Response of a shallow Mediterranean lake to nutrient diversion: does it follow similar patterns as in northern shallow lakes?

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SUMMARY

1. In view of the paucity of data on the response of warm shallow lakes to reductions in nutrient loading, this paper presents a long-term limnological data set to document changes in the food-web of a shallow Mediterranean lake (Lake Albufera, Valencia, Spain) that has experienced reductions in phosphorus (P) (77%) and nitrogen (N) (24%) loading following sewage diversion.

2. Nine years after sewage diversion, P concentration in the lake was reduced by 30% but remained high (TP = 0.34 mg L⁻¹), although the mean water retention time in the lake was only 0.1 years. Nitrate concentrations did not significantly change, probably because the lake continued to receive untreated effluents from ricefields.

3. Chlorophyll *a* concentration was reduced by half (annual mean of 180 μ g L⁻¹). Cyanobacteria abundance remained high but its composition changed towards smaller species, both filamentous and chroococcal forms.

4. Cladocera abundance increased and reached peaks twice a year (December to March and July to September). After nutrient reduction, short-term clear-water phases (up to 5 weeks) occurred during February to March in several years, concomitant with annual flushing of the lake and lower fish densities. The abundance of Cladocera in winter contrasted with the spring peaks observed in northern restored shallow lakes. The zooplankton to phytoplankton biomass ratio remained lower than in northern temperate shallow lakes, probably because of fish predation on zooplankton.

5. Improvement of the water quality of Lake Albufera remained insufficient to counteract littoral reed regression or improve underwater light allowing submerged plants recolonise the lake.

6. Sewage diversion from Lake Albufera impacted the food web through the plankton, but higher trophic levels, such as fish and waterfowl, were affected to a lesser degree.

Although the fish species present in the lake are mainly omnivorous, long-term data on commercial fish captures indicated that fish communities changed in response to nutrient level and trophic structure as has been observed in restored shallow lakes at northern latitudes.

7. Phosphorus concentrations produced similar phytoplankton biomass in Lake Albufera as in more northern shallow lakes with abundant planktivorous fish and small zooplankton. However, in Lake Albufera, high average concentrations were maintained throughout the year. Overall, results suggest that nutrient control may be a greater priority in eutrophicated warm shallow lakes than in similar lakes at higher latitudes.

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Introduction

It is generally accepted that control of nutrient inputs is a crucial factor in restoring lakes from cultural eutrophication, especially in shallow lakes where nutrient recycling is usually faster than in deep lakes (Moss, Madgewick & Phillips, 1996a). Restoration of shallow lakes has mainly been carried out in northern temperate regions and recent reviews emphasise the need for a wider knowledge of lake restoration in south temperate, subtropical and tropical lakes to establish general models (Jeppesen et al., 2003). In northern temperate shallow freshwater lakes reduction of eutrophication symptoms and re-establishment of submerged macrophytes appear to occur when total phosphorus (TP) concentration in the lake is reduced to below $0.1-0.05 \text{ mg L}^{-1}$ (Jeppesen *et al.*, 2000). Critical thresholds for warmer lakes are still unknown, but there is experimental evidence from the Mediterranean zone showing that nutrient concentrations for oligotrophication and the recovery of submerged macrophyte are lower than in northern temperate shallow lakes (Romo et al., 2004).

After nutrient reduction, a delayed response and biological resistance to change are often observed in shallow lakes because of internal phosphorus loading (Søndergaard, Jensen & Jeppesen, 2001). In addition, in very shallow lakes wind-induced sediment resuspension may significantly increase internal phosphorus (P) recycling, which is further enhanced by high water temperature (Søndergaard et al., 2001). According to the alternate stable-states model for shallow lakes (Scheffer et al., 1993), P reductions may lead to abrupt shifts in phytoplankton biomass rather than a linear decline. Such nonlinear relationships between TP and chlorophyll a concentrations have indeed been found in both northern temperate and subtropical lakes (Quirós, 1997; Mazumder & Havens, 1998). Some studies of subtropical shallow lakes have shown that a nutrient loading reduction may lead to improved lake water quality (Lowe et al., 2001; Scasso et al., 2001). There is also evidence that mesozooplankton can improve water transparency in subtropical and southern temperate shallow lakes, although only during short periods because of intensive fish predation on zooplankton (Quirós, 1997; Scasso et al., 2001;

