Limnological changes in a sub-tropical shallow hypertrophic lake during its restoration: two years of a whole-lake experiment

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ABSTRACT

1. Lake Rodó is a turbid system, a condition attributed to algal biomass. The proximal source of the eutrophication was stormwater discharges from an ill-defined urban area. This paper describes an attempt to restore the water quality of Lake Rodó, the first time this has been done in Uruguay. In spring 1996 it was drained, sediments were removed and stream inputs were diverted. Groundwater was used to re-fill the lake. Due to its high nutrient concentration a re-circulation system was designed, pumping water from associated pools covered with free-floating plants.

2. After the lake was refilled, the system was characterized by oxygen saturation or over-saturation, neutral to basic pH, and high phosphorus, nitrogen and silicate concentrations. Ratios of total nitrogen (TN):total phosphorus (TP) and chlorophyll *a* (Chl *a*):TP indicated that phosphorus was the primary limiting nutrient during the period of groundwater supply. Once groundwater pumping had ceased, there was a decrease in TN:TP and Chl *a*:TP ratios, suggesting N-limiting conditions prevailed in some periods.

3. Before restoration, the phytoplankton community was dominated year-round by *Planktothrix agardhii*; since restoration the community has been more diverse. This change has favoured grazing by mesozooplankton, and the onset of clear-water phases in spring.

4. Abundant populations of small omnivorous fish maintained a high predation pressure on zooplankton, restricting the abundance of large-bodied herbivores, which, in turn, allowed an increase in phytoplanton biomass and a decrease in water transparency. Based on this observation, together with the phosphorus concentration and the low abundance of filamentous cyanobacteria compared with previous studies, we suggest that top-down control has played a key role in increasing transparency in Lake Rodó.

5. A nutrient reduction programme, by the mechanical harvest of floating plants, and a removal of small omnivorous fishes and stocking strictly with piscivores, could be key factors in the achievement of a stable clear-water phase. However, if blooms of *Microcystis* or other similar genera occur in summer, additional measures (e.g. reduction of the hydraulic residence time) will be needed to improve water transparency.
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KEY WORDS: eutrophication; urban lake restoration; nutrient load reduction; food web structure

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INTRODUCTION

From the 1960s to the 1990s in Europe and North America, the strategy for restoring lakes from eutrophication gradually evolved from simply controlling phosphorus input towards a more comprehensive and ecosystem-based approach. This included the control of non-point nutrient sources, and the application of in-lake measures such as dredging, flushing and biomanipulation (Hosper, 1997).

Evidence indicates that in temperate regions the most effective and economically suitable means for restoring shallow lakes is through the simultaneous application of nutrient load reduction and biomanipulation measures (Shapiro *et al*., 1975; Carpenter *et al*., 1987; Kasprzak, 1995; Moss *et al*., 1996; Jeppesen, 1998; Scheffer, 1998). Not every aquatic system shows the same responses to the application of these techniques, making it necessary to understand the structure and functioning of the ecosystem under consideration.

Some sub-tropical and tropical lakes support a substantial coverage of free-floating plants (i.e. *Eichhornia crassipes*, *E. azurea* or *Pistia stratiotes*) which strongly influence nutrient dynamics (Camargo and Esteves, 1995; Mazzeo *et al*., 1995; Esteves, 1998) and, consequently, the bottom-up input to the food web. However, their role is much less understood in comparison with the role of submerged plants of shallow temperate lakes. Furthermore, the applicability of the 'classical' food-web manipulation to tropical and sub-tropical lakes has been controversial because top-down links between piscivores and planktivores in warm lakes are weaker. Filtering omnivores are dominant and large pelagic piscivores are frequently replaced by less efficient and smaller predators (Lazzaro, 1997; Pinel-Alloul *et al*., 1998). Simultaneously, zooplankton grazing pressure on phytoplankton is also weakened by the lack of large-bodied *Daphnia* due to all year-round intensive invertebrate predation, and quasi-permanent size-selective predation from many larvae and juvenile fish (Lazzaro, 1997; Pinel-Alloul *et al*., 1998).

Whole-lake manipulation and experimental studies of sub-tropical and tropical aquatic systems have contributed to an understanding of their functioning and have promoted the testing of hypotheses that originate from temperate ecosystems. The main objectives of the present study were to analyse the principal physical, chemical and biological characteristics of a sub-tropical, shallow and hypertrophic lake during its restoration, and to analyse the more significant responses to the measures applied on classical food web structure (including phytoplankton, zooplankton, benthos and fish communities), determining their consequences for water quality. Finally, measures are proposed to restore the lake for amenity and recreational purposes, with a consideration of their applicability to other shallow sub-tropical ecosystems.

METHODS

Study area

Eutrophication is the most important form of degradation shown by aquatic ecosystems in Uruguay. Lake Rodó (34°55″S, 56°10′W) is a small, shallow (Table 1) and turbid system, a condition principally attributed to algal biomass. This man-made lake was constructed in 1917 in a park in Montevideo (1.5 million inhabitants). The lake is used for amenity and recreational purposes (walking, jogging, boating, and fishing) and cultural activities. The main consequences of eutrophication have been the loss of aesthetic and recreational value. Since spring 1996, this urban lake has been undergoing restoration — the first attempt at restoring a shallow lake in Uruguay. It was completely drained and sediments were removed. Now it has no stream inputs, but, until December 1997, it received stormwater with a high nutrient load from an ill-defined urban area. Groundwater (360 m^3 day^{-1}) with high nutrient concentration was used to re-fill and, subsequently, maintain the lake, between January 1997 and January 1998. Groundwater pumping then ceased and, since July 1998, the lake has been connected to two

Table 1. Morphometric data of Lake Rodó

Lake form	Concave
Total lake area (ha)	1.5
Lake area (ha)	1.2
Mean depth (m)	1.7
Maximum depth (m)	2.5
Volume (m^3)	20 794
Maximum length (m)	257
Maximum width (m)	75
Shoreline length (m)	807
Shore development[a]	2.1

[a] Index of shoreline regularity; for a circular lake, index = 1.0.

associated pools (covered with free-floating plants), and a water re-circulation system implemented (Figure 1). Aquatic plants (especially *E. crassipes* and *Spirodela intermedia*) were cultivated and mechanically harvested before autumn.

