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Contribution of omnivorous tilapia to eutrophication of a shallow tropical reservoir: evidence from a fish kill

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SUMMARY

1. We examined whether a large stock of tilapia (>750 kg ha^{-1}, in littoral areas >1300 kg ha^{-1}), mostly *Oreochromis niloticus* (L.) and *Tilapia rendalli* (Boulenger), could contribute to the eutrophication of a tropical reservoir (Lago Paranoá, Brasília, Brazil) by enhancing P-loading.
2. We took advantage of an extensive fish kill (>150 tons removed) during May–August 1997 in a hypereutrophic branch of the reservoir to compare water quality characteristics 1 year before and after this event by means of BACI statistics. We also measured P-excretion rates in laboratory trials to assess the P-loading of the reservoir by the tilapia relative to tributary inputs and loading from a sewage treatment plant.
3. Concentrations of chlorophyll *a* (decline from 84 to 56 μg L^{-1}, $P = 0.018$) and total P (decline from 100 to 66 μg L^{-1}, $P < 0.001$) decreased significantly in the branch of the reservoir affected by the fish kill, compared with a similar but unaffected branch that served as a control. Because P-loading by both a sewage treatment plant and tributaries remained high after the incidence, the fish kill was likely to contribute to the observed water quality improvement.
4. Removing 150 tons of dead tilapia corresponded to 20 days of external total phosphorus load (TP-load) to the branch, and resulted in a reduction of 5.1 kg P day^{-1} in internal recycling via tilapia excretion, which is equivalent to 12% of the external TP-load.
5. Implementing professional tilapia cast-net fisheries could be an efficient biomanipulation approach to improve water quality and limit the occurrence of cyanobacteria blooms and fish kills in hypereutrophic branches of Lago Paranoá and similar tropical lakes.

Keywords: biomanipulation, echosounding, eutrophication, fish winterkill, tilapia

Introduction

Omnivorous cichlids often dominate fish communities in warm-water lakes and reservoirs. They have a much greater carrying capacity than visually feeding planktivores, reaching a high biomass (>1000 kg ha^{-1}) and production in eutrophic systems (Fernando, 1994; Lowe-McConnell, 2000). Tilapias (>70 species) are particularly successful (Kolding, 1993), because of their plasticity in feeding behaviour, which enables them to exploit mixed food sources. Adaptive traits such as year-round spawning, parental brood care, and highly flexible growth rate and maturation size facilitate adjustment of these fishes to various environmental conditions.

Enclosure and small-scale field experiments have demonstrated that high stocks of omnivorous fishes contribute to sustaining eutrophication by enhancing nutrient cycling (Starling & Lazzaro, 1997; Datta &

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Jana, 1998; Starling, 1998). Consequently, controlling tilapia abundance to reduce the internal nutrient loading of lakes should receive special attention to manage tropical and subtropical eutrophic lakes and reservoirs. However, whole-lake studies indicating that tilapia indeed affect nutrient cycling under field conditions are virtually lacking. One way to test this hypothesis is to assess changes in water quality following natural fish kills (Vanni *et al.*, 1990), which are quite common in shallow warm-water lakes (Brinkmann & Santos, 1973; Ochumba, 1990).

We took advantage of a large-scale natural fish kill in a shallow hypereutrophic tropical reservoir to address two objectives: (a) evaluate the effects of fish mortality and subsequent removal of fish biomass on eutrophication, and (b) estimate the contribution of internal nutrient loading mediated by tilapia compared with external loading. During 1 year before and after the fish kill, we compared total phosphorus (TP) concentrations, loadings of TP, and chlorophyll *a* concentrations between two hypereutrophic branches of the reservoir. One branch was affected by the fish kill, whereas no mortality occurred in the other branch, which served as a control. We computed the direct contribution of the tilapia population to internal P-loading, and we also calculated the internal P-loading prevented by the removal of dead fish. To do so, fish biomass estimates from a comprehensive echosounding survey were combined with information on tilapia size-structure derived from simultaneous gillnet catches and with P-excretion rates of tilapia measured in laboratory trials.

