Chapter 9
Biomanipulation: A Useful Tool for Wetland Rehabilitation

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Abstract Food web manipulation, or biomanipulation, is a frequently applied lake management tool, aiming to restore water quality and vegetation characteristics through interventions in the fish communities. Despite the strong management appeal of biomanipulations, this tool found so far little application in wetlands. This chapter highlights pros and cons of biomanipulations in wetlands, and suggests that an extension of the current biomanipulation paradigm beyond fish management, to consider interventions in other components of wetland communities, can be useful for rehabilitating degraded wetlands such as Las Tablas de Daimiel.

9.1 Introduction

Las Tablas de Daimiel is one of many examples of large-scale ecosystem degradation as a result of excessive waste water discharge from nearby urban areas, combined with other anthropogenic stressors (e.g., disruption of the natural hydrological regime, introduction of exotic species, increased agricultural use in its catchment (e.g. Chapter 1, Alvarez-Cobelas et al. 2001). These impacts have profoundly altered the ecosystem structure and function, and Las Tablas de Daimiel shows symptoms of degradation that differ little from those observed in temperate shallow lakes affected by anthropogenic eutrophication. Elevated concentrations of nutrients, increased turbidity, shifts in the primary producer community from submerged macrophyte dominance to phytoplankton dominance, decreased biomass of large-bodied zooplankton, increased biomass of planktivorous and/or benthivorous

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fish and losses of piscivores characterize degraded lakes (Jeppesen 1998; Jeppesen et al. 1998) and wetlands (Whillans 1996; Chow-Fraser et al. 1998; Alvarez-Cobelas et al. 2001). In addition to these symptoms, eutrophied wetlands may show changes in the structure of emergent vegetation, an important biotic compartment in many riparian wetlands (Mitsch and Gosselink 2000; Alvarez-Cobelas et al. 2008).

The similarity of these symptoms suggests that both ecosystem types could benefit from similar rehabilitation strategies. In the practice, however, wetland eutrophication abatement schemes have been curiously different when compared to those of shallow lakes. Most notably, management of shallow lakes has made use of, and contributed itself a great deal to, a large body of scientific evidence that interventions in food webs hold potential to rehabilitate degraded sites (Falk et al. 2006). In addition to interventions in catchments (e.g., control of point and diffuse sources of pollution) and in situ (macrophyte implantation, sediment dredging, nutrient precipitation, water column aeration), lake management has typically focused on top-down manipulations of fish communities as a rehabilitation tool (Jeppesen and Sammalkorpi 2002; Cooke et al. 2005). The enhancement of piscivores or reduction of zooplanktivores and/or benthivores can induce shifts in plankton and benthos community dynamics and lead to improved water quality. Biomanipulation has served as a field test of classic food web models, mainly in north-temperate lakes, and a significant amount of studies has accumulated in the literature that document successes and failures of biomanipulations (Søndergaard et al. 2007; Gulati et al. 2008).

Despite the strong conceptual appeal of biomanipulation for improving the environmental quality of aquatic ecosystems, wetland restoration has frequently ignored or violated ecological theory (Zedler 2000). Based on increased evidence that biotic interactions shape wetland communities and ecosystem processes, some studies suggested that biomanipulations may also be useful for wetland rehabilitation (e.g., Angeler et al. 2003a; Schrage and Downing 2004; Ruggiero et al. 2005; Evelsizer and Turner 2006). Following examples in lakes, studies in wetland biomanipulations have focused chiefly on the top-down manipulation of fish communities (Angeler et al. 2003a; Potthoff et al. 2008).

This chapter will expand on a previous review (Angeler et al. 2003a), and incorporate more recent results to demonstrate potentials and limitations of interventions in the fish communities as a wetland rehabilitation tool. In its original form, biomanipulation was proposed to target different communities and habitats (Shapiro et al. 1975), and the present chapter will also show that biomanipulations targeting communities other than fish can be especially suitable for rehabilitating Las Tablas de Daimiel and perhaps other wetlands. Examples will discuss the potentials and limitations of manipulations of vegetation structure and the populations of an invasive crayfish. A conceptual model will show that the current biomanipulation paradigm could be broadened by extending ecological theory beyond the application of trophic cascades and alternative stable states to consider sedimentation as a threat to wetland disappearance in the long term.

