

Chapter 2

THE ROLE OF FISH COMMUNITIES IN THE EUTROPHICATION OF SHALLOW LAKES

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ABSTRACT

The progressive anthropogenic eutrophication, the uncontrolled introduction of exotic fish species, and the lack of conservation and management strategies are highlighted as the main causes explaining the long-term changes in water biological quality in freshwater ponds and their surrounding aquatic ecosystems worldwide. Experimental evidence shows that fish direct and indirect effects on lake food web lead to algal growths and increased turbidity and nutrients concentration in fish-added treatments. Consequently, submerged macrophytes and epiphytic algae usually decline at increasing nutrient levels. Additionally, many freshwater fishes exhibit a generalist diet with an important contribution of non-planktonic components, and ontogenic shift towards benthic-detrivory has been observed in several species. Field studies on the feeding ecology of both endemic and introduced taxa show that demographic changes and facultative predation influence food webs in freshwater ponds by both direct predation and indirect effects (sediment bioturbation and excretion), however, cascading effects caused by introduced fish species may be more relevant for the food webs in certain bioclimates, e.g. Mediterranean shallow ponds and wetlands, where almost no piscivorous species are recorded and, in general, omnivorous species dominate independently of lake trophic state. Thus, the role of direct and indirect effects of fishes and the importance of their dietary features are stressed as key factors for understanding the causes that control the trophic status of freshwater ponds. Fishes affect biodiversity, quality and water transparency. Restoration of eutrophic ponds must involve control of nutrient inputs and fish communities, with adequate policies for fish and plant management and conservation.

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1. INTRODUCTION

1.1. General Scope

This chapter deals with some of the most fruitful theoretical paradigms in recent limnology, namely the trophic cascade theory (Carpenter and Kitchell 1993) and the ecology of shallow lakes (Jeppesen 1998, Scheffer 1998). Both are providing research frames intended to improve our knowledge of freshwaters and shallow lakes, particularly in respect of those aspects, among others, affected by anthropogenic perturbations. Lentic and shallow lakes and ponds are habitats of great relevancy as they contribute substantially to the world biogeochemical cycles and constitute very important biodiversity reservoirs. Additionally, they provide water for domestic, recreational, industrial and agricultural use. In spite of their fundamental importance, these freshwater systems have been severely affected by a multitude of anthropogenic disturbances, which have led to serious negative effects on their ecological status. Their diversity is currently threatened by a number of human actions, which includes increased nutrient loadings, pollution with toxic substances and the introduction of exotic species (Hansson and Brönmark 2002). Eutrophication in ponds often leads to the decline of submersed macrophytes, the increase in turbidity and algal biomass, and the dominance of benthivorous and zooplanktivorous fishes over piscivores (Moss 1998). High quality in shallow lakes is generally related to the presence of submerged plants and water transparency (Moss et al. 1996, 2003).

In this context, several international scientific projects have been developed to study the structure and functioning of shallow lakes in Europe. In the International Mesocosm Experiment (IME) a total of eleven parallel mesocosm experiments were carried out in six lakes located in Finland, Sweden, England, The Netherlands and Spain during 1998 and 1999. They investigated the climatic and latitudinal relationships between nutrient loading and zooplanktivorous fish and how these affected benthic and plankton communities in shallow lakes. Comprehensive discussions of the results are compiled in a special volume of *Freshwater Biology* (n° 49, 2004). As a general trend, it was found that the influence of nutrient loading is inversely proportional to latitude. The effects of fish were, however, more variable, but they were acknowledged to be a main structuring component of the food web in shallow lakes.

1.2. Ecological Particularities of Freshwater Ponds

Ponds and shallow lakes are numerically the most abundant waterbodies in the world (Wetzel 1990), and have been the aim of increasing scientific interest (e.g. Jeppesen 1998, Scheffer 1998). In brief, they differ from deep lakes in their naturally higher trophic status and their potential for having aquatic plants as the main primary producers. Several authors have demonstrated a refuge effect of macrophytes in maintaining high populations of zooplankters -especially cladocerans- that are able to control phytoplankton density and stabilizing thereby a clear-water phase in shallow lakes (Timms and Moss 1984, Schriver et al. 1995, Persson and Crowder 1998, Bertolo et al. 1999b). However, submerged plants also increase resources and habitat diversity for macroinvertebrates (Diehl and Kornijów 1997),

and some studies indeed show a positive relationship between macrophytes and fish growth rates (e.g. Richardson et al. 1998). Macrophytes also help to maintain high water clarity by competing with algae for nutrients and light (Van Donk et al. 1993, Perrow et al. 1997), increasing sedimentation of suspended particles (James and Barko 1990), and in some cases suppressing algal growth by allelopathy (Wium-Anderson et al. 1982, Gross 2003). Jeppesen et al. (1997) show that in fact P concentrations are noticeably higher in eutrophic shallow lakes without macrophytes. Conversely, fish populations can also affect the abundance of macrophytes: they can feed directly on them or their epiphytes, uproot mats, or increase nutrients in the water column and particulated matter on the plants through sediment resuspension (Jeppesen et al. 1998a). Fishes enhance thereby the succession from macrophytes towards other primary producers, accelerating the eutrophication processes (Brönmark and Vermaat 1997, Hansson et al. 1997) (Figure 1).

Recent limnological research has started to focus in the ecology of subtropical and tropical ponds (Jeppesen et al. 2003, 2005), as well as those in the Mediterranean zone (Romo et al. 2004, 2005, Villena 2006, Beklioglu et al. 2007). Mediterranean shallow ponds are characterized by a relatively more fluctuating water depth, which can allow the maintenance of submersed macrophytes at intermediate nutrient levels, but it seems that they can turn into a turbid state at lower nutrient loadings that shallow lakes at central and northern Europe (Moss et al. 2004, Fernández-Aláez et al. 2004, Romo et al. 2004). There is controversy about if some theories on the ecology of shallow lakes can be generalized to other systems, especially they have to be tested in other climatic zones, such as the Mediterranean, tropical and subtropical areas (Jeppesen et al. 2003, Jeppesen et al. 2005, Beklioglu et al. 2007).

