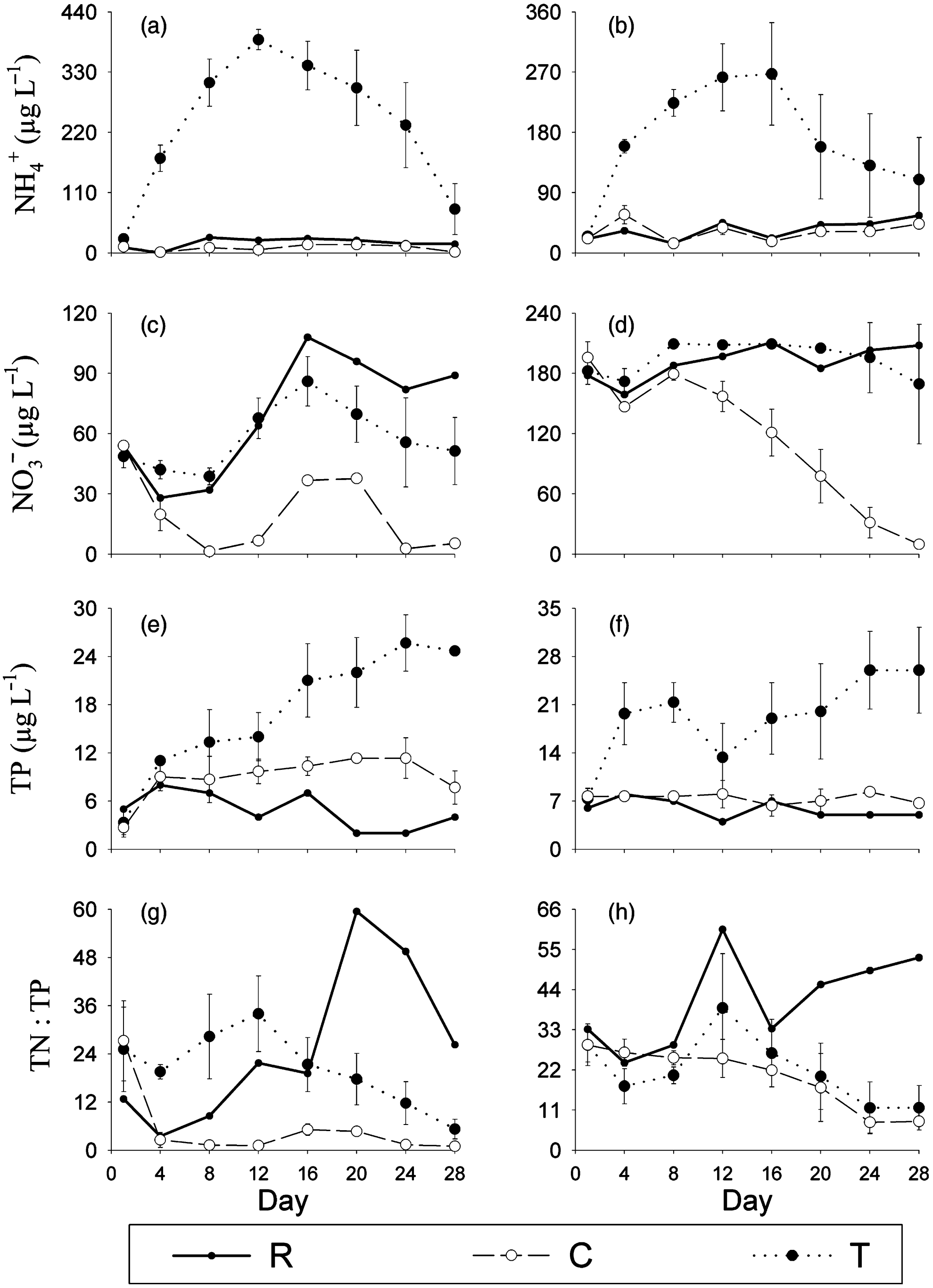

Fig. 1 Variation in nutrient concentrations and N:P ratio during the 28-day experiments [(a), (c), (e) and (g) = experiment 1; (b), (d), (f) and (h) = experiment 2; T, tilapia enclosure; C, control enclosure; R, reservoir]. All data are means of three replicates ±SD (bars that are no visible are hidden by the symbols).