Materials and methods

Water samples were collected weekly from January to April 1997 and bi-weekly until January 1999 at four stations (Figure 1). In the deepest part of the lake (station 2) water samples were taken with a Ruttner
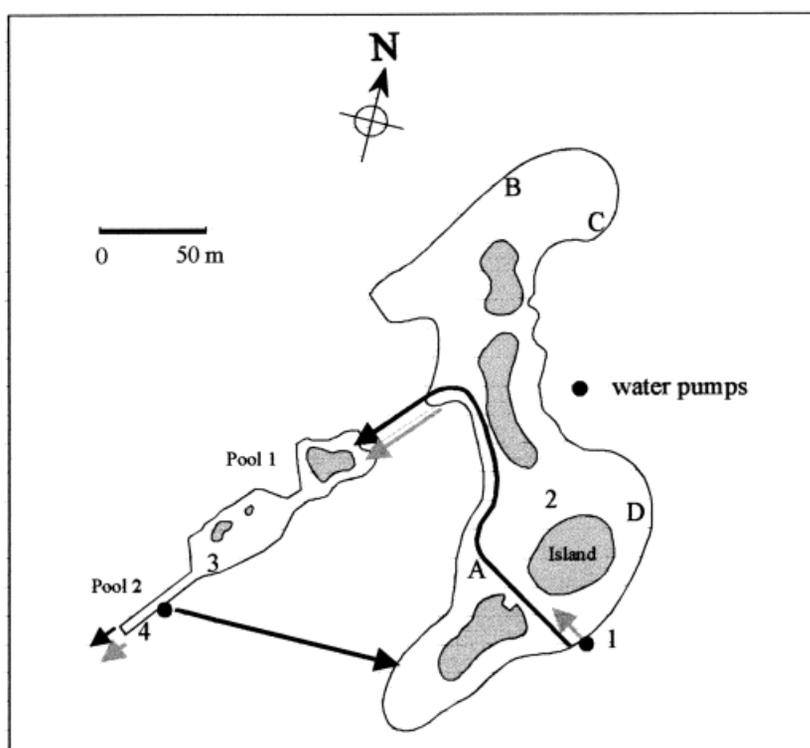

Figure 1. Map of Lake Rodó indicating the physical and chemical sampling stations (1, 2, 3 and 4), benthos and plankton sampling stations (2), and fish sampling stations (A, B, C and D). Arrows indicate the previous (grey) and present (black) water circulation patterns.

Table 2. Average, minimum and maximum values of physical and chemical parameters of Lake Rodó

Parameter	1997	1998
Temperature (°C)	20.1 (10.1–31.2)	19.3 (10.9–28.6)
Dissolved oxygen (mg litre^{-1}) surface	9.7 (5.2–17.0)	8.0 (3.7–19.5)
Dissolved oxygen (mg litre^{-1}) bottom	9.4 (5.2–17.1)	5.1 (0.2–10.9)
Oxygen saturation (%)	110.3 (60.1–175.1)	83.1 (42.3–136.9)
pH	8.1 (7.5–8.5)	8.1 (7.7–9.0)
Conductivity (μS cm^{-1})	975 (889–1061.5)	728.3 (427.7–1103.0)
Alkalinity (mg CaCO$_3^{-1}$)	298.7 (115–380)	236.8 (116.7–301.0)
TN (mg litre^{-1})	10.9 (4.1–27.5)	2.9 (0.7–8.3)
TP (mg litre^{-1})	0.13 (0.07–0.22)	0.21 (0.10–0.58)
SiO$_2^{-2}$ (mg litre^{-1})	8.4 (0.18–18.5)	11.0 (0.33–22.0)
TN/TP (by weight)	85.9 (22.6–253.1)	15.0 (2.0–51.4)
SiO$_2^{-2}$/TP (by weight)	68.4 (1.1–161.9)	57.5 (2.7–138.9)
Chl *a*/TP (by weight)	0.9 (0.0–2.4)	0.5 (0.0–1.3)

bottle just below the surface and close to the bottom. Temperature, dissolved oxygen, conductivity, pH and transparency (Secchi disc depth) were measured *in situ*. These same variables (except for transparency) were also measured in the associated pools (stations 3 and 4) and in the outlet of groundwater pumping (station 1). Methods used for analysis were as follows: Alkalinity and suspended matter — APHA (1985); soluble reactive phosphorus (SRP) — Murphy and Riley (1962); total phosphorus (TP) and total nitrogen (TN) — Valderrama (1981); nitrate — Müller and Widemann (1955); ammonium — Koroleff (1970); silicate (SiO$_2^{-2}$) — Mullin and Riley (1955); and chlorophyll *a* (Chl *a*) — Nusch (1980). At station 2, sediment samples were taken every 2 months with a 6-cm diameter Kajak-corer. The organic matter content was determined by gravimetry (Håkanson and Jansson, 1983). TN and TP content in the sediment were analysed according to Valderrama (1981).