Beklioglu, Ince & Tuzun, 2003). In northern shallow lakes, fish communities often react to oligotrophication by an increasing proportion of piscivorous fish (Jeppesen, Jensen & Søndergaard, 2002). This response seems unlikely in warm-water lakes, where piscivorous species are scarce and frequently replaced by smaller facultative predators, with a predominance of omnivorous species (Fernando, 1994; Lazzaro, 1997; Blanco et al., 2003). Subtropical and tropical lakes typically host small-bodied zooplankton, and in consequence, top-down effects on phytoplankton are reduced (Crisman & Beaver, 1990; Fernando, 1994; Lazzaro, 1997). In addition, cyanobacteria are generally more common in tropical and sub-tropical freshwaters (Komárek, 1985; Pollingher & Berman, 1991; Talling & Lemoalle, 1998), and can dominate phytoplankton communities during both turbid and clear, macrophyte-dominated phases in southern temperate shallow lakes (Romo et al., 2004).

Few studies on food-web changes after nutrient diversion have been made on southern temperate, tropical or subtropical shallow lakes (Lowe et al., 2001; Scasso et al., 2001; Beklioglu et al., 2003; Coveney et al., 2005). This paper presents food-web responses to nutrient reduction in a shallow Mediterranean lake based on a long-term limnological data set, which is compared with published data from northern shallow lakes. We hypothesised that in warm temperate lakes (i) phosphorus inputs support comparable phytoplankton biomass to that in northern shallow lakes, but seasonal average of phytoplankton biomass is higher, leading to prolonged low water transparency; (ii) cyanobacteria are resilient to nutrient reduction; (iii) the zooplankton to phytoplankton biomass ratio remains lower after nutrient reduction, owing to predation of omnivorous fish on zooplankton; and (iv) large zooplankton (mainly Cladocera) can only temporarily influence water clarity and phytoplankton community structure and biomass after nutrient reduction.

Methods

Study site

The Albufera of Valencia is a shallow, oligohaline (salinity $1-2\infty$) and polymictic lake located in the

Natural Park of Albufera (210 km²) on the Mediterranean Spanish coast (39°20'N, 0°21'W). Lake Albufera is the largest Spanish coastal lake with a surface area of 23.2 km², a mean depth of 1.2 m, and a high water renewal rate of about 10 year⁻¹. Since the 18th century rice has been cultivated intensively in the areas surrounding the lake, and the lake water level is regulated for irrigation by sluice gates situated at its three outlet channels which flow into the Mediterranean Sea. The hydrological cycle has two main periods of water renewal during emptying of the rice fields (January to March) and harvest (September to October), and periods of long or intermediate water-table stability during the remaining months. The Albufera of Valencia is a southern temperate lake, with an annual mean air temperature for 1980-2000 of 18 ± 5 °C and 615 ± 228 mm of annual mean rainfall, concentrated in spring and autumn. Average air temperature has risen by 1 °C and rainfall has decreased by 120 mm during the 20-year period from 1980 to 2000.

Lake Albufera was densely covered by macrophytes (Chara, Potamogeton, Myriophyllum, Ceratophyllum) during the first half of 20th century (Arévalo, 1916; Pardo, 1942), but since the 1960s, eutrophication rapidly resulted in a turbid phytoplanktondominated state (Blanco, 1974; Dafauce, 1975). The lake has a near-shore bed of emergent vegetation and several small in-lake reed stands, whose total area has been severely reduced. The phytoplankton community was dominated by cyanobacteria during 1980-88 (Romo & Miracle, 1993, 1994), and zooplankton comprised mostly cyclopoids and rotifers, with periods of sporadic cladoceran presence (Alfonso & Miracle, 1990; Oltra et al., 2001). Water physical and chemical data for the 1980s are reported elsewhere (Soria, Miracle & Vicente, 1987; Soria, 1997). Until the 1990s, urban and industrial discharges went directly to the lake through irrigation channels and gullies, and represented 17% of the annual water input, while 67% came from rice fields (Soria & Vicente, 2002). In 1991, a restoration plan for the lake started by removing 30% of the nutrient-rich sewage discharge, mainly from urban and industrial sewage located in the northern and western part of the lake. However, untreated nitrogen-rich effluents from rice fields, mainly located in the south of the lake, continued to be discharged into the lake. By 1999, total external P loading to the lake was reduced by 77% (from 18 to 4 g P m⁻² year⁻¹) and N loading by 24% (from 324 to 247 g N m⁻² year⁻¹). The TN : TP loading ratio increased from 8 to 61 between 1988 and 1999.