viduals), with Chlorophyta subdominant (30%). The second experiment began with Chlorophyta dominance (approximately 50%), but with a high contribution of Cyanobacteria, Bacillariophyta and Dinophyta/Cryptophyta species (Fig. 4). On the first day of each experiment phytoplankton community structure in the enclosures was similar to that in the reservoir (Figs 3 & 4). Community structure remained stable in the reservoir throughout the experimental periods (Figs 3 & 4).

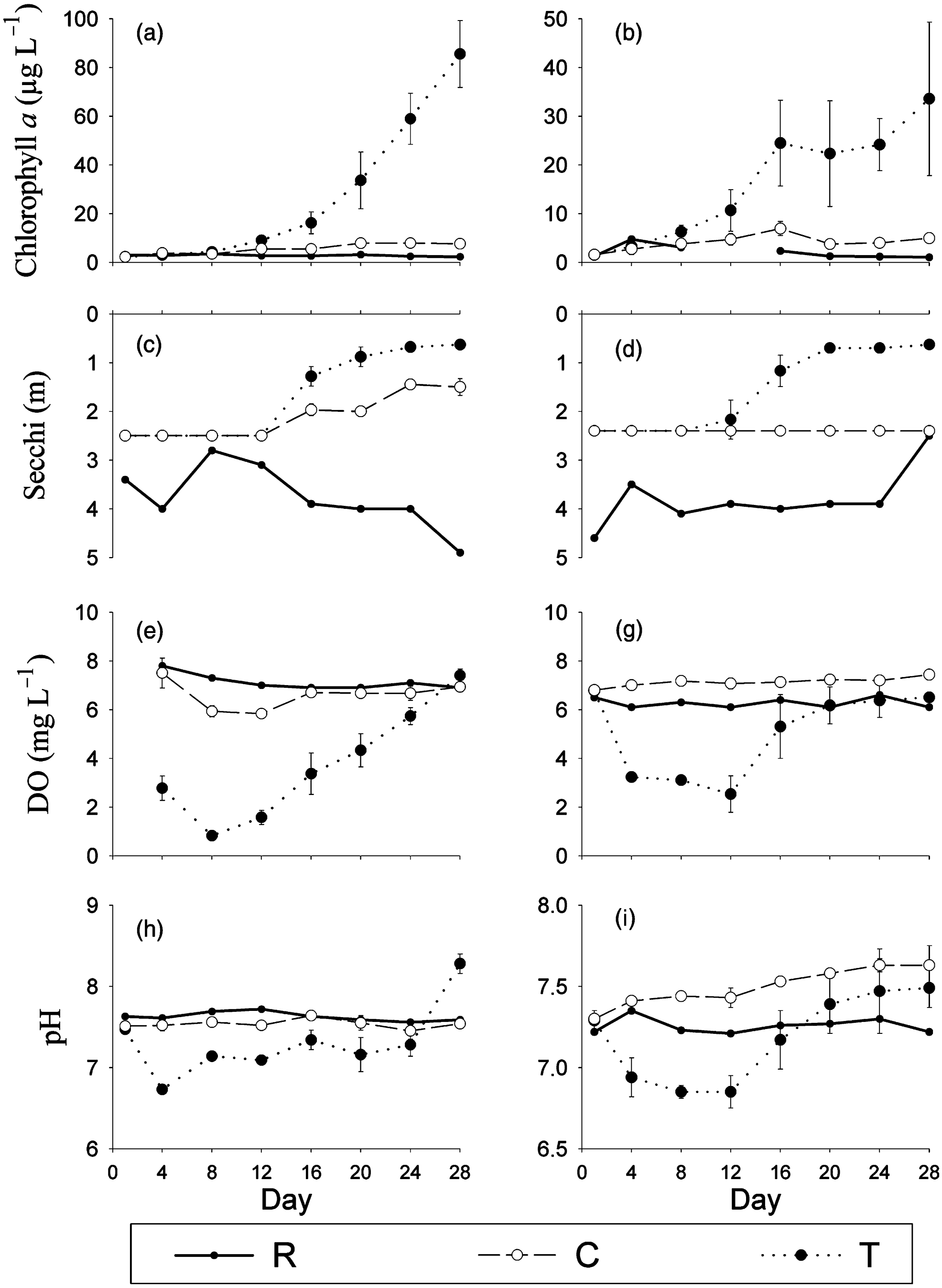

Fig. 2 Variation in chlorophyll *a* content and physical and chemical parameters during the experiments [(a), (c), (e) and (g) = experiment 1; (b), (d), (f) and (h) = experiment 2; T, tilapia enclosure; C, control enclosures; R, reservoir). All data are means of three replicates ±SD (bars that are no visible are hidden by the symbols).