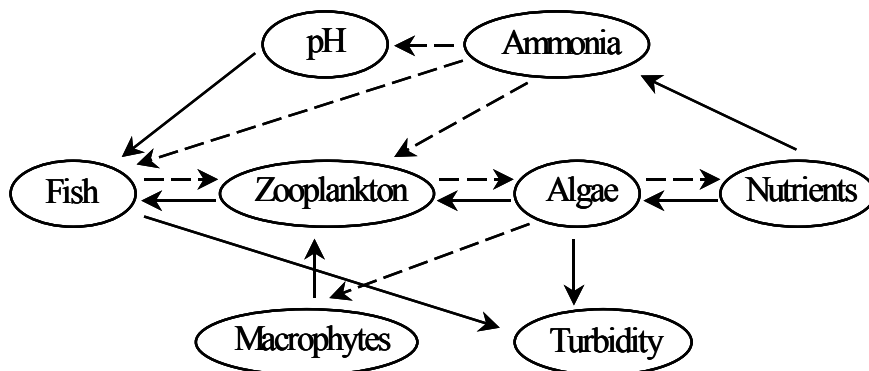


Figure 1. Main ecological interactions between abiotic and biotic factors in freshwater ponds. Solid arrows: direct relationships. Dotted arrows: inverse relationships.

1.3. Food Webs and Trophic Cascades in Lakes

Trophic cascades are defined as a set of reciprocal effects between predators and preys that change the abundance, biomass or productivity of a certain population, community or trophic level through more than one bond in a food web (Pace et al. 1999). Traditionally, food web theory gives great importance to predation as an structuring force in ecosystems (Carpenter et al. 1985, Carpenter and Kitchell 1993, Bertolo et al. 1999b). Trophic cascade

theory states that nutrient input establishes the potential productivity of a lake, while deviations from this potential are due to food web interactions. Selective predation, variability at the top of food webs is transmitted down to zooplankton, macroinvertebrates and phytoplankton, which influence ecological processes (Carpenter et al. 1985, Carpenter and Kitchell 1993). Thus, the concept of trophic cascade explains the differences in productivity between lakes with similar nutrient supplies by means of their differences in food webs (Carpenter et al. 1985).

Food web structure in most of the lakes is regulated by top-down and bottom-up processes. Top-down control implies the regulation of a lower trophic level by a higher level predator. In this process, planktivorous fishes reduce the abundance of large zooplankton and enhance phytoplankton (e.g. Vanni et al. 1997). Bottom-up control leads to the regulation of food web components via primary producers or by limiting their resources e.g. nutrients (Pace et al. 1999). Several studies show that both abiotic factors and fish predation regulate the primary productivity in many limnosystems (Carpenter et al. 1997). According to Jeppesen et al. (1998b), changes in trophic dynamics, turbidity and other variables can be attributed to modifications in fish abundance and structure, rather than to nutrient loads. In shallow lakes and ponds, fishes are known to increase significantly turbidity by bioturbation of the sediment, as well as by indirect mechanisms that influence algal biomass and phosphorus (Drenner et al. 1990, Christoffersen et al. 1993, Jeppesen 1998, Lacroix et al. 1999). In contrast, experimental results (Carpenter and Kitchell 1988, Hessen 1997, Meijer 2000) show that a reduction of planktivorous fish may improve water quality and transparency and this has been used as a remediation technique in shallow and deep lakes (Moss et al. 1996, Drenner and Hambright 1999).

Therefore, food web structure and the effects of fishes on lower trophic levels through predation and nutrient recycling are important processes for the ecology of freshwater ecosystems (Holopainen et al. 1992). Fish predation can be the main factor regulating zooplankton biomass in lakes (Morgan et al. 1980). Intense top-down effects of fishes on zooplankton have been well documented (e.g. Declerck et al. 1997, Bertolo et al. 1999b), and the effects may increase with lake productivity (Hessen et al. 1995, Persson et al. 1996, Kitchell and Carpenter 1993b). Top-down control can be important in shallow lakes (Jeppesen et al. 1990a, 1997), where planktonic algal growth may be related to fish density (Threlkeld 1987).

On the other hand, some studies point out that the effects and responses to a reduction in external nutrient inputs can be more intense than those related to a reduction in zooplanktivorous fishes. Zooplankton population density may be affected more by bottom-up forces, e.g. changes in food availability, than by changes in rates of fish predation (Threlkeld 1987). Vanni (1987b) showed that, under eutrophic conditions, the presence of fishes was unrelated to phytoplankton abundance. Drenner et al. (1990) found that nutrients modulate the predatory effects of fishes in the food web. Therefore, biomanipulation requires the reduction of nutrients until certain thresholds to obtain a desirable response (Moss et al. 1996, Jeppesen et al. 1990b, Drenner and Hambright 2002). The effects of the trophic cascade generally attenuate along the food web (Bertolo et al. 1999b). According to Lacroix et al. (1999), energy transfer between phytoplankton and zooplankton is low in eutrophic shallow lakes.

It is now widely accepted that predators also affect their preys by indirect ways. They can control primary producers by altering the amount and quality of their resources and by recycling nutrients by means of excretion (Persson and Crowder 1998, Drenner and

Hambright 2002). Nutrient excretion by fishes can represent substantial amounts of N and P into the system and a flow from benthic to planktonic habitats. For example, Holopainen et al. (1992) showed that high fish densities are generally related to high nutrient concentrations. Therefore, fishes can also be determinant in biogeochemical cycles and hence in the dynamics of primary producers. Nutrient recycling and transformation by zooplankters is also acknowledged as a relevant source for algal growth (Persson and Crowder 1998). High densities of planktivorous fish in the food web produce that phosphorus excreted by fish is essentially accumulated into the phytoplanktonic biomass, when algae are not limited by herbivorous zooplankters (Vanni and DeRuiter 1996). These effects contribute substantially to the structuration of aquatic food webs (Hessen 1997, Vanni et al. 1997, Mehner et al. 1998a, Bertolo et al. 1999a) and they increase in synergy with nutrient inputs (Drenner et al. 1998). Vanni (1987a) also suggested that such indirect effects could be more intense in eutrophic lakes.