Data collection

Monthly or bimonthly water samples for physical and chemical analyses were collected from 1994 to 2000 after sewage diversion, chlorophyll a was analysed from 1995 onwards and plankton samples were collected from November 1997 to December 2000. During clear-water phases, samples were collected every 3-7 days. Sampling was carried out at three sampling points in the lake used in previous studies before nutrient diversion during 1980-88 (1984 was not sampled). The average value of all the sampling points is reported in this study. Prior to sewage diversion, zooplankton and TP concentration in the lake were only monitored in 1986 and 1988, respectively. Samples were taken from the upper 50 cm of the water column. Water was analysed using standard methods (APHA, 1992). Phytoplankton community composition and biovolume were determined according to Romo & Miracle (1993), and a multiplication factor of 0.12 was used to convert biovolume to dry mass (McCauley & Kalff, 1980). The greatest axial length or diameter for phytoplankton (GALD) based on phytoplankton biovolume was estimated following Reynolds (1984). Zooplankton was concentrated in situ by filtering 3-L water samples through a 35-µm mesh and fixed in 4% formaldehyde. Counting was carried out using an inverted microscope and dry mass was determined by length-weight relationships for Crustacea and rotifers according to Dumont, Van de Velde & Dumont (1975) and Bottrell et al. (1976), after measuring up to 25-50 individuals. Fish community structure was derived from annual commercial captures from 1950 to 2001. In addition, the composition and fish weight and length of the pelagic and benthic fish stock was determined during summer 2000 and spring 2002 using fyke nets and multiple mesh-sized gill nets (6.5, 8, 10, 12, 17, 21, 25, 29, 32, 36, 42, 47, 60 and 75 mm). The length of each size section and depth of gill nets was 3 and 1.5 m, respectively. Four gill and fyke nets each were homogenously distributed

in the lake and the fish catch per unit effort was kept constant in each sampling period (Jeppesen *et al.*, 1997). Wintering (January census) and breeding bird numbers were monitored from 1984 to 2001 by the Spanish Bird Society, according to international wetland protocols for Ramsar and ZEPA zones, which include Lake Albufera and its catchment (Martí & Del Moral, 2002).

Data analysis

To homogenise data size and sampling interval of the limnological variables for statistical analyses, monthly means of each variable for the pretreatment (1986–88) and post-treatment (1997–2000) periods were analysed using Wilcoxon's test for matched pairs. Mann–Whitney *U*-test was used to compare vertebrate annual data before pretreatment 1980–89 (fish) and

Table 1 Limnological and biological variables before (1986–88) and after (1997– 2000) sewage diversion from Lake Albufera of Valencia (Spain). Probability values (*P*) refer to Wilcoxon's test on monthly means. 1984–90 (waterfowl), with those of 1991–2001 to search for differences after nutrient diversion. Waterfowl were categorised as piscivorous, herbivorous, wading birds, diving ducks and surface-feeding ducks. Spearman's correlation analyses were used for some limnological variables.