Responses of the different algal groups were similar in the two experiments, as follows. First, cyanobacteria were excluded or drastically reduced in all enclosures, but the process was accelerated in the tilapia tanks. Cyanobacteria in our experiments were represented by large colonial and filamentous species. Following their decrease Cyanobacteria did not reappear, even in the fish enclosures, despite the fact that nutrients increased greatly in concentration (Fig. 1).

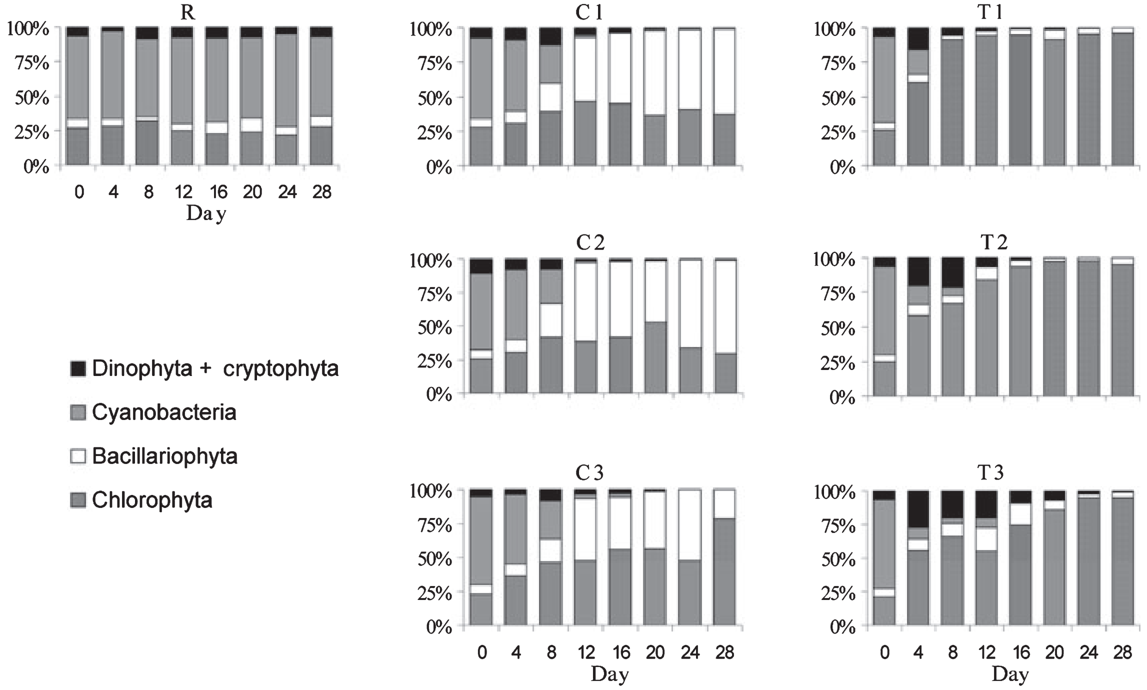

Fig. 3 Phytoplankton community structure in the reservoir (R), control enclosures (C) and tilapia enclosures (T) during experiment 1.