1.4. Zooplanktivorism and Omnivorism in Lentic Systems

Prey density is controlled by environmental characteristics that influence the role of predation, such as habitat complexity or light regimes (Persson and Crowder 1998). Visual zooplanktivorous fishes tend to feed on large-sized zooplankters, leading to the dominance of smaller individuals, which are usually less efficient for phytoplankton grazing (Vanni 1987a, Hansen and Jeppesen 1992). Prey size and motility are some of the main factors controlling their predation for fishes (O'Brien 1987, Hansen and Jeppesen 1992, Hambright and Hall 1992). They explain the generalized fish preference for cladocerans over other micro and macrozooplankters. This justifies the general dominance of small zooplankton taxa in lakes with abundant planktivorous fish (Moss 1998, Gyllström et al. 2005). However, high water turbidity may inhibit predation on cladocerans (O'Brien 1987, Drenner et al. 1988). Furthermore, fish population characteristics -size, age structure- together with dietary features -mainly elective feeding- may play a key role in lake ecological processes (Kitchell and Carpenter 1993b, Vanni and DeRuiter 1996).

Nevertheless, very few fish species are strictly zooplanktivorous. Several studies show that different taxa exhibit somewhat omnivorous and facultative dietary patterns (Granado-Lorencio 1996). The trophic ecology of fish may be controlled to a great extent by prey density and availability (Lammens and Hoogenboezem 1991, Granado-Lorencio 1996, Christoffersen and Bosselmann 1997). Omnivory in freshwater ecosystems is often related to higher water turbidity, by enhancing periphyton and phytoplankton growth and, in general, eutrophication by increasing nutrient recycling (Schaus and Vanni 1990). Deficient utilization of food by fish leaves a considerable amount of material available for bacteria and other autothrophs (Margalef 1983, Schaus and Vanni 1990). For instance, cyprinid fishes constitute a large variety of specialists and generalists that feed on all trophic levels (Lammens and Hoogenboezem 1991). Their adaptative success depends on their wide dietary spectra and their ability to feed under high turbidity conditions (Peltonen et al. 1999). Cyprinids are especially abundant in very productive lakes and have been related directly to eutrophication processes in European lakes (Holopainen et al. 1992, Tammi 1999). In shallow warm lakes, fish communities are dominated by small species with scarce piscivores, which have consequences in the configuration of their food webs (Lazzaro 1997, Lazzaro et al. 2003), and

possibly in the measures for the recovery of eutrophic shallow ponds in these zones (Jeppesen et al. 2003, 2005).

1.5. Epiphytic Algae and Fish

Epiphytic algae constitute an important component, both structurally and functionally in shallow lakes (Ten Cate et al. 1991, McCormick and O'Dell 1996). Nutrients and fish may regulate epiphytic algae and plant growth in shallow lakes. In plant-dominated shallow lakes, macrophytes may limit the growth of epiphyton through competition for nutrients in the water (Ozimek et al. 1993), by shading (Kairesalo 1984; Sand-Jensen and Borum 1991; Cattaneo et al. 1998) and by harbouring grazers (Timms and Moss 1984; Lauridsen et al. 1996). On the other hand, epiphyton and phytoplankton can restrict submerged plants by shading and biomass of algae be controlled by interactions between herbivores and fish (Philips et al. 1978, Sand-Jensen and Søndergaard 1981, Balls et al. 1989, Romo et al. 2007). It is generally postulated that organic turbidity (i.e. mainly phytoplankton) is the main cause for plant decline during eutrophication. However, in very shallow lakes or in ponds where grazers of epiphytic algae are scarce, extensive growth of epiphyton enhance the disappearance of aquatic vegetation (Philips et al. 1978, Sand-Jensen and Søndergaard 1981; Neundorfer and Kemp 1993, Romo et al. 2007). Fish can play an important role also by transferring energy between the benthic and planktonic food webs. A high percentage of the carbon assimilated by fish can originally be fixed by periphyton, pointing out the relevance of the links between the planktonic and benthic food webs (Hecky and Hesslein 1995, Blumenshine et al. 1997).

Table 1. Main limnological parameters of the studied lakes. Mean values from different recent periods. Data from Blanco (2007).

Parameter	Sentiz	Xeres a	Albufera	Baldoví	Cap de Terme	Hond o	Caba nes
Area (ha)	4.7	0.5	2320	0.5	3.5	11	2.3
Mean depth (m)	0.8	0.6	1.2	1.8	2.2	1	2.1
pH	7.6	8.8	8.8	7.7	8.5	8.1	8
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	392	1864	2335	3020	2665	18380	1269 3
Total phosphorus ($\mu\text{g}\cdot\text{L}^{-1}$)	34	20	376	13	140	89	14
Chlorophyll-a ($\mu\text{g}\cdot\text{L}^{-1}$)	9	7	249	3	93	25	2

2. FIELD STUDIES

2.1. Study Sites

Aformentioned ecological hypotheses have been tested in several Spanish Mediterranean ponds (see Blanco 2007). The main limnological parameters of the studied systems are summarized in Table 1. Experimental work with *in situ* mesocosms was undertaken in two

shallow ponds, Lake Sentiz and Lake Xeresa (Figs. 2 and 3). Lake Sentiz is a small, mesotrophic shallow pond situated in north-west Spain (Figure 3), where Tertiary clay deposits cover relatively impermeable low-altitude plateaux (900 m a.s.l.). Water chemistry is dominated by chloride and calcium ions (Fernández-Aláez et al. 2002). The climate in the area is dry moderate Mediterranean, with hot dry summers and cool rainy winters. Highest mean temperatures (20° C) and driest periods (<20 mm) typically occur in July and August, causing annual fluctuations in the lake water level. The lake bottom is almost entirely covered by a diverse submerged macrophyte community dominated by *Myriophyllum alterniflorum* DC. in Lam. and DC., which may reach a biomass of 180 g dry mass m² (Fernández-Aláez et al. 2002). A high macrophyte biomass is maintained for long periods during the year (mean annual biomass of 76 g dry mass m²), in part because *M. alterniflorum* is perennial in the pond. There are only two fish species in Lake Sentiz: *Tinca tinca* L., which is the dominant species, and *Chodrostoma arcasii* (Steind).