Results

Physical and chemical variables

Several limnological variables of Lake Albufera changed significantly within 9 years after starting sewage diversion (Table 1). The concentration of soluble reactive phosphorus (SRP) dropped significantly from an average of 0.17 to below 0.01 mg L^{-1} , and annual mean TP concentration decreased from 0.5 to 0.3 mg L^{-1} , with the greatest monthly

Variable	Before sewage diversion	After sewage diversion	<i>P</i> -value
Conductivity (µS cm ⁻¹)	1784 ± 389	1878 ± 306	0.67
Mean annual temperature (°C)	18.7 ± 6.9	19.4 ± 6.2	0.21
рН	8.8 ± 0.4	9.0 ± 0.4	0.05
Secchi depth (m)	0.21 ± 0.08	0.27 ± 0.15	0.59
Nitrate (mg N L ⁻¹)	0.94 ± 0.61	0.97 ± 1.00	0.75
Ammonium (mg N L^{-1})	0.99 ± 1.66	0.81 ± 0.49	0.78
Soluble reactive phosphorus (mg P L ⁻¹)	0.17 ± 0.25	< 0.01	< 0.01
Total phosphorus (mg P L^{-1})	0.49 ± 0.2	0.34 ± 0.14	0.03
Chlorophyll a ($\mu g L^{-1}$)	269 ± 68	180 ± 53	< 0.01
Chlorophyll <i>a</i> : TP	0.56 ± 0.26	0.61 ± 0.29	0.12
Phytoplankton biovolume (mm ³ L ⁻¹)	174 ± 99	140 ± 66	0.81
Phytoplankton abundance $(10^5 \text{ individuals mI}^{-1})$	3.1 ± 3.0	6.8 ± 3.7	< 0.01
GALD biovolume $\leq 50 \text{ µm (mm}^3 \text{ L}^{-1})$	19 + 12	65 + 23	< 0.01
GALD biovolume >50 μ m (mm ³ L ⁻¹)	128 ± 104	73 ± 50	< 0.01
Phytoplankton biovolume (mm ³ L^{-1})			
Cyanobacteria	136 ± 100	108 ± 61	0.43
Filamentous Cyanobacteria	129 ± 102	74 ± 54	< 0.01
Chroococcal Cyanobacteria	8 ± 11	34 ± 22	< 0.01
Chlorophyta	2.6 ± 1.1	7.4 ± 4.7	< 0.01
Bacillariophyta	5.9 ± 2.8	23 ± 16	< 0.01
Cryptophyta	0.66 ± 0.40	1.3 ± 1.1	0.27
Dinophyta	0.22 ± 0.22	0.77 ± 0.8	< 0.01
Euglenophyta	1.15 ± 2.53	0.22 ± 0.19	0.03
Zooplankton biomass (ug dry mass L^{-1})	291 ± 111	474 ± 259	0.12
Rotifera (ug dry mass L^{-1})	66 ± 67	84 ± 61	0.43
Cladocera (ug dry mass L^{-1})	10 ± 13	128 ± 168	0.02
Cyclopoid Copepoda (μg dry mass L ⁻¹)	215 ± 72	262 ± 123	0.35
Zooplankton biomass :	0.021 ± 0.017	0.038 ± 0.036	0.18
phytoplankton biomass			
Zooplankton biomass : chlorophyll a	1.08 ± 0.27	3.23 ± 2.7	0.02

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decrease occurring in spring and autumn (Table 1; Fig. 1). The annual SRP : TP ratio declined from 0.35 to 0.03 after sewage diversion, and the ratio of summer to annual mean TP concentration approached one. Mean annual nitrate concentration in the lake water did not significantly change between the compared periods (Table 1), and maximum concentrations corresponded with the emptying of surrounding rice fields (January and September to October; Fig. 1). The annual water temperature rose by $0.7 \,^{\circ}$ C during the last two decades (Table 1), with monthly mean water temperatures ranging between 9.7 and 28.4 $^{\circ}$ C (Fig. 1). Mean annual Secchi depth did not significantly increase in the lake, except during December to March (Table 1; Fig. 1).



Fig. 1 Seasonal changes in water temperature; Secchi depth; concentrations of DIN, TP and chlorophyll *a*; phytoplankton abundance and biomass; and zooplankton biomass in Lake Albufera of Valencia (Spain), before (1986–88; filled circles and solid line) and after (1997–2000; open circles and stippled line) sewage diversion in 1991. Symbols represent monthly means for the periods and vertical bars standard errors.