Methods

Study site

Lago Paranoá is a shallow eutrophic reservoir (area 38 km^2, volume 498×10^6 m^3, mean depth 14 m) created in 1959 when Brazilia, the capital of Brazil, was built. In 1997, mean water residence time was 0.82 years, conductivity 20–100 µSi cm^{-2}, the TP concentration 48 µg L^{-1}, the total nitrogen (TN) to TP (TN : TP) ratio 30 : 1, the concentration of chlorophyll *a* 58 µg L^{-1}, and primary productivity 662 g C m^{-2} year^{-1}. Brazilia's population was expected to reach 0.5 million inhabitants in 2000, but has now passed 2 millions. The two sewage plants located at the southern and northern ends of the plane-shaped pilot plan of Brazilia (Fig. 1) were unable to treat all sewage produced. Lago Paranoá hence suffered from accelerated eutrophication resulting from the input of both raw and inadequately treated sewage. Phytoplankton became dominated by cyanobacteria, mainly *Microcystis aeruginosa* (Kützing) Kützing and *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju. Blooms were prevented by copper sulphate addition. The zooplankton community became dominated by rotifers (500–700 ind. L^{-1}, mainly *Brachionus*, *Keratella*, *Anuraeopsis*, *Trichocerca* and *Polyarthra* species) that exert little grazing pressure on the dominant algae. Exotic omnivorous fish species, such as Nile tilapia (*Oreochromis niloticus* Linnaeus) and Congo tilapia (*Tilapia rendalli* Boulenger) and benthivorous common carp (*Cyprinus carpio* L.) were introduced in the 1960s. They dominate the fish community today. Since 1993, the Brazilia Water and Sewage Corporation (CAESB) has reduced the external nutrient loading by 70%, using an advanced tertiary treatment with biological removal of P and N (Cavalcanti *et al.*, 1997). Nevertheless, over three decades of intensive discharge by the two sewage plants, a layer of organic sediment (sludge) up to 3 m thick has accumulated upstream of the two branches of the reservoir that receive the sewage plant effluents (Fig. 1).

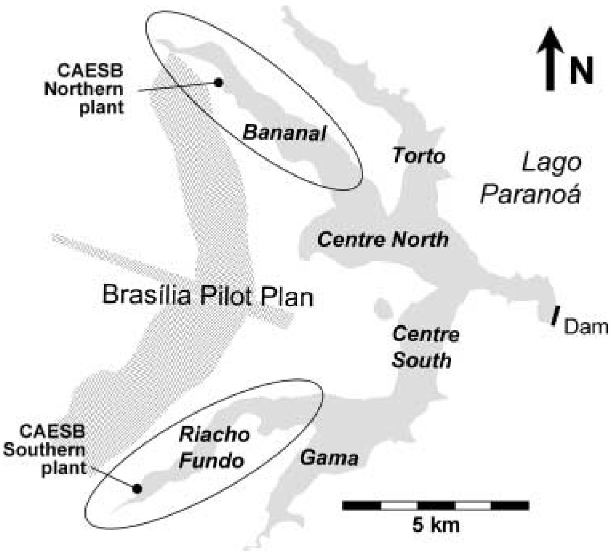

Fig. 1 Map of man-made Lago Paranoá showing the Riacho Fundo and Bananal branches, the other four regions of the reservoir, and the two sewage treatment plants, in relation to Brasília's plan-shaped pilot plan.

Massive fish mortality

From May to September 1997, an extensive fish kill occurred upstream in Riacho Fundo, one of the two most eutrophic branches of Lago Paranoá, and extended downstream. From all fishes lost from the system and allowed to decompose, a total of 150 tons were manually removed from the reservoir, mostly tilapias. During this winter, prior to the fish kill, air temperature during the night had dropped to 12 °C and difference between day and night increased abruptly from 1.5 to 7.4 °C. This rapid cooling provoked a vertical circulation of the water column that brought sediment organic matter and increased gas emission in the epilimnion, such as methane in the epilimnion, increasing the oxygen demand. Less pronounced fish kills mediated by oxygen depletion had been previously recorded in Lago Paranoá in 1981, 1982, 1987, 1988, 1989 and 1993. Compared with previous years, the 1997 mortality was larger, in part because of a strong pulse in P-loading a few weeks before the event resulting from operational problems in the active sludge system in the sewage treatment plant (CAESB, unpublished data). The intensified enforcement of the ban of cast-net fishing also may have contributed to an increase in tilapia biomass from 1995 to 1997 (Walter, 2000) and thus enhanced the magnitude of the die-off.

BACI approach

We chose a statistical approach called BACI (Before, After, Control and Impact), which is suited for detecting effects in non-replicated situations (Stewart-Oaten, Murdoch & Parker, 1986). This approach uses *t*-tests to compare the differences between the 'Impact' (Riacho Fundo) and 'Control' (Bananal) sites of variables measured before and after an incidence.

We applied this procedure to TP and chlorophyll *a* concentrations measured weekly and to densities of total zooplankton and macrozooplankton determined monthly. We sampled the Riacho Fundo and Bananal branches (Fig. 1) at midlength at 1-m depth. External TP-loading was recorded daily by CAESB at the Southern and Northern treatment plants during the year before (May 1996 to April 1997) and after the fish kill (October 1997 to September 1998). The average discharge of the tributaries and their TP concentrations were monitored on a weekly basis to calculate the total point-source loadings. Overall external TP-loadings were computed as the sum of the loadings from the sewage plant and the tributaries. Diffuse loadings in this urban branch of the reservoir is of limited importance as they contribute <15% to the total external input (Cavalcanti *et al*., 1997). Zooplankton densities and TP and chlorophyll *a* concentrations were determined following APHA's (1998) standard methods.