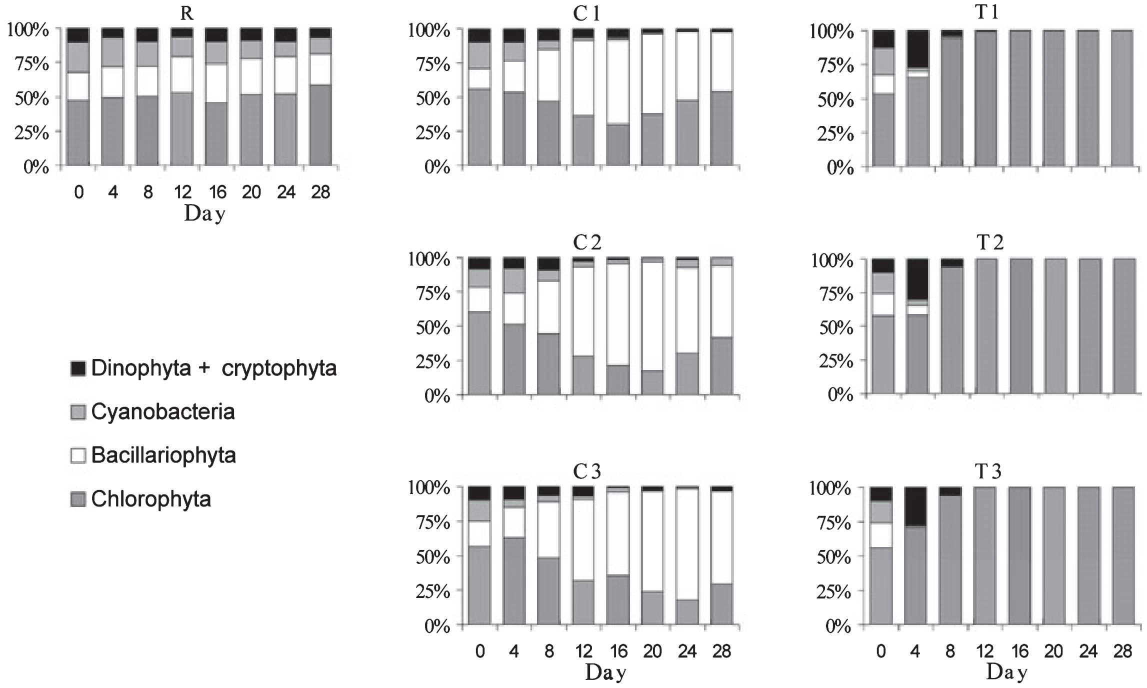

Fig. 4 Phytoplankton community structure in the reservoir (R), control enclosures (C) and tilapia enclosures (T) during experiment 2.

Chlorophyta, however, decreased or remained constant only in the control enclosures. In the tilapia enclosures they became dominant and made up almost 100% of total individuals (Figs 3 & 4). The experimental conditions (water isolation and presence of tilapia) also affected the relative abundance of diatoms (Bacillariophyta; Figs 3 & 4), which became dominant in the control tanks but were relatively less important in the tilapia enclosures (Figs 3 & 4). Dinophyta and Cryptophyta generally were modestly represented, but there was a clear trend for an increase in their densities in the tilapia enclosures early in each experiment, and a decline towards the end (Figs 3 & 4).

The presence of fish also affected the species composition and size structure of the phytoplankton community, with the greatest changes taking place within the Cyanobacteria and Chlorophyta. At the beginning of the experiments the most abundant species were large such as *Cylindrospermopsis raciborskii* Woloszynska (mean length 85 μm), which was dominant in experiment 1 and subdominant in experiment 2. At the end, small chlorophyceans (diameter <8 μm, as *Chlorella vulgaris* Beijerinck, *C. saccharophila* Krüger and one species of *Scenedesmus* Meyen) were favoured in the tilapia enclosures where they achieved more than 98% dominance (Table 3).