The experiments described in Blanco et al. 2004 were carried out in Lake Xeresa, which is located on the Spanish Mediterranean coast (Figure 3). It is a shallow, macrophyte-covered lake (mainly *Chara* spp.) (Table 1). Water level also suffer pronounced annual fluctuations due to evaporation and agricultural use. Helophytic vegetation (mainly *Phragmites australis* [Car.] Trin. ex Steud). cover the surrounding area (Romo et al. 2004). Five more shallow lakes were studied in Blanco et al. 2003 and Blanco and Romo 2006, all of them located in the Spanish Mediterranean coast (Figure 3). These systems are placed in wetlands considered natural reserves. Lake size varied between 0.5 and 2300 ha with a mean depth less than 3 m. They are from oligohaline to brackish waters, with a trophic gradient from mesotrophy to hypertrophy (Table 1).

Further investigations were conducted in the Albufera Lake (Blanco and Romo 2006). This is a shallow, freshwater, polymictic lake located in the Natural park of the Albufera (210 km²) on the Spanish Mediterranean coast (Figure 3). It is the largest Spanish coastal oligohaline lake with a water renewal time of about 7 times per year (Romo et al. 2005). The lake has a belt of emergent vegetation and several small islands with reed beds. Since the 18th century, rice has been cultivated in the surrounding areas of the lake, and the lake has been used as a reservoir for agricultural irrigation. Lake water level is regulated by sluice gates situated at its three outlet channels which flow into the Mediterranean Sea. The hydrological cycle markedly influences phytoplankton dynamics (Romo and Miracle 1993). It has two annual periods of water renewal during the emptying of the ricefields (January-March) and harvest (September-October), with periods of long or intermediate water stability during the remaining months. This shallow freshwater lake was dominated by submerged plants during the first half of the 20th century (Arévalo 1916, Pardo 1942), but from 1960s onwards eutrophication rapidly brought the lake Albufera into a turbid state, dominated by cyanobacteria and characterized by reduced biodiversity in the plankton and benthos (Blanco 1974, Dafaue 1975, Romo et al. 2005). Since 1980 phytoplankton is overwhelmed by cyanophytes (Romo and Miracle 1993, 1994, Villena and Romo 2003) and zooplankton almost wholly composed of rotifers, with sporadic periods of cladoceran presence (Alfonso and Miracle 1990, Oltra et al. 2001). Since the 1980s, the fish community has been mainly composed of mugilids (Blanco et al. 2003, Blanco and Romo 2006), commercially exploited by local fishermen. Water physical and chemical variables for the 1980s are reported in Soria et al. (1987) and Soria (1997) and thereafter in Romo et al. (2005). In 1991, a restoration plan started involving nutrient diversion, through the removal of industrial, agricultural, and urban

sewage waters from the lake catchment area. This has reduced about 77% phosphorus and 24% nitrogen loadings. Effluents from ricefields, mainly in the southern part of the lake area, are still untreated (Romo et al. 2005).

2.2. Mesocosm Experiments and Field Studies

Part of the research consisted in experimental analyses concerning changes in the trophic ecology of fishes under different ecological conditions, using *in situ* mesocosms (Figure 2). Experimental design was in accordance to an international mesocosm protocol to study food webs on shallow lakes (Stephen et al. 2004). Polyethylene film (~750 L) mesocosms were placed in the center of the lakes. Each enclosure received a treatment, except those acting as untreated controls. Experimental factors tested were fish density and nutrient concentration. Three fish-density and four (1998) or five (1999) nutrient-loading treatments were applied.

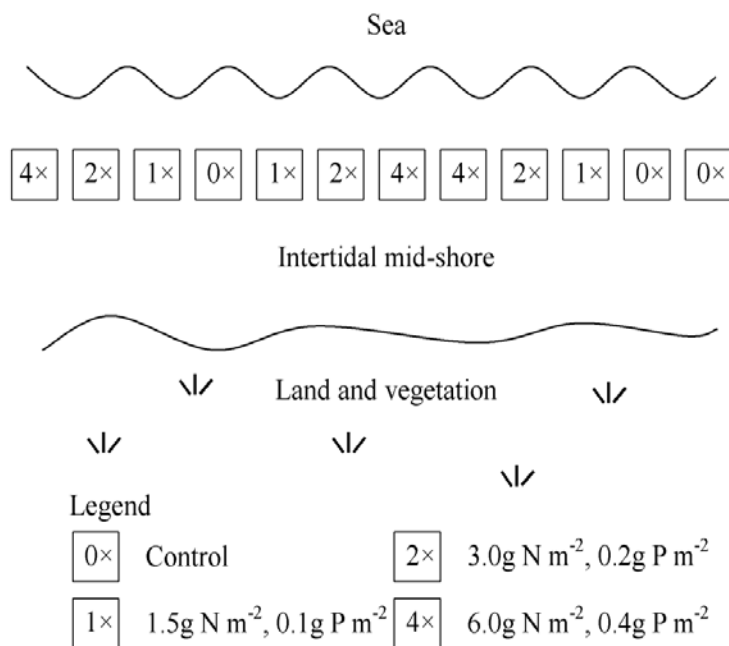


Figure 2. Experimental mesocosms arranged in Sentiz lake (Spain) in summer 1998.

Each combination of treatments was triplicated (1998) or duplicated (1999) and assigned randomly to the mesocosms (Hurlbert, 1984). First sampling week was set as a pre-treatment week for establishment of initial conditions. During nine (1998) and seven (1999) weeks abiotic and biotic variables were studied at weekly intervals (plankton) or during shorter periods (benthos). The physico-chemical variables measured were temperature, pH, total alkalinity, total suspended solids (TSS, only in 1998), Total phosphorus, Soluble reactive phosphorus, nitrate and ammonium. Planktonic chlorophyll-a was extracted from GF/F

filtered samples into 90% ethanol and measured spectrophotometrically. Blanco (2007) describes the protocol in more detail.