P-excretion laboratory trials

We used the maximum P-excretion rates of tilapia measured by Starling (1998) in laboratory trials. P-concentrations were monitored in 40-L indoor plastic tanks, filled with prefiltered reservoir water, aerated and maintained at room temperature (24–26 °C) (Brabrand, Faafeng & Nilssen, 1990). Duplicate treatments with tilapia (*T. rendalli* and *O. niloticus* combined at 50% biomass each) and without fish were randomly assigned to tanks. Two trials were performed, one using sixteen 16-g fishes, the other six 40-g fishes, at an average of 250 g fish per tank in both trials. Soluble reactive phosphorus (SRP) and TP were monitored every 4 h during 48-h periods.

Biomass and P-excretion rate of the tilapia stock in Riacho Fundo

To assess the tilapia-mediated TP-loading in Riacho Fundo, we combined data from acoustic echo-integration and gillnet fishing obtained during a campaign in April–May 1998 (Lebourges-Dhaussy *et al*., 1999). Each of the six regions in Lago Paranoá (Bananal, Riacho Fundo, Torto and Gama branches, and the Northern and Southern Central areas) was surveyed during day and night on two consecutive days along parallel transversal transects (GPS-positioned). A vertically oriented 120-kHz Simrad EY500 split-beam elliptic transducer (4° × 10°) (Kongsberg Simrad Mesotech Ltd, Port Coquitlam, Canada) was used onboard a 4.5-m long Zodiac rubber boat propelled at an average speed of 7 km h^{-1}. In addition, nylon gillnets (50 m long and 2 m high) of 10 different stretched mesh sizes (30–240 mm with a 50% horizontal ratio) were set at five stations per region for 24-h periods, with inspections every 6 h, to estimate fish species composition, relative biomass, and length and weight structure.

To assess the P-excretion rate of the tilapia stock in Riacho Fundo branch, we combined estimates of the diurnal and nocturnal fish densities from the acoustic survey with the tilapia biomass proportions and information on the size-structured biomass obtained from the gillnet catches. To compute tilapia weight-frequency distributions, we used 1-cm class length-frequency distributions from gillnet catches with a fitted wet weight (WW) to total length relationship. We then computed the frequency distribution of P excreted by the tilapia stock by multiplying these weight-frequency distributions by the daily P-excretion rates. The likely range of P-excretion rates by the tilapia stock in Riacho Fundo branch was assumed to be bounded by the sum of TP excreted by all size classes from diurnal (minimum) to nocturnal catches (maximum).

Results

BACI approach

Following mass mortality and before complete fish removal, TP concentrations in Riacho Fundo branch peaked above 300 µg L^{-1}, probably as a result of partial decomposition of dead fish (Fig. 2a). Mean TP values were always higher in Riacho Fundo branch than in Bananal branch. The comparison of the two areas revealed a significant (P < 0.001) decrease of TP in Riacho Fundo branch from 100 ± 41 µg L^{-1} before to 66 ± 22 µg L^{-1} after the fish kill (i.e. a 34% reduction on average).

Chlorophyll *a* concentrations followed the same short-term increase after the fish kill as TP, with a peak above 160 µg L^{-1} (Fig. 2b). The chlorophyll *a* concentration also showed a significant ($P = 0.02$) long-term decrease from 84 ± 42 µg L^{-1} before to 56 ± 18 µg L^{-1} after the fish removal (a 33% reduction). Water transparency, however, was not affected by fish mortality ($P = 0.94$; from a Secchi depth of 0.59 ± 0.12 m before to 0.57 ± 0.10 m after the fish removal; data not shown). Similarly, zooplankton densities did not change following the fish kill ($P = 0.86$ for total zooplankton, $P = 0.63$ for macrozooplankton and $P = 0.47$ for the proportion of macrozooplankton) (Fig. 3).

Although external TP-loading of Riacho Fundo branch was always higher than in Bananal branch, both branches showed similar temporal changes (Fig. 2c). As the Northern and Southern sewage

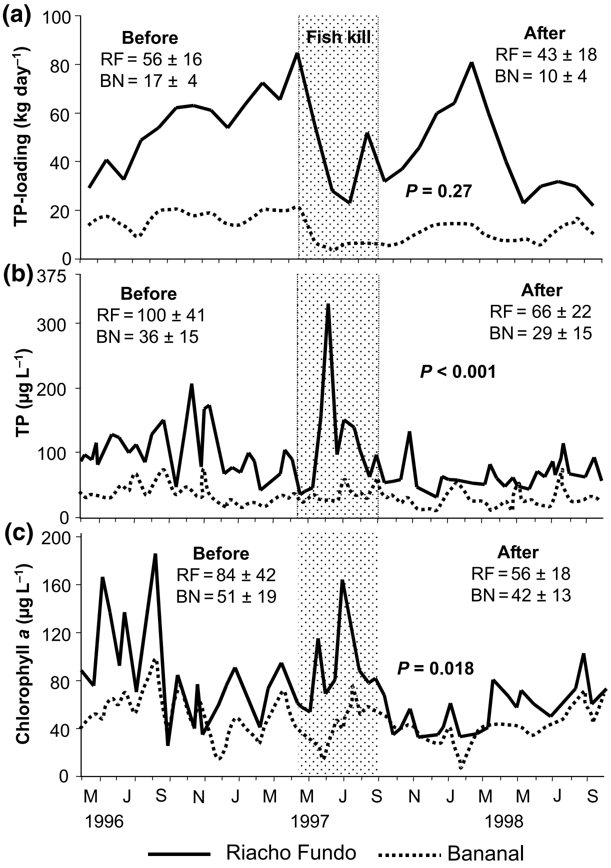

Fig. 2 Results of BACI analyses for (a) TP concentration, (b) chlorophyll *a* concentration and (c) TP-loading in the Riacho Fundo (RF) (impacted area, solid line) and Bananal (BN) (control area, dashed line) branches of Lago Paranoá, before and after the fish kill in RF.