Discussion

The relative importance of 'top-down' and 'bottom-up' forces in controlling algal communities is still unclear (Søndergaard *et al.*, 1990). Focusing on two components of the aquatic community, phytoplanktivorous fishes and phytoplankton, our experiments showed how both forces could contribute to increasing algal biomass. The bottom-up and top-down model proposed by McQueen, Post & Mills (1986) and McQueen *et al.* (1989) suggested that the influence of the top of the chain on the lower level community constituents would be less significant in eutrophic environments. At the beginning of our experiments water conditions in Furnas reservoir were oligotrophic, a situation in which nutrients are generally very important in defining aquatic community structure (McQueen *et al.*, 1986), and algae may show a rapid response to fish excretion (Proulx *et al.*, 1996). Excretion or fish death and decomposition can both result in higher nutrient concentrations (Threlkeld, 1988; Attayde & Hansson, 2001). In our experimental enclosures, tilapia enhanced algal biomass and the state of eutrophication by promoting P and N recycling in the water.

The indirect influence of fish on phytoplankton through nutrient excretion may surpass the top-down pressure via a trophic cascade (Threlkeld, 1988), causing an increase in chlorophyll concentration in experimental enclosures containing zooplanktivorous,

Table 3 Changes in the relative abundance of dominant phytoplankton species during the two experiments

	Dominant species [relative abundance (%)]			
	7 October 1998	15 October	23 October	4 November
Experiment 1				
R	*Cylindrospermopsis raciborskii* (32)	*C. raciborskii* (41)	*C. raciborskii* (34)	*C. raciborskii* (33)
C1	*C. raciborskii* (44)	*C. raciborskii* (21)	*Cyclotella* sp (46)	*Synedra* sp. (50)
C2	*C. raciborskii* (40)	*Cyclotella* sp. (22)	*Cyclotella* sp. (47)	*Synedra* sp. (62)
C3	*C. raciborskii* (45)	*C. raciborskii* (17)	*Spondylosium papillosum* (31)	*S. papillosum* (51)
T1	*C. raciborskii* (39)	*C. vulgaris* (67)	*C. vulgaris* (36)	*Monoraphidium komarkovae* (37)
T2	*C. raciborskii* (42)	*C. vulgaris* (28)	*Scenedesmus* sp. (47)	*M. komarkovae* (34)
T3	*C. raciborskii* (45)	*C. vulgaris* (20)	*Cyclotella* sp. (16)	*Tetrallantos lagerheimii* (24)
	13 May 1999	21 May	29 May	10 June
Experiment 2				
R	*Chlorella vulgaris* (18)	*C. vulgaris* (17)	*Cyclotella* sp. (20)	*C. vulgaris* (18)
C1	*C. vulgaris* (21)	*Rhizosolenia* sp. (18)	*Cyclotella* sp. (36)	*S. papillosum* (22)
C2	*C. vulgaris* (21)	*Cyclotella* sp. (22)	*Rhizosolenia* sp. (50)	*Synedra* sp. (22)
C3	*C. vulgaris* (24)	*Cyclotella* sp. (28)	*Cyclotella* sp. (44)	*Cyclotella* sp. (43)
T1	*C. vulgaris* (20)	*Chlorella saccharophila* (87)	*C. saccharophila* (99)	*C. saccharophila* (98)
T2	*C. vulgaris* (24)	*C. saccharophila* (87)	*C. saccharophila* (99.6)	*C. saccharophila* (99)
T3	*C. vulgaris* (20)	*C. saccharophila* (87)	*C. saccharophila* (99)	*C. saccharophila* (99.7)

R, reservoir; C, control enclosures; T, Tilapia enclosures.
Authorities for species not cited in the text: *M. komarkovae* Nygaard, *S. papillosum* West & G.S. West, *T. lagerheimii* Teiling, *Cyclotella* Kützing, *Synedra* Ehrenberg, *Rhizosolenia* Brightwell.

omnivorous or benthivorous fishes (Mazumder *et al.*, 1988; Tátrai *et al.*, 1990a; Drenner *et al.*, 1998; Angeler *et al.*, 2002; Lazzaro *et al.*, 2003). However, few authors have paid much attention to potential bottom-up forces, and have related their results to trophic cascade effects that may not be the main driving forces promoting phytoplankton growth.