Benthic communities were sampled every 2 months with a 6-cm diameter Kajak-corer and sieved through a 500-μm mesh (10 replicates). Phytoplankton-net tows were taken (25 μm mesh size), and integrated triplicate samples were collected with a 5-litre Schindler trap, while triplicate counting was carried out using a 1-mL Sedwick-Rafter chamber. Biovolume was calculated from microscopic measurements using the criteria of Hillebrand *et al.* (1999). Zooplankton samples for qualitative analysis were collected with a 68-μm net and triplicate samples were taken with a 5-litre Schindler trap at the mean depth. Triplicate counts were made according to Paggi and De Paggi (1974) using a Sedwick-Rafter chamber of 1–5 mL. Fish were collected using a 20 × 2 m seine net (1 mm mesh size). Individuals were counted and weighed and fish density and biomass were calculated.

Parametric (non-linear) and non-parametric (Spearman) correlation analyses were performed for physical and chemical data, and for sediment data, respectively.

RESULTS

Lake Rodó is a warm polymictic lake with a water temperature range of 10–31°C, characterized by oxygen saturation or super-saturation, neutral to basic pH, and high phosphorus, nitrogen and silicate concentration. During summer 1998, anoxic conditions were recorded close to the bottom (Table 2). Nutrient concentrations were higher in groundwater than in the lake. Conductivity, SRP and nitrate varied among the sampling sites (Figure 2), with a clear gradient of decrease from groundwater to pool 2. These observations led to the design and installation of a re-circulation system pumping water from pool 2 towards the lake (Figure 1). The results are thus segregated into three periods: (i) when the lake
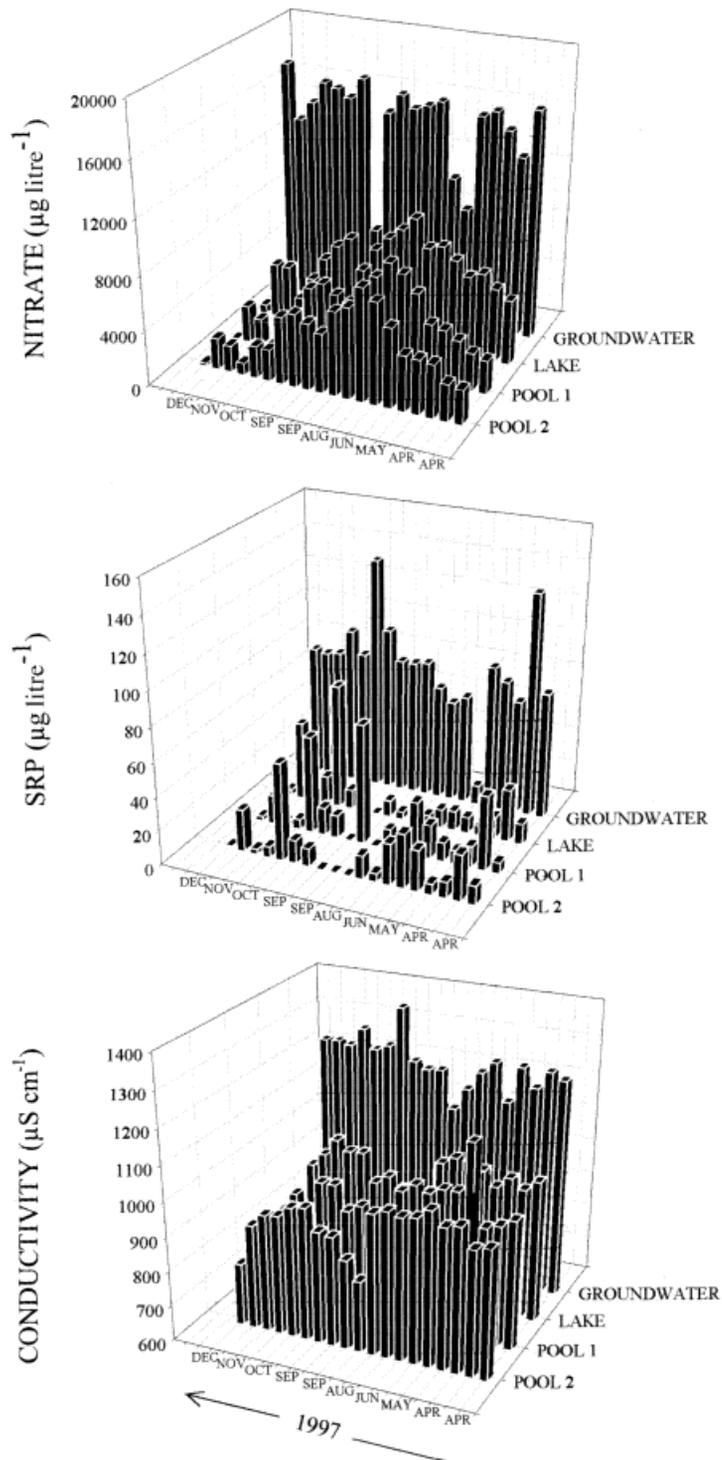
Figure 2. Spatial and temporal variation of conductivity, SRP and nitrate during groundwater supply in the four sampling stations at Lake Rodó.

received groundwater, (ii) when the groundwater supply was stopped, and (iii) when the water was re-circulated.