Phytoplankton

Mean annual chlorophyll *a* concentration almost halved after sewage diversion (Table 1; Fig. 2). Concentrations decreased for all seasons including summer (from 317 to 200 μ g L⁻¹, *P* < 0.01). Annual and summer means of the chlorophyll *a* : TP ratio were similar and below one (summer ratio 0.55 and 0.65 before and after nutrient diversion, respectively). Chlorophyll *a* and suspended solids were significantly correlated (Spearman R = 0.60, P < 0.01). The lowest chlorophyll a concentrations were recorded during clear-water phases in March 1999 and February 2000, with concentrations of 1.6 and 0.2 μ g L⁻¹, respectively (Fig. 2). Clear-water phases coincided with the periods of highest annual water renewal in the lake when the rice fields are emptied, and lasted 11 and 30 days, respectively. Secchi depth reached the lake bottom during these periods (Fig. 3). Chlorophytes [Ankyra cf. judayi (G. M. Smith) Fott, Chlorella vulgaris Beijer and Chlamydomonas spp.] and diatoms (Cyclotella spp.) dominated the phytoplankton during the monitored clear-water phases (65-85% of total phytoplankton biovolume), which replaced slender filamentous cyanobacteria (Fig. 3).

Although mean annual chlorophyll *a* concentration decreased after nutrient diversion, the mean annual phytoplankton biovolume remained the same, while total phytoplankton abundance increased significantly (Table 1; Fig. 1). Total cyanobacteria biovolume was reduced by 15–20% in the lake, among which filamentous cyanobacteria declined from 78% to 48% of total phytoplankton biovolume after sewage diversion. However, this decrease in the proportion of

filamentous cyanobacteria was partly compensated by the significant increase of small chroococcal species (Table 1). *Chroococcus dispersus* (Keiss.) Lemm., *C. minutus* (Kütz.) Näg and *Aphanocapsa incerta* (Lemm.) Cronb. Kom. reached peaks between June to October for the period 1997–2000. Apart from euglenophytes, which decreased significantly, other groups increased their contribution to total phytoplankton biomass, especially diatoms and chlorophytes (Table 1). Mean biovolume of phytoplankton based on GALD decreased significantly (both large and small algae) after nutrient diversion (Table 1). Phytoplankton species richness did not vary between the two study periods (about 130 species).

Zooplankton

Annual zooplankton biomass increased by 38% after nutrient reduction, with a significant contribution of Cladocera (Table 1), mostly Daphnia magna Straus (December to March, 33-55% of total zooplankton biomass) and Moina micrura Kurz (July to September, 8-30% of total biomass; Fig. 1). Before sewage diversion, Cladocera (D. magna) appeared only in January and February and represented <30% of total zooplankton biomass. The mean individual weight of Cladocera almost doubled between the compared periods (from 8 to 14 µg individuals⁻¹). Daphnia magna dominated during the clear-water periods, with large fluctuations in its population size (Fig. 3). Annual mean biomass of rotifers and copepods also increased after nutrient reduction, but not significantly (Table 1). In fact, their contribution to the total zooplankton biomass diminished (15-20%). Copepods were only



Fig. 2 Long-term changes in chlorophyll *a* concentrations in Lake Albufera of Valencia (Spain). The start of sewage diversion and occurrence of clear-water phases are indicated by arrows.

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Fig. 3 Phytoplankton main groups and the dominant Cladocera (*Daphnia magna*) during monitored clear-water phases in 1999 (duration of 2 weeks) and 2000 (duration of 5 weeks). Upper panel shows the water level of the lake during these 2 years, with the greatest changes between January and March indicating regular water flushing for rice field drainage prior to tilling and sowing.

represented by the cyclopoid Acanthocyclops robustus Sars during both study periods. The main rotifer taxa were Synchaeta oblonga Ehrenberg, Polyarthra spp., Keratella spp., Brachionus angularis Gosse, B. variabilis Hempel, B. calyciflorus Pallas, Asplanchna brightwelli Gosse, Trichocerca pusilla Lauterborn and Proalides tentaculatus-digitus De Beauchamp-Donner. Although Brachionus variabilis was a facultative epibiont on D. magna it remained present for several weeks after D. magna populations declined during clear-water phases (Fig. 3). Zooplankton species richness increased after nutrient reduction. The zooplankton to phytoplankton biomass ratio was always low, although it increased slightly after sewage diversion (Table 1). The zooplankton to chlorophyll a ratio significantly changed from 1 to 3 (Table 1).