From the beginning of our experiments ammonium, the main nitrogenous excretion compound in fishes, increased in the experimental fish tanks. After a few days, however, ammonium was consumed completely by the growing phytoplankton, as previously observed by Karjalainen, Seppälä & Walls (1998) and Angeler *et al.* (2002) in similar experiments. Both ammonium and nitrate are potential N sources for algae (Karjalainen *et al.*, 1998), although ammonium at high concentrations might inhibit nitrate assimilation by phytoplankton and it is generally used first because of its energetic advantage in the assimilation process (Mallet, Charpin & Devaux, 1998). In the tilapia enclosures nitrate consumption occurred only after total depletion of ammonium, but it decreased faster in the control enclosures, where nitrate was the main N source.

Through excretion (Mazumder *et al.*, 1988; Attayde & Hansson, 2001) and sediment resuspension (Scheffer, Portielie & Zambrano, 2003) the role played by fish in the P dynamics of a waterbody may be more important than allochthonous inputs (Starling, 1998). Tilapias have high excretion rates of SRP (Starling, 1998) that can be assimilated and accumulated rapidly by algae (‘luxury consumption’). As found by Angeler *et al.* (2002) and Lövgren & Persson (2002), the increase in algal biomass at the end of all our experiments resulted in high P consumption and consequently lower SRP concentration in fish enclosures. TP however, showed a constant increase in the fish enclosures until the end of the experiments, confirming the role of tilapia as an important P source.

Additional changes also registered in similar biomanipulation experiments were observed in our fish enclosures. A reduction in water transparency for instance (Fig. 2) is expected in such enclosures (Mazumder *et al.*, 1988; Drenner *et al.*, 1998; Starling, 1998; Radke & Kahl, 2002; Parkos *et al.*, 2003) as a consequence of massive phytoplankton growth and suspended faecal pellets. Oxygen concentration was very low in the fish enclosures at the beginning of the experiments, because of the high consumption rates by tilapia. However, as *O. niloticus* is highly resistant to low oxygen levels (Fernandes & Rantin, 1986) it survived these critical periods. Later, growth of algal biomass regenerated O_2 supplies, decreased CO_2 concentration and increased pH. In a study on the impact of net cages containing seabass (*Lates calcarifer* Bloch) on water quality in two mangrove estuaries in Malaysia, Alongi *et al.* (2003) found a similar correlation among O_2, CO_2 and pH.

Even with no significant modification of total biomass, top-down effects of tilapia can alter relative phytoplankton species abundances (Tátrai *et al.*, 1990a), thereby modifying phytoplankton community structure (Ramcharan, France & McQueen, 1996). Attempts to predict effects of fish predation on species composition and richness in phytoplankton are rare (Northcote, Arcifa & Munro, 1990). Changes in the size structure of algal populations by omnivorous and herbivorous filter-feeding fishes can occur indirectly by selective capture of zooplankton (Northcote *et al.*, 1990; Ramcharan *et al.*, 1996; Komárková, 1998), or more directly by size selective ingestion of particular algal species (Lazzaro, 1987; Turker, Eversole & Brune, 2003). Food is not selected visually by filter-feeding fishes (Lazzaro, 1987), however the ability of some algae to avoid ingestion or digestion can lead to changes in community structure (Søndergaard *et al.*, 1990; Turker *et al.*, 2003). Species able to escape grazing grow better when released from competition with more vulnerable species (Lövgren & Persson, 2002). As a consequence of these processes, total algal biomass did not decrease and chlorophyll concentrations were higher in our fish enclosures (Fig. 2), although species composition and diversity showed significant changes (Figs 3 & 4).