A marked decline in water transparency was observed during the first 3 months after re-filling, closely related to an increase in phytoplankton biomass ($r = -0.87$, $p < 0.001$) (Figure 3). Higher water transparency (> 1 m Secchi depth) was noted during spring 1997 (groundwater supply) and spring 1998 (water re-circulation regime). These clear-water phases lasted for 2 and 3 weeks, respectively, during which the lowest phytoplankton biomass and the highest ammonium and phosphorus concentrations were observed (Figure 3). Reductions in nitrate (the predominant form of nitrogen) and Chl *a* occurred during the re-circulation regime (Figure 3). However, TP and SRP showed a clear increment during the study period (Table 2, Figure 3). The TN:TP and Chl *a*:TP ratios indicated that phosphorus was the primary limiting nutrient during the groundwater supply period. After groundwater pumping ceased a decrease of
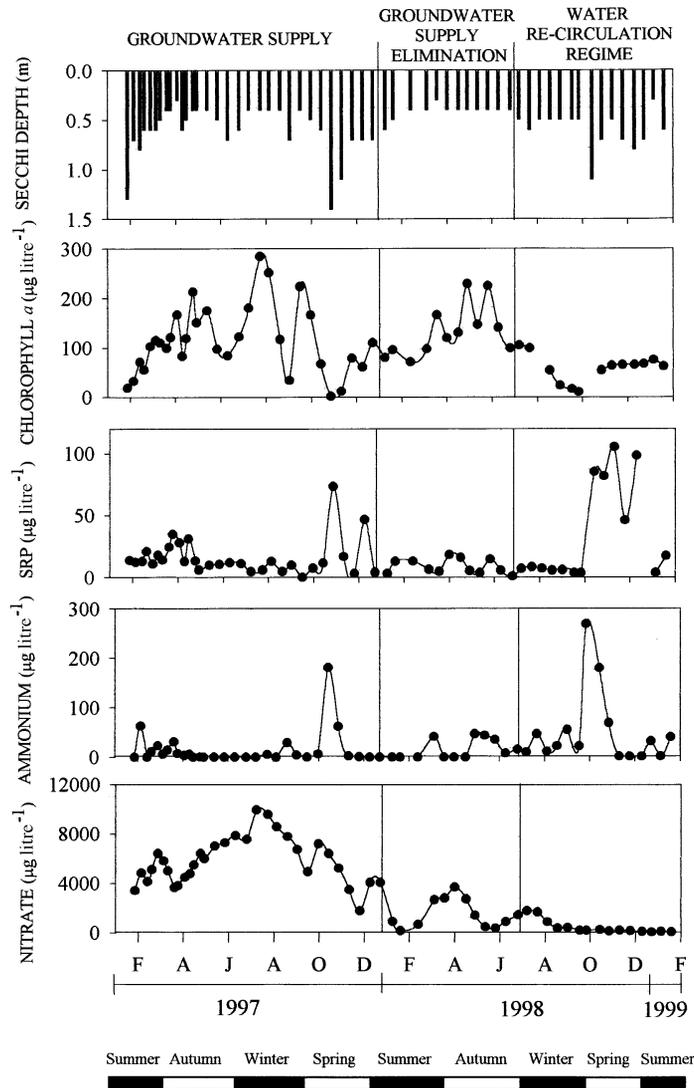

Figure 3. Temporal variation of water transparency (Secchi depth), Chl *a*, SRP, ammonium and nitrate at the lake (station 2).
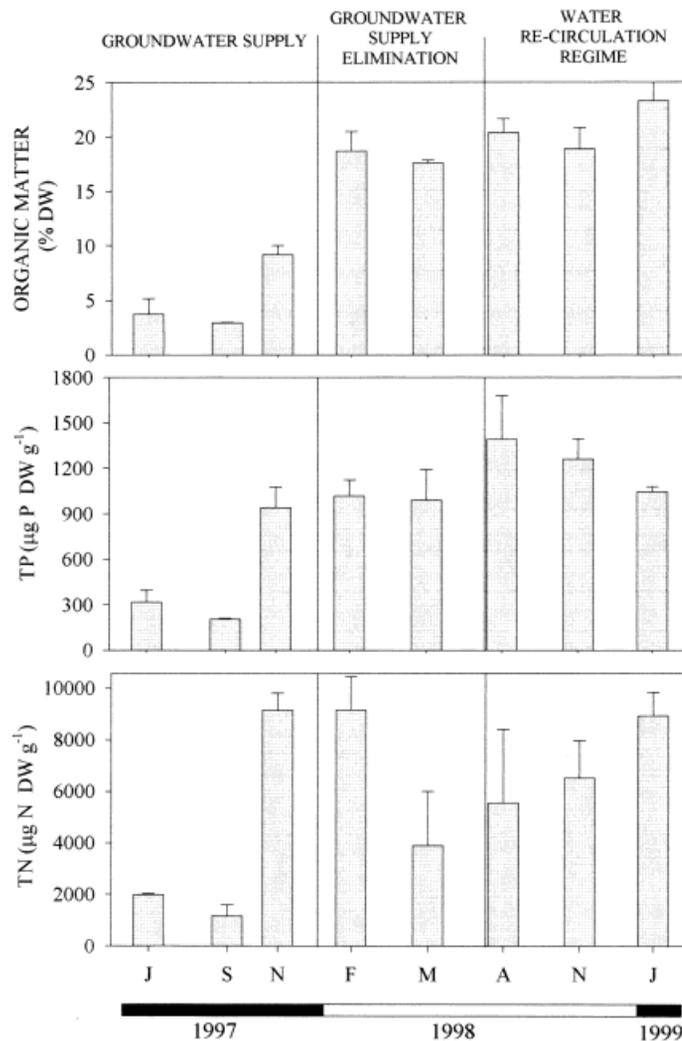
Figure 4. Temporal variation of organic matter, TN and TP content at the sediment surface of Lake Rodó. DW, dry weight.