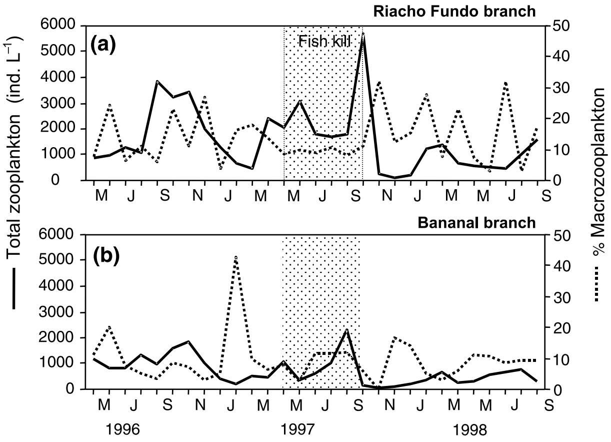

Fig. 3 Changes in total zooplankton density (solid line) and the proportion of macrozooplankton (dashed line; the copepod, *Thermocyclops*, and the cladocerans, *Bosmina* and *Diaphanosoma*) in Riacho Fundo (impacted area) and Bananal (control area) branches of Lago Paranoá.

treatment plants operated under the same tertiary treatment regime, the difference between the two TP-loadings did not change significantly over the study period ($P = 0.27$). Thus, water quality improvements in Riacho Fundo branch during the year following tilapia removal could not be attributed to changes in external P-loading to this branch.

Size-structured biomass of the tilapia stock

Although the extensive fish kill in 1997 had eliminated 150 tons of fish (>50% of the stock), the stock of tilapia had recovered by the time of the acoustic survey in 1998. Total fish stock in Riacho Fundo branch reached 153 (day) and 355 tons (night), with a biomass of 341 and 791 kg ha^{-1}, respectively (Table 1). The nocturnal biomass estimate was twice the diurnal estimate, because tilapia were more active at dusk and dawn than during daytime. These values are probably underestimates, because densely populated littoral areas <1 m in depth could not be surveyed with the echosounder. For example, spreading rotenone on a 80 m^2 littoral area that was quickly isolated by 8 mm mesh netting yielded an overall fish biomass of 1492 kg ha^{-1}, including 1312 kg ha^{-1} of tilapias (88%, mainly Nile tilapia) (Starling, 1998).

The fish biomass of the overall gillnet catch (156 kg) was dominated by tilapias (31%; mainly Nile tilapia) and carp (50%) (Table 2). The contribution of tilapia was probably greatly underestimated, because tilapias can visually detect and actively avoid gillnets by swimming backwards. Tilapias are more efficiently captured by cast-nets and represent >80% of the biomass landed by professional cast-net fishermen in Lago Paranoá (Walter, 2000). To compensate for our gillnet bias against tilapia, we used the more realistic results from a complete fish removal by the quadrat-rotenone technique (Starling, 1998), which indicated that 90% of the acoustically estimated stock were tilapias. In the gillnet catch, the observed frequency distributions of tilapia density with fish body length and biomass with fish body weight showed several modes. These reflect the superposition of patterns between gillnet selectivity and cohort abundances. Combining the size modes from the catch data with the biomass estimates from the echo-integrated acoustic data gives the highest tilapia stocks for the following length classes, with weight classes in parentheses: 10 and 23 tons (during the day and night, respectively; mainly in the central and left margin areas) for 6–7 cm (8–13 g), 21 and 49 tons (upstream and right margin areas) for 18–19 cm (227–268 g), and 17 and 39 tons (upstream area) for 27–28 cm fish (784–877 g).