9.2 Biomanipulation: Theory and Rationale

Despite substantial reduction of external nutrient loading, many aquatic ecosystems remain in a degraded state caused by large amounts of phosphorus that have accumulated in sediments (e.g. Havens et al. 2001). Lake sediments can therefore act as nutrient sources to the water column and provide a means to sustain high algal productivity even if allochthonous nutrient loading is effectively controlled. Under such conditions, ecosystem structure is altered in ways that create a self-sustaining feedback loop which works to maintain hysteresis, and the activities of planktivorous and benthivorous fish play an important role in maintaining these internal stabilising mechanisms (Box 9.1).

Making use of the concept of trophic cascades in lake food webs (Carpenter and Kitchell 1993), and alternative stable state theory (Scheffer et al. 1993), biomanipulation has, at least in some cases, proved useful to disrupt the equilibrium condition, favouring the shift of shallow lakes from the degraded, turbid state to the clear-water state. Both concepts are useful for understanding the ecology of wetlands (summarised in Angeler et al. 2007), and several studies suggest that similar state shifts can be induced through fish manipulations (see Section 9.3).

Box 9.1 Trophic cascades and alternative stable states in shallow aquatic ecosystems

In degraded shallow lakes and wetlands, phytoplankton is the dominant primary producer, while zooplanktivores and/or benthivores dominate the fish community. Zooplanktivorous fish contribute to eutrophication, chiefly via food-web mediated effects. The biomass of efficiently grazing zooplankton (the main ones being large-bodied cladocerans) is effectively controlled by zooplanktivores, thereby relieving phytoplankton from top-down control. The resulting high phytoplankton standing crop contributes to high turbidity, which in turn constrains submerged macrophytes. On the other hand, benthivorous fish favours phytoplankton growth by transferring sediment-bound nutrients to the water column during bottom foraging. The foraging activity of benthivores also contributes to sediment re-suspension which causes high non-algal turbidity. Furthermore, benthic feeding inflicts mechanical damage to submerged macrophytes.

Community structure in shallow lakes differs at lower nutrient concentrations, i.e. in the desirable clear water state. Submerged macrophytes are the dominant primary producers, as a result of an improved light climate. Plants consolidate sediments and provide predation refugia for large cladocerans, thus contributing to more control of phytoplankton via zooplankton grazing. Submerged plants also control phytoplankton via competition for light and nutrients and/or by allelopathic activity. In the clear-water state, fish communities tend toward higher piscivore to planktivore ratios, ultimately relieving large daphnids from predation by zooplanktivorous fish.

Ecosystem internal management by means of biomanipulation may be particularly useful in wetlands to reduce eutrophication effects through features that are inherent to wetlands. By definition, wetlands are shallow ecosystems (<2 m). This suggests that the effects of planktivorous and benthivorous fish increase with decreasing water depth in shallow aquatic ecosystems (Jeppesen et al. 1999; Chow-Fraser 1999; Angeler et al. 2002). Such effects are manifest in: (1) high zooplankton production per unit volume, as a result of high primary production; hence, strong top-down control of fish on zooplankton is possible, (2) the limitation of zooplankton refugia in shallow, turbid systems, especially when macrophytes are absent, (3) fish ingestion of sediment with high nutritive value due to low settling times in the water column; thus, populations of obligate and facultative benthivores are sustained, even when invertebrates are scarce, and (4) the more pronounced effects of sediment re-suspension by benthic-dwelling fish in shallower systems, because turbidity may affect the entire water column.

Wetlands can also show considerable variability in flood frequencies and hydroperiods, features that distinguish them well from physically less disturbed shallow lakes (Mitsch and Gosselink 2000). Fish reduction schemes should therefore have potentially positive effects in many deteriorated wetlands when their inundated area is at minimum levels. Catch per unit effort should increase with decreasing water column depth and when fish are hydrologically confined. Thus, it has been suggested that biomanipulation, when appropriately timed as a function of hydrological disturbance regimes of wetlands, may be a low cost–high benefit tool for wetland eutrophication abatement (Angeler et al. 2003a). However, landscape settings, vegetation characteristics and other inherent features of many wetlands may complicate intervention.

9.3 Biomanipulation in Wetlands: Applying a Lake Restoration Tool

Biomanipulation attempts in Las Tablas de Daimiel are limited to an enclosure study which was carried out during a summer draw down in 1999 (Angeler et al. 2002). This study assessed impacts of three exotic fishes that dominate the degraded wetland's fish community (Chapter 8). Because of the seasonally-pronounced changes of inundated area as a result of the climatic conditions, fish concentrate during severe summer droughts, thereby reaching very high biomass levels. Simulating the biomasses of the fish under such hydrological confinements, Angeler et al. (2002) tested for the impacts of common carp (*Cyprinus carpio* L.), pumpkinseed sunfish (*Lepomis gibbosus* L.) and mosquito-fish (*Gambusia holbrooki* Girard) on water quality and zooplankton.