There is no general consensus about the effect of fishes on Cyanobacteria in biomanipulation experiments. They were excluded from all our experimental tanks, but Tátrai *et al.* (1990a)) observed an increase in the biomass of this group in enclosures containing the benthivorous fish *Abramis brama* Linnaeus. In contrast, Turker *et al.* (2003) registered a decrease in Cyanobacteria abundance as a consequence of grazing by *O. niloticus*. Starling (1993) observed that the carp *Hypophthalmichthys molitrix* Valenciennes brought about the decline of several species of cyanobacteria in Paranoá Lake (Brazil). In this lake, the carp did not modify total cyanobacteria biomass, because it could not alter the abundance of the dominant species

C. raciborskii. When studying the effects of tilapia, Starling (1998) on the other hand found that high fish densities substantially increased the biomass of *Microcystis aeruginosa* (Kützing, 1846), while diminishing the population of *Cylindropermopsis raciborskii*.

In our study, the consumption of cyanobacteria by tilapia must have been the main cause of their decrease in the experimental tanks. In many systems the abundance of cyanobacteria is ascribed to the inefficiency of filtering fishes in digesting and assimilating them as a food source, as they often have low nutritional value and resist the predation of many fish species (see review of Lazzaro, 1987). Tilapia, however, are considered efficient cyanobacterial consumers thanks to their ability to digest them at very low stomach pH (1.25) (Lazzaro, 1987). Although cyanobacteria frequently dominate eutrophic environments, their abundance did not increase in our fish enclosures despite the higher nutrient concentration. The absence of cyanobacteria from the fish enclosures may also have been a result of their lower growth rates compared with those of chlorophyceans. Thus, after their initial reduction by fishes, they may have been unable to recover in an environment dominated by other fast-growing species.

It is also possible that the tilapia in our experiments fed more intensively on cyanobacteria because of their greater size. The most abundant cyanobacteria species in Furnas reservoir was the filamentous *C. raciborskii* (Table 3), followed by the colonial *Epigloeosphaera brasilica* Azevedo et al., each of which could be caught by the tilapia filtering system. Selective ingestion of large cyanobacteria by fishes was observed by Lazzaro (1987), and was reported for *O. niloticus* by Turker *et al.* (2003). Because of the selectivity determined by the mesh size of their gill rakers, *O. niloticus* preferentially feeds on bigger algae, and has a low capacity to capture algal species smaller than 8 μm (Turker *et al.*, 2003) and consequently reducing their biomass.

The decrease in Cyanobacteria in control enclosures was not explained by a change in the N : P ratio, as this variable did not change at the beginning of the experiment when the cyanobacteria disappeared. Therefore, other factors must have affected cyanobacterial growth. Vertical migration into a nutrient-rich hypolimnion, for instance, can provide an important competitive advantage for these organisms (Ganf & Oliver, 1982) and isolation from the deeper zone of the lake in our experimental enclosures may have contributed to their exclusion in all treatments.

Among the chlorophyceans that became abundant in the fish enclosures were several species that seemed to resist tilapia predation through the possession of mucilaginous sheaths, thick cell walls and/or reduced size. Some chlorophycean species cannot be digested and pass intact throughout the digestive tract (Moriarty & Moriarty, 1973; Getachew & Fernando, 1989), thanks to the protection against digestive enzymes given by thick cellulose cell walls (Vörös *et al.*, 1997) and gelatinous cover (Porter, 1977; Lazzaro, 1987). Furthermore, small algae can escape passively from grazer pressure, and become dominant. An increase in biomass of green algae is generally associated with fish presence (Northcote *et al.*, 1990; Turker *et al.*, 2003). *Oreochromis niloticus*, for example, is efficient at digesting cyanobacteria (Lazzaro, 1987) but not chlorophyceans (Moriarty & Moriarty, 1973; Getachew & Fernando, 1989), which, by avoiding fish pressure are likely to dominate. In addition to grazing resistance, their growth in our experimental enclosures was supported by the high N and P concentrations. Probably because their higher growth rates, green algae can dominate in eutrophic environments, particularly small, highly enriched waterbodies, with relatively high levels of N (Reynolds, 1984), as found in the fish enclosures.