Table 1 Mean characteristics of fish stocks in Riacho Fundo and Bananal branches of Lago Paranoá, as estimated by echo-sounding in May 1998 (Lebourges-Dhaussy *et al*., 1999). For comparison, fish biomass within Lago Paranoá was lowest in Torto branch (day 168 kg ha^{-1} and night 185 kg ha^{-1}) and highest in Gama branch (day 640 kg ha^{-1}) and Riacho Fundo branch (night 751 kg ha^{-1})

	Riacho Fundo		Bananal	
Variable	Day	Night	Day	Night
Target strength (dB)	−46.37	−45.40	−46.52	−42.74
Total body length (cm)	15.0	15.9	14.9	19.3
Body wet weight (g)	73.4	89.1	76.5	183.1
Density (ind. ha^{-1})	4343	8879	2549	3167
Biomass (kg ha^{-1})	341	791	195	580
Total stock (tons)	153	355	105	313

Contribution of tilapia to internal P-loading

Maximum P-excretion rates reached 1.5 and 0.5 μg SRP g^{-1} WW h^{-1} and 1.73 and 1.12 μg TP g^{-1} WW h^{-1}, for 16 and 40 g tilapia, respectively. These rates are low compared with literature values for various fishes (Table 3). To assess the P-excretion rates of tilapia in Riacho Fundo branch, we weighted these excretion rates on a daily basis by means of the weight-frequency distribution of the fish (i.e. 24 h × 1.73 μg TP g^{-1} WW h^{-1} for tilapia <40 g, and 24 h × 1.12 μg TP g^{-1} WW h^{-1} for tilapia = 40 g; Starling, 1998).

The abundance of fish in the two size classes above is reflected in the size-dependency of TP-excretion rates (Fig 4a,b). The overall TP excreted by the tilapia stock ranged from 3.9 (day) to 9.1 kg TP d^{-1} (night). This estimate is conservative, because the gillnets used (mesh size >30 mm) did not capture the smallest individuals, which were most abundant. For comparison, the external TP-loading to Riacho Fundo branch from tributaries and the sewage treatment plant (September 1997 to June 1998) was 43 kg day^{-1} during the 10-month period after the fish mortality (CAESB, personal communication). The internal TP-loading by the tilapia stock

Table 2 Biomass of tilapias and common carp captured from gillnets in Riacho Fundo and Bananal branches (kilogram of wet weight with percentage of total catch in parentheses)

	Riacho Fundo			Bananal		
Fish species	Day	Night	Total	Day	Night	Total
Nile tilapia	15.6	40.8	56.4	1.6	4.4	6.0
(*Oreochromis niloticus*)	(27.5)	(29.9)	(29.2)	(17.8)	(16.6)	(16.9)
Congo tilapia	1.8	1.4	3.2	0.2	0.9	1.1
(*Tilapia rendalli*)	(3.1)	(1.0)	(1.6)	(2.2)	(3.4)	(3.1)
Common carp	19.9	76.8	96.7	2.0	5.1	7.1
(*Cyprinus carpio* L.)	(35.1)	(56.4)	(50.1)	(22.2)	(19.2)	(20.0)
Total catch	56.6	136.3	192.9	9.0	26.5	35.5

Table 3 Ranges of phosphorus excretion rates for different fish species

Fish species	P excretion rate (μg SRP g WW^{-1} h^{-1})	N : P ratio excreted (in weight)	Comment	Reference
Yellow perch				
Perca flavescens (Mitchill)	0.8–3.2	–	Yoy	Nakashima & Leggett (1980)
	4.2	13–47	Yoy	Kraft (1992)
Roach				
Rutilus rutilus (Linnaeus 1758)	2.0–7.6	12	–	Brabrand *et al.* (1990)
	3.0–12.0	–	–	Persson (1997)
	11.0–35.0	5–7	–	Attayde & Hansson (1999)
Common carp				
Cyprinus carpio (L.)	1.0–10.0	–	10 g fish	Lamarra (1975)
	0.4–1.0		>500 g fish	
	0.2	–	Starved fish	Nuttall & Richardson (1991)
Gizzard shad				
Dorosoma cepedianum (Lesueur 1818)	1.0–1.3	15–16	Adult, starved	Mather *et al.* (1995)
	2.0–13.7	1–16	Adult, fed	
	0.3–1.2	10–41	Yoy, fed	
	2.2–21.4	1–18	2–210 g, fed	Schaus *et al.* (1997)
Tilapia				
Tilapia rendalli	1.6 max.	–	16 g fish	Starling (1998)
(Boulenger) and *Oreochromis niloticus* (L.)	0.5 max.	–	40 g fish	

SRP = soluble reactive phosphorus; WW = wet weight; Yoy = young of the year.

is hence estimated to represent 9–21% of the external TP-loading.

Reduction of internal P-loading by tilapia removal

To assess the potential reduction in internal TP-loading resulting from fish removal, we computed the TP-loading to Riacho Fundo that the 150 tons of removed tilapias could have generated, considering two processes:

(1) Prevention of internal TP-loading via fish excretion. Because nearly all dead fish collected were tilapia, we assumed that 150 tons of tilapia were removed, of which roughly 75 tons were small (<40 g) and 75 tons were large individuals (= 40 g). Given the P excretion rates of small and large tilapia determined in the present study, the 150 tons of removed tilapias would be equal to an excretion of 5.1 kg TP day^{-1} (1.73 μg TP g^{-1} WW h^{-1} $\times$ 24 h $\times$ 75 $\times$ 10^{6} g + 1.12 μg TP g^{-1} WW h^{-1} $\times$ 24 h $\times$ 75 $\times$ 10^{6} g). Most of this phosphorus comes from tilapia feeding on the reservoir bottom (Grando, 1989), excretion in the water column, and possibly the physical release of P from the sediment into the water column as a