Fish

Commercial fish catches changed with the changes in the plankton community. Total fish captures of the main species (*Mugil* and *Liza* species) increased by 84%between 1950 and 2001, from 80 to 490×10^3 kg year⁻¹ (Fig. 4). In contrast, the captures of piscivorous species was severely reduced with increasing eutrophication, including eel (Anguilla anguilla L.; from 90 to 3.5×10^3 kg year⁻¹) and sea bass captures (*Dicentrarchus labrax* L.; from 30 to $0.25 \times$ 10^3 kg year⁻¹). The proportion of piscivore to total fish captures varied from 60% to 0.8% between 1950 and 2001. There was a main inflexion point of this ratio by 1974, with a suggestion of an earlier change by around 1966. Thus, the ratio of piscivore to total fish captures varied from 90% to 2% between 1950-66 and 1980-2001. During the last two decades before (1980-89) and after (1991-2001) sewage diversion, total mean annual fish captures represented about 150 kg ha⁻¹. Mugilidae catches did not differ statistically (P = 1.0) between these two decades (mean 335×10^3 kg year⁻¹), but the piscivore captures decreased significantly (P = 0.01), owing to a 50% reduction in eel catches (from a mean of 12 to 5×10^3 kg year⁻¹), although sea bass tended to increase slightly (mean from 30 to 110 kg year⁻¹;



Fig. 4 Long-term changes (1950–2001) in commercial fish captures in Lake Albufera for the main piscivorous (*Anguilla anguilla* L. and *Dicentrarchus labrax* L.) and plankti-benthivorous species (*Mugil* spp. and *Liza* spp.).

P = 0.28). The fish community in the lake was dominated by individuals larger than 10 cm (73%). Mean individual body mass of all fish was 140 g and for piscivores 105 g. Other fish species, most of them non-native, were also abundant in the lake, although they are not usually captured owing to their low commercial value. They included, for instance, carp (*Cyprinus carpio* L.; representing about 40% of the total fish biomass), pumpkinseed sunfish (*Lepomis gibbosus* L.) and mosquitofish (*Gambusia holbrooki* Girard). Total fish species richness decreased from about 28 to nine species between 1950 and 2001.

Waterfowl

The relative abundance of wintering waterfowl did not differ between the periods before (1984–90) and after (1991–2001) sewage diversion, with populations of around 7 and 6×10^5 individuals year⁻¹. Only wintering diving ducks decreased significantly (from 12 000 to 6000 individuals year⁻¹; P = 0.01). On the contrary, total number of breeding birds almost doubled between the compared periods (from 5000 to 9000 breeding pairs year⁻¹; P < 0.01). Breeding piscivorous birds (mainly *Larus* spp., *Sterna* spp., ardeids and great cormorant, *Phalacrocorax carbo* L.),

herbivorous (mostly coots, Fulica atra L.) and waders increased significantly after sewage diversion (P < 0.01). Breeding piscivorous birds increased especially from 1994 onwards, from 3000 to 7000 breeding pairs year⁻¹ for the compared periods, after the creation of reserve areas near the lake. Waders increased from a mean of 250 to 450 breeding pairs year⁻¹. Herbivorous waterfowl (*F. atra* and Porphyrio porphyrio L.) had low densities in the aquatic reed stands of the lake in all study years (from seven to 37 breeding pairs year⁻¹). The number of breeding pairs of diving and surface-feeding ducks did not change after sewage diversion, with a mean of 60 and 1350 pairs year⁻¹, respectively. During the clear-water phases, some Anas species fed on Cladocera in the lake, but otherwise preferentially used the rice fields. Waterfowl species richness did not vary for the last two decades. There were about 28 species, comprising 16 piscivorous birds, seven ducks and five wading species.