An increase in diatoms as found in the fishless tanks has also been described in other biomanipulation studies (Northcote *et al.*, 1990; Proulx *et al.*, 1996). In conditions of low P concentration, such as those in the control enclosures, diatoms generally show competitive advantages because of their lower demand for P (Smith, 1983) and strong capacity to store this nutrient (Karjalainen *et al.*, 1998). *Oreochromis niloticus*, however, is an efficient predator of large diatoms, which can constitute an important item of its diet (Spataru & Zorn, 1978; Getachew & Fernando, 1989). Thus two main factors may be related to the lack of increase in the relative abundance of diatoms in the fish enclosures: the reduction of their competitive superiority at high nutrient concentrations and the predatory pressure exerted by fishes.

According to the McQueen model, top-down forces should be stronger at higher trophic levels and bottom-up forces should be stronger at the base of the food chain. The food chain incorporating tilapia and phytoplankton is very short, and in our experiments, both forces were important in determining the responses of the phytoplankton to fish presence. The

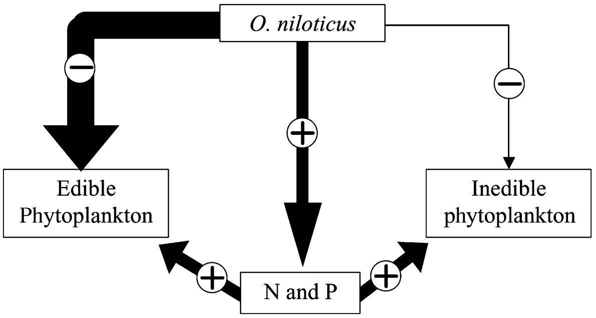

Fig. 5 Schematic summary of the impact of *Oreochromis niloticus* on the phytoplankton community of Furnas reservoir.

increase in phytoplankton biomass was a consequence of tilapia excretion (bottom-up), however, because of selective grazing, the top-down response was more than a simplified cascade of linear events. Fish-grazing affected the structure of the phytoplankton community as a result of differences in species vulnerability but alone it was not sufficient to decrease total phytoplankton biomass (Fig. 5).

Our study has demonstrated that environmental problems may arise in aquatic environments after the introduction of *O. niloticus*. In habitats with low water renewal time (Alongi *et al.*, 2003), such as the littoral bays of the Furnas reservoir, impacts can be severe. The use of net cages is spreading rapidly in these bays and cultivation methods, especially the daily addition of food, may quicken environmental damage. Furthermore, the feeding activity of tilapia on sediments (Getachew & Fernando, 1989) may exacerbate the changes being an additional nutrient source to the water column (Angeler *et al.*, 2002; Scheffer *et al.*, 2003; Parkos *et al.*, 2003).

We have shown that the complexity of trophic interactions, combined with the particular characteristics of specific players, can lead to unique and unpredictable results. Earlier studies have verified the utility of phytoplanktivorous fishes to control and remove some dominant cyanobacteria in eutrophic reservoirs (Starling, 1993, 1998; Turker *et al.*, 2003), and our results were consistent with them. However, apparently encouraging results have to be assessed carefully. Nutrient inputs by fishes to oligotrophic systems, for instance (like many sites in the Furnas reservoir), ultimately will result in degradation of water quality. Additionally the top-down removal of cyanobacteria, diatoms and other large sized species in these low-biomass systems may result in proliferation of small, faster-growing algae like chlorophyceans. Therefore because of the negative consequences of tilapia introduction, this form of biomanipulation may not be a successful tool for water management.

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