TN:TP and Chl *a*:TP ratios at the lake were observed (Table 2), suggesting N-limiting conditions in some periods (principally during the re-circulation regime).

The nitrogen, phosphorus and organic matter content of the sediment showed substantial increase after the end of the groundwater supply period (Figure 4). The benthic genera recorded were *Coelotanypus*, *Procladius*, *Larsia*, *Polypedium*, *Goeldichironomus* (Chironomidae), *Helobdella* (Hirudinea) and *Limnodrilus hoffmeisteri* (Oligochaeta) (Figure 5). The density of benthic invertebrates varied greatly, including some periods (during water re-circulation) when no organisms were found. The temporal variation in organic matter was correlated with sediment phosphorus content and total benthic abundance ($rs = 0.93$, $p < 0.001$; $rs = -0.76$, $p < 0.05$, respectively).

More than 150 phytoplankton taxa were identified. The succession during 1997 began with small invasive chlorophytes (C-strategists, characterized by rapid nutrient absorption, assimilation and replication rates). This group was followed by R-strategists (with a high surface area/volume ratio that maximizes their suspension, light harvesting and metabolic rate), including pennate diatoms (*Synedra*

acus) and filamentous cyanobacteria (*Limnothrix* sp. and *Pseudoanabaena* spp.). Finally, larger chlorophytes (C-strategists) appeared at the end of 1997 (Figure 6). After groundwater supply ceased the sequences of temporal replacement continued with coccal cyanobacteria, and then by nitrogen-fixing and filamentous cyanobacteria (S-strategists, with a modest surface area/volume ratio, control buoyancy, slow growth and complex perennation mechanism) such as *Anabaena* spp., *Aphanizomenon flos-aquae* and *Raphidiopsis mediterranea*. During spring and summer 1998, chlorophytes dominated once again. The main change following the cessation of groundwater supply was the reduction in diatoms. During the second clear-water phase (spring 1998), chlorophytes dominated with higher biovolume (associated with *Sphaerocystis*), compared with 1997. Small incremental increases in cyanobacteria biovolume (*Microcystis* spp., *Coelomoron tropicalis* and *Gomphosphaeria* spp.) were observed in this period, but they did not dominate until late summer (Figure 6).

The zooplankton community was largely composed of small herbivores (Figure 7), mainly rotifers (*Keratella tropica*). Copepods (*Notodiaptomus incompositus*, *Metacyclops mendocinus* and *Tropocyclops prasinus meridionalis*) showed a clear temporal pattern, with higher abundance at the beginning of the spring. Cladocerans were less abundant with peaks in spring 1997 and summer 1997–1998 (in response to the presence of *Moina micrura* in spring and *Diaphanosoma birgei* in summer). *Daphnia pulex* was only observed in spring. The abundance of mesozooplankton herbivores was higher in spring and summer and decreased after groundwater supply had been eliminated (Figure 7).

Conservation groups with no connections to the restoration programme kept alive some native fish during the drainage process and introduced them later to the lake, during re-filling. The species composition and abundance of fish stocked are therefore unknown, but the community was rapidly characterized by a high fish biomass (Figure 8) dominated by small omnivorous fish and an absence of
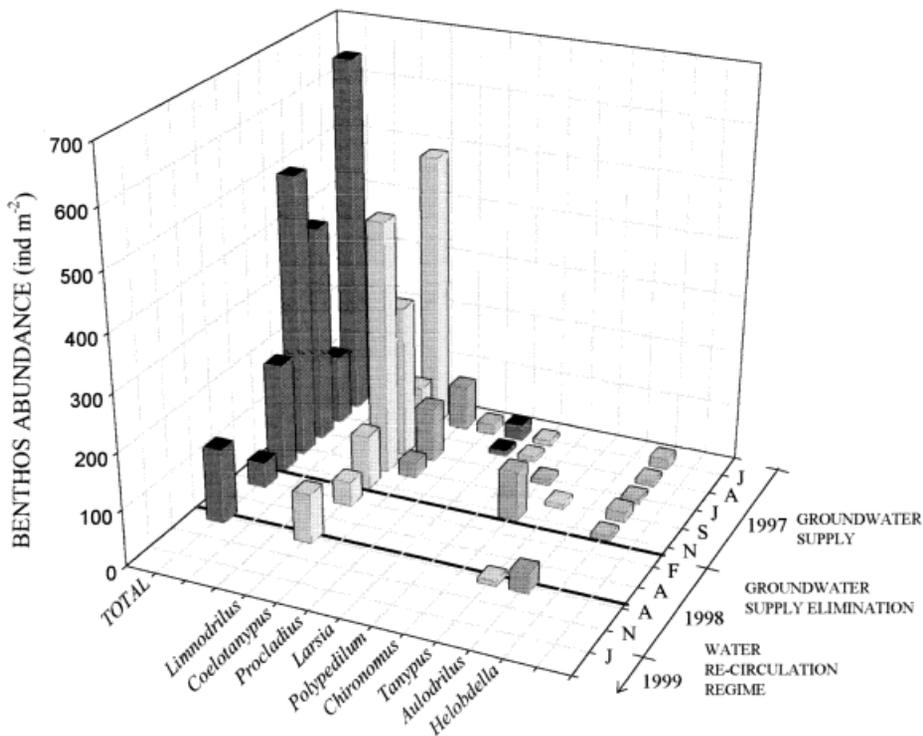