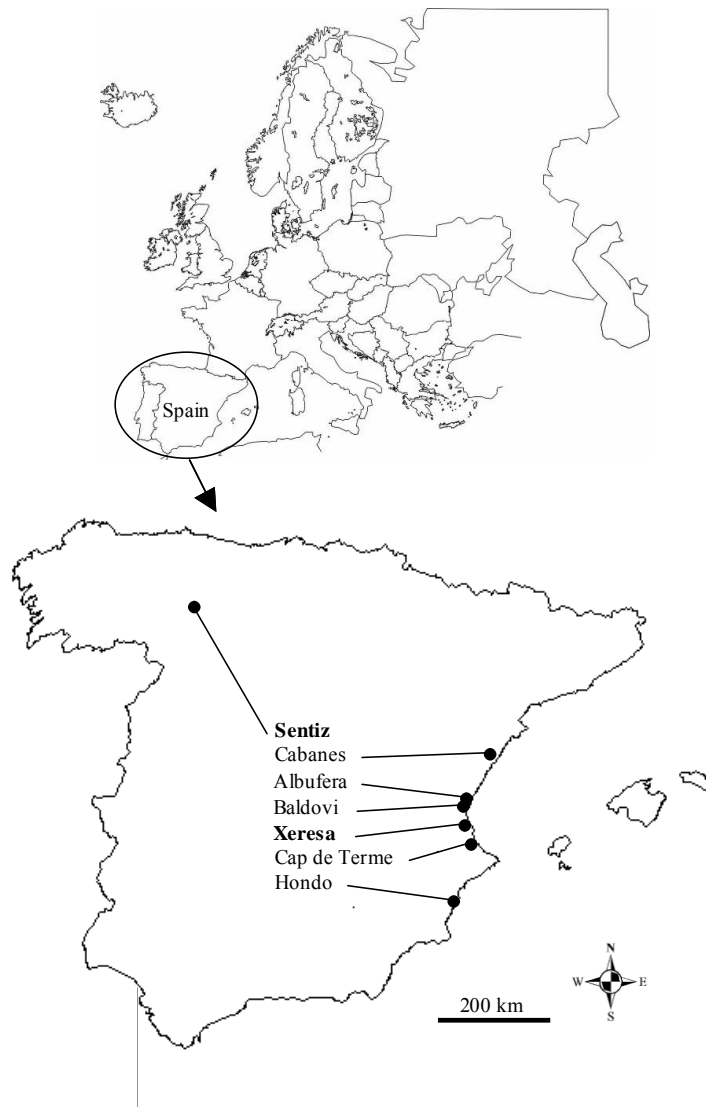


Figure 3. Geographic location of the study lakes.

2.3. Analysis of Gut Content in Fishes

Fish effect on food webs is usually assessed in relationship with prey population changes (O'Brien 1987), but these dynamics may respond to causes other than predation (e.g. Mehner et al. 1998b). Thus, gut content analysis is an approach providing empirical evidence for top-down interactions in aquatic food webs. However, these studies only reflect dietary patterns occurring over a few hours (Persson and Hansson 1999), and may underestimate the most digestible items (Margalef 1974). Gut content analyses are especially difficult in cyprinids, which have pharyngeal teeth that break up prey (Horppila 1994; Lammens and

Hoogenboezem 1991). In the presented studies, fish gut content analyses were carried out according to Granado-Lorencio (1996) and Hyslop (1980) and a detailed protocol is reported in Blanco (2001).

Fishes were captured and preserved in formaldehyde (4 % v/v) until processed. Biometric variables for fishes and guts were measured in order to take into consideration presumable ontogenic dietary shifts (Persson and Hansson 1999). In most cases fish size made impossible to differentiate between gut sections, therefore the entire digestive tract was analyzed from pharynx to anus (Hyslop 1980, Byström and Garcia-Berthou 1999). In each individual, abdominal cavity was opened laterally and the digestive was removed and separated from gas bladder and other organs. The gut was then placed in deionized water and cut into several sections, each one of which was emptied with water using a micropipette. The resulting suspension was eventually homogenized using a magnetic agitator or an ultrasonic sonicator, allowing the gut content to be analyzed using a 40x stereomicroscope. Firstly, a semi-quantitative visual estimation of the abundance of dietary components (zooplankton, macroinvertebrates, macrophytes, algae, detritus, sediment, etc.) was made on the basis of five categories: absent (0%), very rare (25%), rare (50%), abundant (75%) and very abundant (100%) (see Collares-Pereira et al. 1996 and Blanco et al. 2003). Animal debris were more easily recognized after inventorying the community of available preys in the environment (Granado-Lorencio 1996). Thereafter, individual biomasses could be back-calculated according to the conversion factors of Christoffersen et al. (1993). For each prey species, the Minimum Number of Individuals (MNI) was calculated (Hodgson et al. 1993). Zooplankton composition was identified following Alonso (1996), Dussart (1969), Amoros (1984) and others. Numerical data were used to calculate common dietary indices detailed in Blanco et al. (2008) (Lindquist et al. 1994, Donaldson and Clavijo 1994, Pike and Lindquist 1994). Hyslop (1980) recommends the use of both occurrence and frequency parameters since they reflect complementary aspects of a dietary pattern, especially if biomass variables are taken into account. Dietary preferences can be evaluated using electivity indices that compare the proportion of prey items between gut contents and the available community. Ivlev's (1961) index is the most commonly calculated and it is used in the study of the diet of *Chondrostoma arcasii* (Blanco et al. 2008). However, it was criticized by Strauss (1979) who proposed a new index, that was the one used in the dietary study of *Gambusia holbrooki* (Blanco et al. 2004).