Discussion

After nutrient reduction Lake Albufera has shown some changes in nutrient level and trophic structure. Our results agree with the data compiled by Sas (1989)

who concluded that a response in chlorophyll a concentration is only expected when SRP concentrations drop below 0.01 mg L^{-1} . The decline in the lake of nutrient concentrations was more marked for SRP, which now remains at undetectable levels throughout most of the year, suggesting that P limitation for phytoplankton has become more significant in recent years. With sewage diversion, the TP concentration in Lake Albufera decreased by about 30%, but mean annual values (0.34 mg L^{-1} between 1997 and 2000) were still too high to reduce chlorophyll a concentrations below eutrophic levels or re-establish submerged macrophytes (TP $\leq 0.05 \text{ mg L}^{-1}$; Romo *et al.*, 2004). The decline of P concentration in the lake following reduction of P loading was similar to that observed in other restored shallow lakes (Jeppesen *et al.*, 2005), although high P levels (>0.2 mg L^{-1}) were maintained all the year round (Fig. 1). Phosphorus concentrations in Lake Albufera produced a phytoplankton biomass similar to that in northern temperate shallow lakes with abundant planktivorous fish and small zooplankton (Moss et al., 1996b; Jeppesen et al., 2000), but the high average levels were maintained throughout the year and were comparable with those observed in subtropical shallow lakes (Quirós, 1997; Scasso et al., 2001). Some experiments suggest that the influence of nutrient loading on phytoplankton biomass is greater in southern shallow lakes, indicating that nutrient control may have to be a greater priority in these systems than in more northern lakes (Moss et al., 2004). Mazumder & Havens (1998) showed that there was a significantly lower transparency in subtropical lakes in Florida than in temperate lakes, both with small zooplankton. Accordingly, in a Mediterranean shallow lake a rapid switch to a turbid state was observed after P loadings of only 0.1–0.15 mg L^{-1} (Romo *et al.*, 2004). In Lake Albufera, removal of 77% of the P load proved to be insufficient to reach the loading threshold suggested for initiating complementary restoration measures, such as biomanipulation $(1-2 \text{ g P m}^{-2} \text{ year}^{-1}; \text{ Jeppe-}$ sen et al., 1990). Although biomanipulation in combination with nutrient reduction temporarily increased water transparency in some warm shallow lakes (Scasso et al., 2001; Beklioglu et al., 2003), even above the threshold of $2 \text{ g P m}^{-2} \text{ year}^{-1}$, this effect was unstable in the absence of macrophytes.

The zooplankton to phytoplankton biomass ratio in Lake Albufera was low compared with restored

northern shallow lakes (Jeppesen et al., 2005). Fish captures in Lake Albufera were above the suggested 20 kg ha⁻¹ to prevent removal of large zooplankton by fish in shallow lakes (McQueen & Post, 1988; Breukelaar et al., 1994). Nutrient reduction led to an increase in Cladocera biomass in Lake Albufera, as described for other restored shallow lakes (Jeppesen et al., 2002, 2005), but they were only able to control algae and influence water transparency for short periods during winter. As observed in some temperate and subtropical lakes (Köhler, Behrendt & Hoeg, 2000; Scasso et al., 2001; Köhler et al., 2005), the large filamentous cyanobacterium Planktothrix agardhii (Gom.) Anag. & Kom. was replaced by smaller species after nutrient reduction, which facilitated cladoceran grazing and the occurrence of clear-water phases. In temperate lakes, these clear-water phases often occur between April and August (Scheffer et al., 2001; Jeppesen et al., 2005), but in Lake Albufera they appeared earlier (February to March). This was possibly because of changes in phytoplankton community composition and size of species, to phytoplankton biomass reduction by flushing, to mild winter water temperatures (winter mean of 12 °C) enabling Cladocera to achieve net growth, and to a decrease of fish predation on zooplankton following annual maximum captures by commercial fishermen. Top-down control of phytoplankton biomass by large zooplankton was short-lived, partly because of high fish stocks and intense predation by most of the fish species present in the lake, as indicated by fish stomach analyses (Blanco et al., 2003). This finding is in agreement with plankton and fish studies of subtropical and tropical lakes (Fernando, 1994; Quirós, 1997; Scasso et al., 2001).