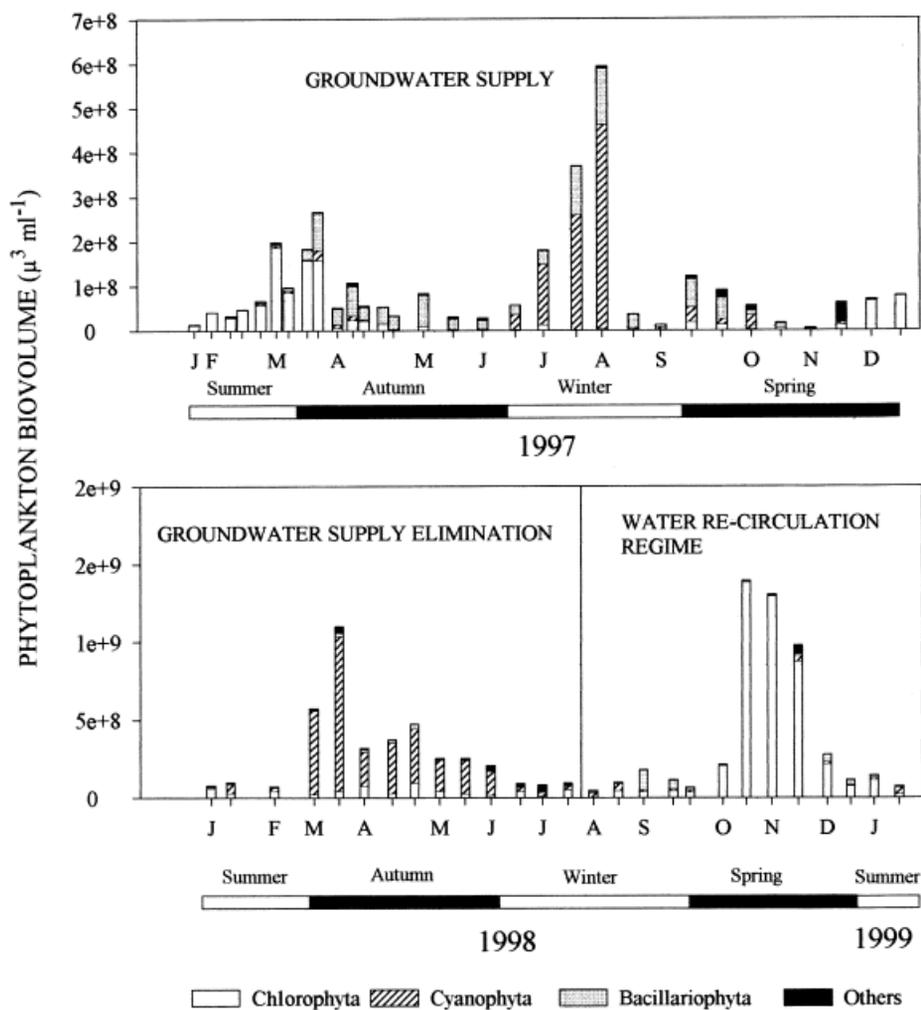Figure 5. Temporal pattern in density of benthic genera of Lake Rodó.

Figure 6. Sequential replacement of the principal phytoplankton groups of Lake Rodó.

piscivores. The mean biomass estimates for 1997 and 1998, respectively, were 300 and 160 kg ha^{-1}. *Cnesterodon decemmaculatus* (Poeciliidae) was clearly the dominant species with average densities of 97000 ha^{-1} in 1997 and 41000 ha^{-1} in 1998. This species, together with *Jenynsia lineata* (Jeninsiidae) (both small omnivorous fish), represented 96% of the total fish biomass in 1997 and 60% in 1998. *Gymnogeophagus rabdotus* and *Cichlasoma facetum* (Cichlidae), which can probably prey on the previously mentioned species, represented 4% and 34% of the total biomass each year. All fish found are native species.

DISCUSSION

Until this study, the available limnological data for Lake Rodó were obtained from samples taken between January and December 1992 (Sommaruga, 1993, 1995; Sommaruga and Psenner, 1995; Sommaruga and Conde, 1997). The principal differences are a change in water transparency from a mean

of 0.2 to 0.5 m Secchi disc depth, coinciding with a reduction in phytoplankton biomass (> 50%). The other main physical and chemical changes compared with previous studies were a decrease in TP (69% during the groundwater supply period), and a significant increase in TN (300%) which returned to the previous concentrations after the water re-circulation system was installed. The mean TN:TP ratio (by weight) varied from 8.5 to 85.9, turning the supportive capacity of the lake from N-limited to P-limited during the groundwater supply period, and changed to 11.4 during the water re-circulation regime, returning to N-limiting conditions for some periods. Water re-circulation seems to be an effective tool for reducing nitrogen (assisted by plant assimilation and denitrification processes) and probably phosphorus.

Before the beginning of the restoration activities (spring 1996), the phytoplankton was dominated year-round by *Planktothrix agardhii*, representing between 82% and 99% of the total phytoplankton biomass (Sommaruga, 1995). Now, the community is more diverse; more than 150 taxa have been recorded, while Sommaruga (1995) found only 27 using the same counting procedure. The structural modification in the phytoplankton community before and after restoration could have been caused by changes in the TN:TP ratio, and the SiO_2^{-2} concentration. Elimination of constant nutrient supply (by groundwater pumping) appears to have had a significant impact on the phytoplankton, leading to the presence of S-species (adapted to resource-limiting conditions) and to an increase in nitrogen fixers.