2.4. Epiphyton Analyses

For the study of epiphytic algae (Blanco et al. 2007), macrophyte samples were taken during the pre-treatment week and at the end of the mesocosm experiment in lake Sentiz in 1998. Samples were taken using a Kornijów's sampler (Kornijów 1998). Epiphyton was removed from the plant by gently shaking in one litre of deionized water for a standardized time of two minutes (Zimba and Hopson 1997). Thereafter, macrophytes were dried until their weight remained constant and then weighed. Subsamples of 125 mL were preserved in Lugol's solution (4% v/v) for later epiphyton identification and counting. Epiphytic algae were identified under microscope to the lowest taxonomic level. Plant-associated animals were also sampled at the end of the experiment using a Kornijov's sampler. The number of individuals of the main animal associated-plants per gram of macrophyte dry weight was estimated.

3. EXPERIMENTAL RESULTS

Blanco et al. (2008) studied the trophic ecology of *Chondrostoma arcasii* (Steind.), an Iberian endemic cyprinid, by means of a bifactorial mesocosm experiment performed in a shallow pond, testing different nutrient concentrations and fish population densities. The results showed that high water turbidity are maintained in fish-added treatments, but decrease in higher enriched mesocosms due to cladoceran proliferation. Fish exhibited a generalist diet with an important contribution from non-planktonic components. An ontogenic shift towards benthic-detritivory was observed. The proportion of zooplankton in gut contents increased with nutrient additions. Fishes selected preferentially cladocerans over copepods and rotifers, these latter dominating in the resulting zooplankton community. Some fish-added mesocosms kept high water transparency probably as a consequence of physiological alterations related to high ammonium concentrations. Authors concluded that the dietary spectrum of this species, despite showing electivity patterns, depended greatly on prey availability. A similar experiment (Blanco et al. 2004) had been designed to analyse the dietary patterns of the introduced mosquitofish, *Gambusia holbrooki* Girard. The results confirmed that it is a planktivorous species, but also ingested large amounts of algae and detritus. Nutrient fertilization caused almost no changes in the feeding behavior of this species, but larger mosquitofish stocks induced a shift to zooplanktivory and a decline in detritivory. When macrophytes were present, the predation effect focused on zooplankton and plant-associated animals, otherwise predation on bottom macroinvertebrates increased. Females preyed upon almost all groups more intensely, including detritus. Males and juveniles did not overlap in diet, the former preferentially selected ostracods, while juveniles consumed detritus, rotifers and cladocerans. The data support the idea that mosquitofish can cause important top-down effects in shallow lakes under a wide variety of ecological conditions, being an important zooplanktivore in both turbid and plant-dominated shallow Mediterranean lakes.

Fish communities and food web interactions in some shallow Spanish Mediterranean lakes were studied in Blanco et al. 2003. Gut contents were analysed to determine the foraging pattern of each species and the influence on the lake food web. Almost no piscivore species were recorded and in general omnivorous species dominated independently of lake trophic state. Fish dietary differences were found among lakes and prey availability. Maximum fish biomass and diversity were found in the Albufera Lake (Spain), where mugilids (*Mugil cephalus* and *Liza aurata*) and *Cyprinus carpio* dominated. The other lakes had young populations of *Atherina boyeri* and *Liza ramado* endemic species (*Barbus guiraonis*, *Aphanius iberus*) or introduced species (*Lepomis gibbosus*, *Micropterus salmoides*, *Gambusia holbrooki*). Fish were mainly detritivorous and shifted to zooplanktivorous in response to the abundance of large zooplankton. Changes in fish demography and facultative prey influenced food webs of the lakes both by direct predation and by indirect nutrient recycling (sediment bioperturbation and excretion). An exhaustive historical review of the ichthyofauna data of the Albufera lake (Spain) is undertaken in Blanco and Romo (2006), together with fishery records, while in addition fish communities were studied during the summer of 2000 and the spring of 2002. The results showed a remarkable reduction in the richness of fish species, especially from the 1950s, a noteworthy increase in the populations of exotic species, and an increase in mugilid captures. These trends concur with the severe eutrophication, disappearance of submerged macrophytes and over-fishing of some species in

earlier periods. Seasonal cycles were observed for the specific composition of the captures, related to the population dynamics of each species and the manipulation of the hydrological cycle of the lake for rice cultivation. The largest commercial fish captures occurred between October and January, reducing the predation on macrozooplankton and increasing water transparency, which had other consequences on the lake food web.

Blanco et al. (2007) covers experimental results concerning the effect of fish (*Chondrostoma arcasii*) and nutrients on the epiphyton ecology of Lake Sentiz. Nutrient additions caused significant decreases in the total epiphyton biovolume, especially of bacillariophyceans and zygmatophyceans, together with an increment in the abundance of cyanobacteria. The presence of planktivorous fish enhanced the abundance and biovolume of all algal groups except cyanobacteria. The different response of algal groups at higher nutrient treatments is attributed to their ecophysiological constraints and resistance to toxicants (ammonium) accumulation. Fishes had an inconsistent effect on the abundance of plant-associated animals and on epiphytic algae. Fish indirect effects (e.g. release of nutrients) are suggested as the main cause for algal growth in fish-added mesocosms. Submerged macrophytes and epiphyton decreased at increasing nutrient levels, as a result of the phytoplankton increase.

4. DISCUSSION

4.1. Top-down vs. Bottom-up Control and Fish Indirect Effects

The structure of planktonic community differs between clear and turbid shallow ponds, and some of these differences have been attributed to differences in the cascading effect of fish on prey populations (Van de Meutter et al. 2005). Data presented in Blanco et al. 2003, 2004, 2008 and Blanco and Romo 2006 support the idea that some fish species can cause important top-down effects in shallow lakes under a wide variety of ecological conditions, both in turbid and plant-dominated shallow lakes. According to Jeppesen et al. (2003), fish control on large-bodied zooplankton is higher in nutrient-rich lakes and generally higher in shallow than deep lakes. Horppila and Liljendahl-Nurminen (2005) also concluded that the importance of fish predation is greater in shallow waters. According to Jeppesen et al. (1997), benthic-planktivorous fish are less dependent on zooplankton prey in shallow lakes, due to their ability to shift to zoobenthos predation. These dietary shifts modify the impact of fish species on phytoplankton through both top-down and bottom-up effects (Schaus et al. 2002).