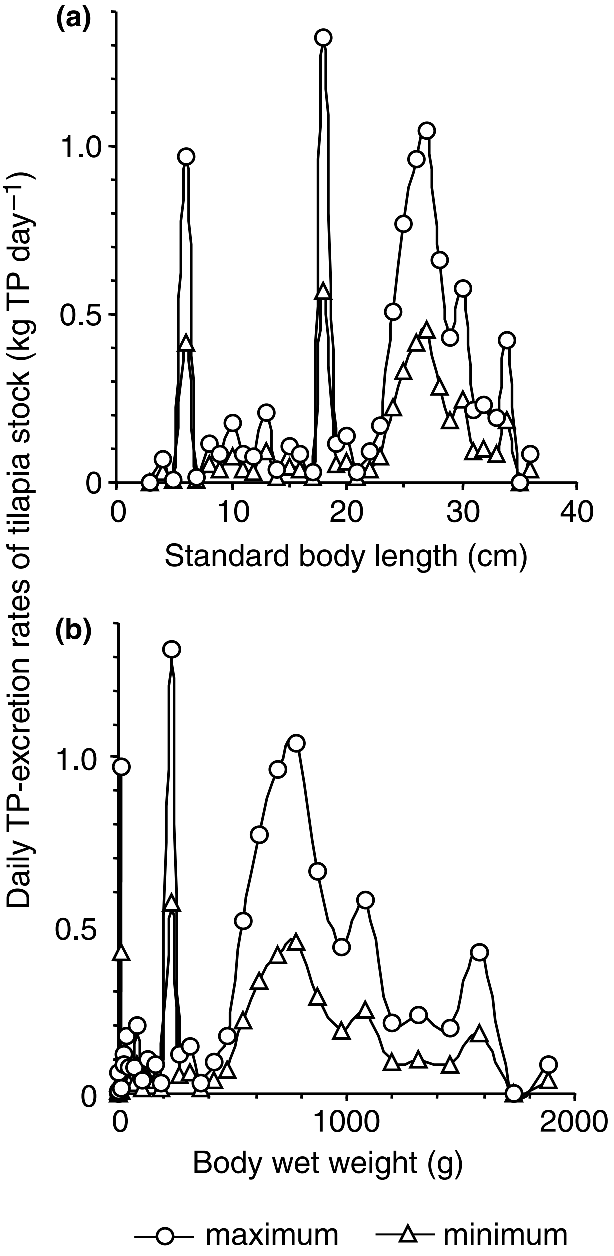

Fig. 4 Total phosphorus-excretion rates of the tilapia stock (*O. niloticus* plus *T. rendalli*) in Riacho Fundo branch as a function of tilapia (a) body-length and (b) body-weight. Estimates are based on the fish biomass from an acoustic survey and the size-frequency distribution of tilapia in the catch of an experimental gill-net fishing campaign in 1998. Minimum (open triangles) and maximum (open circles) estimates refer to fish biomass estimates for the daytime and nighttime, respectively.

result of bioturbation. Given an external TP-loading of 43 kg TP d^{-1} (see previous subsection), the tilapia-mediated internal TP-loading prevented by the removal of 150 tons of dead fish reached 12% (5.1/43) of the external TP-loading to Riacho Fundo branch during the 12 months following fish mortality.

(2) Removal of P in dead fish biomass. The 150 tons of tilapia wet weight correspond to a dry weight (DW) of 36 tons (using a DW : WW ratio of 24%; Drenner *et al.*, 1997) and 857 kg of P (using a P-content of 2.39% of fish dry weight). This amount is equivalent to the external loading received by Riacho Fundo branch during 20 days after tilapias had been removed.

Discussion

Four decades after their introduction, tilapias have become extremely abundant in Lago Paranoá, especially in the studied branches. During the 1970s and 1980s, cast-net fisheries were well established, because net fisheries, although prohibited, were poorly controlled. Daily catches by more than 100 fishermen were estimated to reach 1–2 tons day^{-1} (L.D. Dornelles, personal communication). Starting in 1995, increased enforcement gradually reduced the fishing activity. During the 1990s, the total fish biomass in littoral areas of Bananal branch was estimated by the quadrat-rotenone technique to range from 1100 (Starling & Lazzaro, 1997) to 1500 kg ha^{-1} (Starling, 1998). In the present study, a comprehensive acoustic survey coupled with experimental fishing estimated the overall fish stock of Lago Paranoá to exceed 1400 tons, corresponding to >368 kg ha^{-1}. In hypereutrophic Riacho Fundo branch, the fish stock was estimated at >350 tons or >763 kg ha^{-1}, 200 tons of which (including >100 tons of tilapias) were concentrated upstream near the sewage plant where fish mortality took place. As indicated by previous data on total fish removal in littoral areas, these biomass figures are underestimates, because the most productive shallow areas (<1 m in depth) could not be assessed by echosounding.