The structure of the zooplankton community was fairly similar before and after restoration in terms of their species composition and relative abundance. However, the abundance of rotifers was lower than in the past, while medium-sized herbivores were more abundant. The small, but higher, proportion of edible algae compared with past monoculture of *P. agardhii* could be an important factor explaining these differences, as *P. agardhii* is a filamentous alga resistant to grazers because of its trichome size (Gliwicz, 1990). The new community composition favoured phytoplankton grazing, leading to a stronger control of
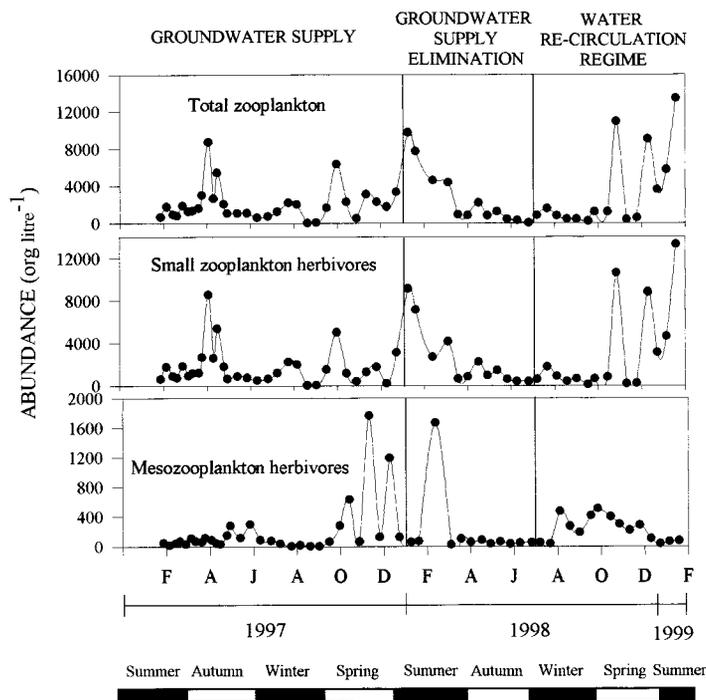

Figure 7. Abundance of total zooplankton, small zooplankton herbivores, and mesozooplankton herbivores and their temporal variability.
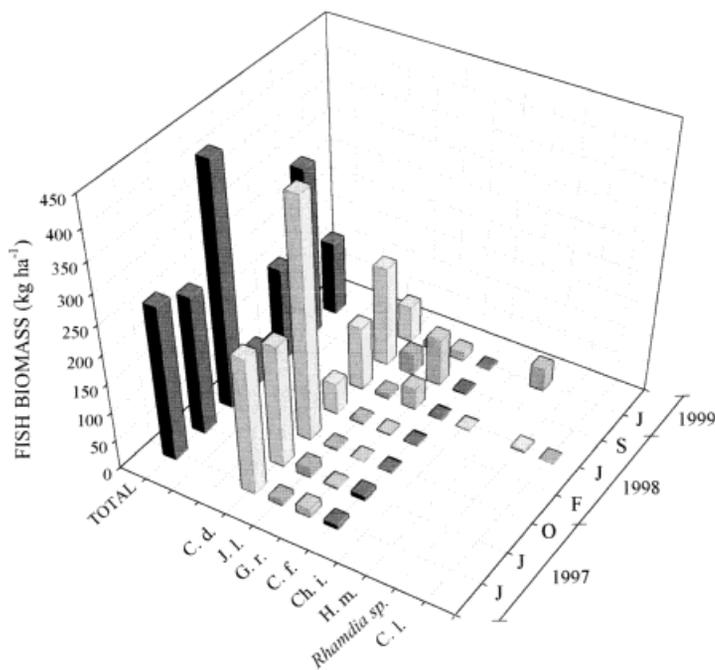
Figure 8. Total and specific fish biomass using seine net captures. C.d., *Cnesterodon decemmaculatus*; J. l., *Jenynsia lineata*; G. r., *Gymnogeophagus rabdotus*; C. f., *Cichlasoma facetum*; Ch. i., *Cheirodon interruptus*; H. m., *Hoplias malabaricus*; C. l., *Crenicichla lacustris*.

algal development by mesozooplankton that produced the clear-water phase observed in spring. In this sense, it is remarkable that before restoration the spring increment of mesozooplankton herbivores (Sommaruga, 1993, 1995) was not concomitant with a clear-water phase.

The physical and chemical changes observed during clear-water periods indicate how important the variation of the food web structure is for system functioning. The ammonium and phosphorus pulses observed during the clear-water phases have been associated with lower phytoplankton assimilation and higher zooplankton excretion (Lampert and Sommer, 1997). On the other hand, the high biomass and algal sedimentation produced an increase in the nitrogen, phosphorus and organic matter content of the sediment, promoting anoxic conditions (due to organic matter decomposition) during summer. This process might influence the temporal decrease of benthic abundance and prevent colonization of sediments (Frantzen *et al.*, 1994; Popp and Hoagland, 1995).