The fish species studied, *Chondrostoma arcasii* and *Gambusia holbrooki* (Blanco et al. 2003, 2004), have exhibited a high preference for cladocerans over other zooplankters, and higher fish stocks influenced zooplankton composition towards the dominance of copepods and rotifers, that resulted in a lower control of the phytoplanktonic biomass. Schindler and Scheuerell (2002) stated that fishes will preferentially feed on large-bodied zooplankton, such as *Daphnia*, until they become rare, at which point fish will switch to feed on other available prey. However, uncoupling effects in the top-down chain may arise when zooplankton growth is stimulated by nutrient enrichment (external inputs or nutrient recycling). This is reported in Blanco et al. 2008, where fishes, even when having a significant preference for cladocerans among available prey, were unable to control their populations, which filtering effect

increased water transparency at the higher nutrient treatments. Fishes also failed to control epiphyton grazers, since fish treatments unaffected macroinvertebrate abundance or biomass (Blanco et al. 2007). Scheffer et al. (2000) argued that critical fish densities for cladoceran collapse is higher in systems with higher nutrient concentrations. The observed fish response could be induced by high ammonia concentrations at the higher nutrient treatments. Experimental results by Wicks and Randall (2002) confirm that exposure to high ammonia levels causes a variety of negative physiological effects in fishes, including a reduction of food intake.

Fishes can be an important link between benthic and planktonic habitats by removing nutrients from bottom and littoral zones and excreting or moving them into the open water (Shindler and Scheuerell 2002). Many fish species are multi-chain omnivores, exploiting food webs based on both littoral and planktonic primary producers (Blanco et al. 2003, 2004, Hietala et al. 2004). Fishes, in fact, may play an important role as habitat couplers as a result of their high mobility and flexible foraging tactics that lead to inter-habitat omnivory (Gido 2002, Shindler and Scheuerell 2002). Omnivorous feeding patterns and facultative dietary shifts characteristic of several freshwater fishes may enhance water turbidity. Omnivorous fish interact in synergy with the trophic state, thus their limnological effects become more intense with increased eutrophication (Drenner et al. 1996). The trophic ecology of the species studied experimentally in Blanco et al. 2003, 2008 show that their dietary spectrum, despite of showing selectivity patterns, was depended on the available food.

The results suggest that water turbidity was enhanced by indirect fish effects (e.g sediment bioturbation and nutrient recycling) and emphasize the relevancy related to omnivory and benthic-detrivory diet of the fish communities studied in the shallow lakes. Several works have demonstrated how nutrient excretion by benthivorous consumers can account for a substantial fraction of the nutrients in the water column (Shindler and Scheuerell 2002, Kornijów et al. 2005, Tolonen et al. 2000). Additionally, Scheffer et al. (2003) showed that bottom-feeding fish greatly facilitate the resuspension of sediment by waves or currents, as they reduce the erosion resistance of the sediment. Qin & Threlkeld (1990) demonstrated experimentally that nutrient level increases may occur even without sediment bioturbation when benthivorous fish are present.

A critical increase of benthivorous species, such as carps, has been identified as one of the main causes of loss of biodiversity and water clarity in numerous shallow lakes and ponds worldwide (Zambrano et al. 2001). Carps are very common in eutrophic lakes (Egerston and Downing 2004) and in Lake Albufera (Blanco and Romo 2006), and high biomass of carps is known to have important direct and indirect effects on nutrients, turbidity, and suspended solids (Parkos et al. 2003, Khan 2003). Turbidity may affect differentially the foraging capabilities of fish species. Cyprinids are able to maintain high predation pressure both on benthic and pelagic preys (Schiemer and Wieser 1992). Hence, changes in the physical environment induced by eutrophication (decrease in submerged vegetation and increase in turbidity) should affect the competitive interactions among fish populations, promoting the succession from percids to cyprinids observed in some shallow lakes undergoing eutrophication (Diehl 1988; Olin et al. 2002). The changes in fish composition may vary according to the biogeographical distribution of the species.

Anthropogenic eutrophication, habitat modification, and biological invasions severely have modified habitat connections in the Albufera Lake and its fundamental flow of nutrients and energy, such as also observed in other lakes and ponds (Schindler and Scheuerell 2002).

Some introduced fishes in the Albufera Lake and surrounding wetlands (e.g. carps, mosquitofish), seem to have out-competed some native species (Blanco and Romo 2006). For instance, *Gambusia* seems to have caused the displacement of endemic taxa (e.g. Goren and Galil 2005; Planelles-Gomis 1999, Alcaraz 2006, Blanco et al. 2004). Additional perturbations in the Albufera Lake can be attributed to changes in the commercial fish captures. Although fish species present in the lake were mainly omnivorous, long-term data on commercial fish captures indicated that fish communities changed in response to nutrient level and represented a bioindicator of the lake trophic state (Romo et al. 2005). This has been also observed in some restored shallow lakes of northern latitudes (Jeppesen et al. 2003).

4.2. Fish Effects on Epiphytic Algal Communities

Periphyton have received relatively less attention than phytoplankton in lentic studies. However, evidence is increasing that they play a key role in primary productivity, nutrient cycling and food webs, especially in shallow waters (Vadeboncoeur and Steinman 2002). The results described in Blanco et al. 2007 showed a structural change within the epiphytic algal community shifting towards the dominance of cyanobacteria along a nutrient gradient. A similar result was found by Romo et al. (2007) under a mesocosm experiment using *Gambusia holbrooki*. In the mesocosm experiment of lake Sentiz using the fish species *Chodrostoma arcasii* (Blanco et al. 2007), the results suggest that epiphyton increase may be mediated by a fish effect that influenced nutrient balance, provided that fishes did not control the growth of plant-associated macroinvertebrates even at higher fish stocks. This is consistent with the findings of Williams et al. (2002) that reported that the release of nutrients from fish excreta was an important factor stimulating epiphyton growth. In lake Xeresa, however, the increase of total epiphyton biomass and cyanobacteria was directly related to nutrient concentrations and *G. holbrooki* scarcely influenced epiphyton biomass and composition (Villena 2006, Romo et al. 2007). Some studies showed that fishes can exert a weak top-down control on epiphytes (Moss 1976, Marks and Lowe 1989). The studied fish species did not show a high dietary preference for macroinvertebrates (Blanco et al. 2003, 2004, 2008). Nurminen and Horppila (2006) attribute this effect in some cases to water turbidity that prevents efficient grazing of visual fishes on macroinvertebrates. Therefore, high fish densities may enhance epiphyton biomass acting in synergy with external nutrient additions. This situation often drives the system into a turbid state, where microalgae (epiphyton and phytoplankton) replace submersed plants as primary producers at different light and nutrient levels (Romo et al. 2007).