More than 10 years of experimentation in Lago Paranoá have demonstrated that the massive presence of tilapia is closely related to eutrophication symptoms. Cyanobacteria density increased in 2.5 m^3 bag-type enclosures in 1987 (Starling & Rocha, 1990), in 1000 m^3 isolated littoral areas in 1993 (Starling & Lazzaro, 1997), and in a series of experiments with 50–100 m^3 limnocorrals in 1995 (Starling, 1998). In all these experiments, a high biomass of tilapia

(1100–3000 kg ha^{-1}) was related to increases in TP concentrations, chlorophyll *a* concentrations and cyanobacteria densities. These effects were attributed to P-excretion by fish and P-release from sediment via bioturbation by bottom-feeding fishes. Therefore, the desired removal of algae and detritus by grazing tilapia was offset by their stimulating effect on phytoplankton via the enhanced release of nutrients into the water column. The present study substantiates the important role of tilapia in enhancing internal nutrient loading directly by P excretion.

The alternative explanation for the water quality improvements in Riacho Fundo branch would be the classical 'trophic cascade hypothesis' (Carpenter & Kitchell, 1993) of phytoplankton control by increased grazing pressure from herbivorous zooplankton. This explanation is unlikely for two reasons. First, in Lago Paranoá, large-bodied herbivorous zooplankton such as *Bosmina* and *Diaphanosoma* is virtually absent, and inedible algae (mainly colonial and filamentous cyanobacteria) dominate the net-phytoplankton. Secondly, zooplankton densities did not increase after the fish kill (BACI: $P = 0.86$ for total zooplankton and $P = 0.63$ for macrozooplankton), nor did the proportion of macrozooplankton increase ($P = 0.47$).

By experimentally reducing the tilapia biomass from as high as 900 kg ha^{-1} down to 350 kg ha^{-1} within large limnocorrals (100 m^3) in 1996, significant water quality improvements were recorded in terms of reduced turbidity (−46%), TP concentration (−31%), density of bloom-forming nuisance algae (−70%) and total phytoplankton biomass (−38%) (Starling, 1998). In the present study, despite the short-term increases in nutrient and chlorophyll concentrations resulting from partial decomposition of some fishes prior to their removal, the large-scale removal of dead tilapias induced significant water quality improvements, which encourage the implementation of biomanipulation at whole reservoir scale.

Management implications

Our results suggest that it is worth evaluating the feasibility of adopting a whole-lake biomanipulation programme to control tilapia biomass so as to improve water quality and prevent extensive winter fish kills. Since the early 1960s, non-professional fisheries in Lago Paranoá were mostly based on the use of cast-nets to capture tilapias. They produced daily catches of 20–100 kg per fisherman per day (Walter, 2000). Legalising professional cast-net fisheries in Lago Paranoá would contribute to keep tilapia populations under their carrying capacity, and thus reduce the risk of large fish kills in the future. In addition, water quality would be improved because of a reduction of internal nutrient loading.

The fundamental requirement to convince the local government to legalise professional cast-net fisheries in some hypereutrophic areas of Lago Paranoá has been fulfilled by certifying the good sanitary quality of the fishes (Caldas *et al.*, 1999). Although these authors confirmed the absence of contamination in terms of heavy metals, pesticides and pathogenic bacteria, long-term monitoring should be enforced, particularly with regard to preventing consequences from potentially toxic bloom-forming cyanobacteria.

A large-scale tilapia removal campaign using cast-nets carried out in May 1999 (Starling *et al.*, unpublished data) and a comprehensive socio-economic study of the cast-net fisheries in Lago Paranoá (Walter, 2000) convinced the Brazilian Environmental Agency (IBAMA) to legalise the activity of a pilot group of 70 trained professional cast-net fishermen in 2000. Monitored landings of the 15 most productive fishermen reach over 5 tons of tilapia per month, and no further fish mortality has been recorded so far. To establish cast-net fisheries as a biomanipulation strategy, the number of fishing licenses will eventually have to be increased as a result of a systematic monitoring of landing and an accurate evaluation of tilapia recruitment, growth rate and stock dynamics. Additionally, a prerequisite for attracting more fishermen would be a higher market price for tilapia, which could be achieved by increasing the aggregate value of the product through developing specific food processing techniques such as filleting, smoking and 'surimi'.

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References

APHA (1998) *Standard Methods for the Examination of Water and Wastewater*, 20th edn. APHA (American Public Health Association), Washington, DC.

Attayde J.L. & Hansson L.A. (1999) Effects of nutrient recycling by fish and zooplankton on phytoplankton communities. *Oecologia*, **121**, 47–54.

Brabrand A., Faafeng B.A. & Nilssen J.P.M. (1990) Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 364–372.

Brinkmann W.L.F. & Santos U.M. (1973) Heavy fish-kill in unpolluted flood-plain lakes of Central Amazonia. *Brazilian Biology Conservation*, **5**, 146–197.

Caldas E.D., Coelho R., Souza L.C.K.R. & Silva S.C. (1999) Organochlorine pesticides in water, sediment, and fish of Paranoá Lake of Brasília, Brazil. *Bulletin of Environmental Contamination and Toxicology*, **62**, 199–206.