Stable clear-water phases (Secchi depth > 1 m) can be expected at TP < 60 µg litre^{-1} and at 45 µg litre^{-1} of Chl *a*, for mixed phytoplankton in shallow lakes. However, higher TP levels do not necessarily exclude the existence of an alternative clear-water state (Moss *et al.*, 1996; Hosper, 1997). Some eutrophic lakes show a clear-water phase during spring, which sometimes persists for up to 1 month (Gulati, 1983; Sommer *et al.*, 1986; Lampert and Sommer, 1997). This phenomenon was observed in Lake Rodó with TP concentrations higher than 60 µg litre^{-1}. Scheffer (1998) demonstrated that clear-water states could be linked to zooplankton structure (especially to the biomass of large-bodied herbivores) at intermediate nutrient levels. Jeppesen (1998) suggested that fish predation pressure on the large-sized zooplankton may be unimodally linked with nutrient levels. The highest proportions of *Daphnia* in the total biomass of cladocerans during summer in 300 Norwegian and Danish lakes were observed at 50–100 µg litre^{-1} TP, while at 100–200 µg litre^{-1} (similar to P levels in Lake Rodó) the percentages of *Daphnia* were also important and similar to those at 25–50 µg litre^{-1}. The abundant populations of small omnivorous fish

(such as *C. decemmaculatus* and *J. lineata*) are thought to maintain a high predation pressure on zooplankton, leading to the absence of large-bodied herbivores (Lazzaro, 1997) and the temporal variation in the abundance of herbivorous mesozooplankton. The preliminary analysis of stomach contents of the above-mentioned species support this hypothesis (Scasso *et al.*, unpublished data). Based on the evidence of phosphorus concentration, the lower abundance of filamentous cyanobacteria compared with 1992, and the temporal variation in the abundance of herbivorous mesozooplankton during 1997–1998, top-down control could play a key role in influencing the water transparency in Lake Rodó.

The summer decline of mesozooplankton herbivores which has been observed in many temperate lakes (Jeppesen, 1998) can be ascribed to blooms of cyanobacteria or to food limitation. Some shallow temperate lakes dominated by edible phytoplankton species (such as green algae) and with a high biomass of planktivores that feed more actively in summer (Jeppesen *et al.*, 1996, 1998), experience minor phytoplankton grazing pressure during this season. Lake Rodó possibly presents a similar seasonal pattern, as the abundance of mesozooplankton herbivores decreased in early summer, when green algae were still dominating the phytoplankton community. Besides, a clear decrease in the biovolume of cyanobacteria (*Microcystis aeruginosa* and *M. tenuissima*) was recorded in association with a large increase in *Diaphanosoma birgei* during one week in summer 1998. Thus, it could be argued that the predation pressure of *C. decemmaculatus* and *J. lineata* was higher in summer.

The reproductive strategy of *C. decemmaculatus*, the most abundant fish in the lake, is highly successful. It is a viviparous species with up to three reproductive phases per year (Lorier and Berois, 1995). This characteristic, coupled with a short generation time and low predation pressure by piscivores, has favoured the rapid re-colonization of the lake from introduced individuals. This also explains the high biomass reached in a short period.

C. facetum and *G. rabdotus* have broad diets. Ruiz *et al.* (1992) found that a great part of *C. facetum* diet consists of eggs and fish fry, with a high percentage of small poecilids and other fish. The lower relative abundance of *C. facetum* and *G. rabdotus* could have been caused by the short length of time since re-colonization of the lake and their longer generation times compared with those of the small omnivorous species. *C. facetum*, like other cichlids, is a very abundant fish in the littoral zones of many eutrophic lakes, including those where it was introduced as an exotic species (Scasso, 1996). Both species could exercise an effective predation pressure on the small omnivorous fish species, but intensive angling has resulted in populations dominated by small individuals with a high predation pressure on zooplankton (Scasso *et al.*, unpublished data).

Biomanipulation of urban lakes in Uruguay is a complex activity due to the biological characteristics of the dominant omnivorous species and the frequent spread of *C. decemmaculatus* by the public authorities for controlling mosquito larvae. Moreover, fishing activities are not regulated leading to a high pressure on piscivores and large-sized omnivores. Removing small omnivores and stocking with piscivores, combined with a nutrient reduction programme and the mechanical harvest of floating plants, could be the key factors for achieving a stable, clear-water phase. However, if *Microcystis* or other similar genera blooms occur in spring and summer, additional measures (e.g. reduction of the hydraulic residence time) will be needed to improve water transparency.

Sub-tropical lakes show some similar features to temperate lakes, such as the presence of large-bodied zooplankton (particularly *Daphnia* species), but the omnivorous and piscivorous fish communities resemble those of tropical lakes (Lazzaro, 1997). Taking this into account, biomanipulation in sub-tropical areas using native piscivores such as *Hoplias malabaricus* (Erythrinidae) and *Crenicichla lacustris* (Cichlidae) could be more efficient than the removal of planktivorous or small omnivorous fish. The zooplanktivorous species in temperate northern hemisphere regions are generally larger and have lower reproductive rates than *C. decemmaculatus*; therefore, the control of small omnivorous fish in sub-tropical lakes is more difficult. Besides, in South American countries, the spread of omnivorous and

planktivorous fish for controlling mosquito larvae is very common. *Gambusia affinis* (Poeciliidae), analogous to *C. decemmaculatus* in North America, whose predation pressure on zooplankton increases the phytoplankton biomass (Hurlbert and Mulla, 1981), has been introduced in Chile and Argentina (Ruiz, 1993). The consequences of these management activities and the effects of biomanipulation need further experimental analysis in sub-tropical and tropical lakes.

ACKNOWLEDGEMENTS

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