4.3. Fish Trophic Ecology in Warm Lakes

Top-down and food-web dynamics in shallow lakes may also depend on climate (Gyllström et al. 2005). Models developed are mainly based on temperate shallow lakes located in central and northern Europe (Scheffer 1998; Jeppesen et al. 1998b). However, some marked differences have been pointed out for shallow Mediterranean lakes (Beklioglu et al. 2007). Results of Blanco et al. 2003, 2004 and Blanco and Romo 2006 showed that omnivorous fish species dominated in the shallow Mediterranean lakes studied and they exerted by predation a negative effect on macrozooplankton, which enhanced algal biomass.

This structure with dominance of omnivorous species resembles that described for some food webs of tropical and subtropical lakes (Lazzaro 1997). In addition, small fishes, such as *Gambusia* that have several cohorts per year, were able to keep predation high on macrozooplankton, even under dense beds of submerged vegetation (Blanco et al. 2003). Our results show that both fish species studied (*G. holbrooki* and *C. arcasii*) were able to remove macrozooplankton even under dense submerged macrophyte meadows (*Myriophyllum* or *Chara*). The refuge effect of submerged vegetation for zooplankton deserves further studies in shallow lakes.

Bottom-up mechanisms seem to be relevant in warmer lakes and submerged plants are special key factors to maintain water quality and biodiversity (Romo et al. 2004). Processes related to the vegetation and the benthic-planktonic coupling of food webs could be complex but relevant in the ecology of shallow Mediterranean lakes (Beklioglu et al. 2007). Experimental results have shown that the thresholds of nutrient loading and in-lake phosphorus required to avoid a turbid state and to maintain submerged macrophytes were lower in southern than northern shallow European lakes (Romo et al. 2004, Moss et al. 2004, Vakkilainen et al. 2004). Furthermore, zooplankton seems to have a weaker control on phytoplankton biomass at lower latitude (Gyllstrom et al. 2005).

4.4. Management Perspectives

Nutrient control should be a main priority in the restoration of eutrophicated shallow lakes and ponds, especially in warmer regions (Jeppesen et al. 2003, Moss et al. 2004, Romo et al. 2004, Romo et al. 2005). Nutrient load control has been acknowledged as a key factor in shallow lake recovery programs (e.g. Perrow et al. 1997). This often implies the reduction of nutrient external and internal loading (Moss et al. 1996b, Golterman et al. 1998). As a complementary technique for lake restoration (Moss et al. 2006), biomanipulation of fish communities have been carried out mainly in north temperate lakes with diverse success (Drenner and Hambright 1999, Meijer 2000). Its applicability to subtropical, tropical and shallow Mediterranean lakes is under revision and need further studies (Jeppesen et al. 2003, Beklioglu et al. 2003, Jeppesen et al. 2005).

I agree with Mehner et al. (1998a) who state that management strategies in eutrophic lakes must imply changes in their fish communities, since the synergy between intense zooplanktivory and high phosphorus recycling by benthivory are able to stabilize a water turbid phase, even after reducing the external nutrient loading. Interactive feedbacks among fish populations and lacustrine food webs operate to maintain dominance of benthivorous and omnivorous species in highly productive systems. Thus, effective stewardship of shallow lake ecosystems must incorporate holistic food web insights. For example, our historic analysis of water quality changes in the Albufera Lake (Blanco and Romo 2006) highlights the relevance of fish communities for the control and management for the recovery of this ecosystem, with the necessary reduction of some fish species (e.g. cyprinids, mugilids and introduced species).

The study of the ecology of submerged plant communities for the stabilization of clear water phases and connectivity in food webs should be also stressed in shallow lakes, and especially in shallow Mediterranean lakes, where there is an insufficient number of food web studies (see review Beklioglu et al. 2007). Applied issues in the management of shallow lakes should give also importance to the relationship between shallow lakes and its related

ecosystems, because they usually form part of wetlands (Moss 1998, Scheffer 1998). This should imply a stronger environmental policy for conservation and restoration of these zones. Restoration of eutrophic shallow lakes must involve the control of nutrient inputs and fish communities, with adequate policies for fish and plant management and conservation.

5. CONCLUSION

Severe perturbations are affecting the functioning of shallow lakes worldwide. Dramatic changes, mainly associated with human activities, are driving many of these ecosystems into irrecoverable situations or disappearance. Despite of recent efforts in the study of shallow lakes ecology, little is still known about the factors leading to the stabilization of the different ecological states, especially in tropical, subtropical and semi-arid shallow lakes (e.g. Mediterranean). The influence of abiotic and biotic factors for the structure of food webs and how these are affected by climate remain poorly understood (Jeppesen et al. 2003, Jeppesen et al. 2005, Beklioglu et al. 2007). There are still open some questions about the roles of fishes in relationship with nutrients and how these influence primary producers and food webs in shallow lakes, as well as, the complex interactions between fishes and submerged plants (Meerhoff et al. 2006). The role of submerged macrophytes for zooplankton refugia against fish predation and their effect on food webs deserves further investigations, especially in shallow Mediterranean, tropical and subtropical lakes (Meerhoff et al. 2006, Beklioglu et al. 2007). The effects of fish omnivorism on the aquatic food webs also need further studies. In view of the results outlined here, more researches should focus on the trophic ecology of fish communities, in order to assess the relevance of top-down and indirect effects for the ecology of shallow lakes. It should be emphasized that it is relevant to support these studies with dietary analyses. Finally, further research on different aspects of the ecology of shallow lakes are also recommended when planning management strategies for their recovery and conservation.

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