Sas (1989) argued that nutrient loading reduction initially affects phytoplankton biomass and later its community structure, which is in contrast to our results from Lake Albufera. As in some northern temperate lakes undergoing nutrient reduction (Jeppesen *et al.*, 2000, 2005; Köhler *et al.*, 2000), phytoplankton species composition changed in Lake Albufera and the community became more diverse. In addition, euglenophytes, which may indicate organic pollution in the lake (Romo & Miracle, 1994), decreased markedly. Cyanobacteria remained dominant, which agrees with observations in some subtropical lakes receiving reduced P loading (Scasso *et al.*, 2001; Coveney *et al.*, 2005). Summer replacement of filamentous cyanobacteria by chroococcal cyanobacteria, in response to water quiescence and reduced zooplankton grazing, took place in Lake Albufera at P concentrations around 0.3 mg L^{-1} , as also observed in enclosure experiments (Romo et al., 2004). Release of nutrients from the sediment favoured fast-growing species (e.g. mainly chlorophytes) in some northern shallow lakes (Jensen et al., 1994), but in warm lakes small chroococcal cyanobacteria can take advantage of nutrient pulses replacing the more slowly growing filamentous cyanobacteria (Romo et al., 2004). In Florida lakes, the average size of phytoplankton tends to decrease with decreasing total phytoplankton biomass (Duarte, Agustí & Canfield, 1990). Algae with smaller mean size appear to attenuate more light per unit of biomass than larger algae (Carpenter & Kitchell, 1993; Mazumder & Havens, 1998). The phytoplankton succession in Lake Albufera also agrees with Reynolds's model (Reynolds, 1993) for polymictic lakes, where filamentous non-heterocystous cyanobacteria alternate with centric diatoms at high flushing rates, as in Lake Albufera earlier in the year. Accordingly, diatoms (mostly epiphytic) and chroococcal cyanobacteria dominated during the mesotrophic phase of Lake Albufera in the first half of the 20th century (Pardo, 1942; Villena & Romo, 2003).

Sewage diversion from Lake Albufera impacted the food web through the plankton, but apparently had less effect on higher trophic levels, such as fish and waterfowl communities. Waterfowl abundance and diversity are primarily related to habitat diversity and food availability, associated with benthic animals and aquatic plants (Mitchell & Perrow, 1997). The water quality of Lake Albufera has remained too low to counteract littoral reed regression or to improve underwater light sufficiently for submerged plants to re-colonise the lake. In 1965, macrophyte beds in Albufera enabled a high carrying capacity of ducks and coots (e.g. 1000 coot pairs; Dafauce, 1975). Similar requirements apply to fish, especially those associated with aquatic vegetation, resulting in low fish diversity from the second half of the 20th century (Blanco & Romo, 2006).

Mesocosm experiments carried out to elucidate the impact of fish and bird feeding on submerged plants suggest that herbivory may also affect plant recovery (J.M. Benavent, pers. comm.), as in temperate lakes (e.g. Köhler *et al.*, 2005). Although the dominant fish species in the lake are mainly omnivorous (Blanco *et al.*, 2003),

the main changes in the long-term data of commercial fish captures followed the trophic state changes taking place in the lake, as also reported from northern shallow lakes (Moss et al., 1996a; Jeppesen et al., 2003). However, our conclusions are based mainly on an analysis of commercial fish data that are biased towards large fish of commercial interest, changes in fish community composition and biomass have been seen in several other restored lakes (Jeppesen et al., 2005). The ratio of piscivorous to total fish captures was nearly one during the macrophyte-dominated state of the Albufera but remained very low after the establishment of the turbid state. The inflexion point of this ratio around 1974 (Fig. 4), corresponded well with the doubling of the chlorophyll a concentration in this year and the major shift to a eutrophic state (mean of 53 µg chlorophyll $a L^{-1}$; Dafauce, 1975). The lake by then had switched to a state devoid of submerged macrophytes, which had started to decline already much earlier however. In 2005, Lake Albufera is still in a turbid state, which has persisted for more than 30 years.

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