Carpenter S.R. & Kitchell J.F. (Eds). (1993) *The Trophic Cascade in Lakes*. Cambridge University Press, New York.

Cavalcanti C.G.B., Pinto M.T., Freitas H.J. & Moreira R.C.A. (1997) Paranoá Lake restoration: impact of tertiary treatment of sewage in the watershed. *Verhandlungen der Internationalen Vereinigun für Theoretische und Angewandte Limnologie*, **26**, 689–693.

Datta S. & Jana B.B. (1998) Control of bloom in a tropical lake: grazing efficiency of some herbivorous fishes. *Journal of Fish Biology*, **53**, 12–24.

Drenner R.W., Day D.J., Basham S.J., Smith J.D. & Jensen S.I. (1997) Ecological water treatment system for removal of phosphorus and nitrogen from polluted waters. *Ecological Applications*, **7**, 381–390.

Fernando C.H. (1994) Zooplankton, fish and fisheries in tropical freshwaters. *Hydrobiologia*, **272**, 105–123.

Grando J.V. (1989) *Considerações sobre o estágio atual da ictiofauna e aspectos alimentares de quatro espécies de peixes do Lago Paranoá, Brasília-DF*. MSc Thesis, University of Brasília, Brasília.

Kolding J. (1993) Population dynamics and life-history styles of Nile tilapia, *Oreochromis niloticus*, in Ferguson's Gulf, Lake Turkana, Kenya. *Environmental Biology of Fishes*, **37**, 25–46.

Kraft C.E. (1992) Estimates of phosphorus and nitrogen cycling by fish using a bioenergetics approach. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2596–2604.

Lamarra V.A. (1975) Digestive activities of carp as a major contributor to the nutrient loading of lakes. *Internationale Vereinigun für Theoretische und Angewandte Limnolologie, Verhandlungen*, **19**, 2461–2468.

Lebourges-Dhaussy A., Dhaussy Ph., Lazzaro X. & Starling F.L.R.M. (2000) Acoustical fish biomass assessment of Lago Paranoá – Brasilia – Brazil within the framework of a water quality improvement project. In: *Proceedings of the 2nd International Shallow Water Fisheries Sonar Conference*. Seattle, 7–9 September 1999, p. 22. *Aquatic Living Resource*, Elsevier.

Lowe-McConnell R.H. (2000) The roles of tilapias in ecosystems. In: *Tilapias: Biology and Exploitation* (Eds M.C.L. Beveridge & B.J. McAndrew), pp. 129–162. Kluwer, London.

Mather M., Vanni M.J., Wissing T.E., Davis S.A. & Schaus M.H. (1995) Regeneration of nitrogen and phosphorus by bluegill and gizzard shad: effects of feeding history. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 2327–2338.

Nakashima B.S. & Legett W.C. (1980) Natural sources and requirements of phosphorus for fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 679–686.

Nuttall P. & Richardson J. (1991) Nitrogen and phosphorus excretion by European carp. *Chemosphere*, **23**, 671–676.

Ochumba P.B.O. (1990) Massive fish kills within the Nyanza Gulf of Lake Victoria, Kenya. *Hydrobiologia*, **208**, 93–99.

Persson L. (1997) Effects of fish predation and excretion on the configuration of aquatic food webs. *Oikos*, **79**, 137–146.

Schaus M.H., Vanni M.J., Wissing T.E., Bremigan M.T., Garvey J.E. & Stein R.A. (1997) Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology and Oceanography*, **42**, 1386–1397.

Starling F.L.R.M. (1998) *Development of biomanipulation strategies for the remediation of eutrophication problems in an urban reservoir, Lago Paranoá – Brazil*. PhD Thesis, Institute of Aquaculture, University of Stirling, Scotland.

Starling F.L.R.M. & Lazzaro X. (1997) Experimental investigation of the feasibility of improving water quality by controlling exotic planktivore overpopulation in eutrophic Paranoá Reservoir (Brasilia-DF, Brazil). *Verhandlungen der Internationalen Vereinigun für Theoretische und Angewandte Limnologie*, **26**, 789–794.

Starling F.L.R.M. & Rocha A.J.A. (1990) Experimental study of the impacts of planktivorous fishes on plankton community and eutrophication of a tropical Brazilian reservoir. *Hydrobiologia*, **200/201**, 581–591.

Stewart-Oaten A., Murdoch W.W. & Parker K.R. (1986) Environmental impact assessment: 'pseudoreplication' in time? *Ecology*, **67**, 929–940.

Vanni M.J., Luecke C., Kitchell J.F. & Magnuson J.J. (1990) Effects of planktivorous fish mass mortality on the plankton community of Lake Mendota, Wisconsin: implications for biomanipulation. *Hydrobiologia*, **200/201**, 329–336.

Walter T. (2000) *Ecologia da pesca artesanal no Lago Paranoá – Brasília-DF*. MSc Thesis, University of São Paulo, São Carlos, Brazil.

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