With the addition of carp or pumpkinseed sunfish, chlorophyll *a*, total phosphorus, total nitrogen and turbidity increased. The magnitude of this increase depended on the fish species and was most pronounced in the carp treatment. Mosquitofish did not significantly affect water quality as compared to a fishless control (Table 9.1). Zooplankton biomass was significantly lower in the carp treatment. However, no direct negative effects (predation) of carp were observed.

Table 9.1 Comparison of selected water quality and biotic variables in response to biomanipulation in selected wetlands

Site	Secchi depth	Phytoplankton biomass	Tot-P	Tot-N	Turbidity	Cladocerans	Submerged vegetation	Intervention	Type of study/duration	Source
Prairie wetland (USA)	n.d.	–6.1[a]	–1.5[a]	–2.0[a]	–4.7[a] as NTU	+176.8[a]	n.d.	Planktivore elimination with rotenone	Whole ecosystem study; 4 years	Zimmer et al. (2001)
Cootes Paradise Marsh (Canada)	n.d.	n.s.[b]	–1.6[b]	n.d.	–2[b] as NTU	n.s.[b]	n.d.	Carp exclusion	Enclosure study; 15 days	Lougheed and Chow-Fraser (1998)
Tablas de Daimiel (Spain)	n.s.	–2.6[b,c]	–2.3[b, c]	–1.4[b, c]	–3[b, c] as Tot-SS	+ ≈250[b, c]	n.s.	Carp, sunfish and mosquitofish exclusion	Enclosure study; 6 weeks	Angeler et al. (2002)
Ventura marsh (USA)	+2.9[d]	–11.5[d]	–≈1.2[d]	n.d.	n.s.	+ ≈2.3[d,e]	+(n.c.)	Benthivore elimination with rotenone	Whole ecosystem study; 14 months	Schrage and Downing (2004)
Major Lake (Hungary)	+2.1[d]	–(n.c.)	–1.3[d]	n.d.	n.d.	+(n.c.)	+4.6[d]	Planktivore and benthivore removal, piscivore stocking	Whole ecosystem study; 4 years	Tátrai et al. (2005)
Delta marsh (Canada)	n.d.	n.d.	n.d.	n.d.	n.s.	n.d.	+11.9[b]	Planktivore and benthivore exclusion	Exclosure study; ca. 4 months	Evelsizer and Turner (2006)
Pairie wetlands	n.d.	n.s.	n.s.	n.d.	n.d.	+7.03[a]	n.s.	Piscivore stocking	Replicated whole ecosystem experiment; 3 years	Potthoff et al. (2008)

Values indicate the multiplicative change observed in each variable in response to the manipulation

+/–, Increase or decrease of value, respectively, n.d., no data; n.s., not significant; n.c. no calculations possible based on original study (but trends to increase or decrease after the manipulations are indicated)

NTU, Nephelometric Turbidity Units; Tot-P, total phosphorus; Tot-N, total nitrogen; Tot-SS, total suspended solids

[a]Changes observed between a treatment and a reference wetland

[b]Values calculated by comparing enclosures with highest fish stock and fishless controls

[c]Shown are carp data only, given that its effects were most deleterious for water quality

[d]Comparing periods before and after fish manipulations

[e]Values refer to body length and not biomass

Zooplankton biomass did not differ from the control, either with sunfish or mosquitofish treatments. Nevertheless, both fish species affected zooplankton community composition, contributing to a community of ineffective grazing rotifers and copepods. The cladoceran *Ceriodaphnia reticulata* Jurine developed only in the fishless control, and was able to exert some top-down influence on phytoplankton.

Although beneficial effects of fish exclusion on water quality and plankton communities were evident in this study, consistent with predictions made by the trophic cascade theory, it is currently difficult to evaluate to what extent biomanipulations at larger spatial scales will reflect the findings of the enclosure study in Las Tablas de Daimiel. Although the ecological relevance of enclosure studies is limited, other wetland biomanipulation studies in larger fish exclosures and ecosystem scale interventions also successfully tested the application of the trophic cascade theory. These results are encouraging because studies across different spatial extents and climatic areas have shown that top-down manipulations of the wetland fish communities hold potential to improve the environmental quality of the studied systems (Table 9.1). This suggests that biomanipluation beyond the scale of enclosures could be useful in Las Tablas de Daimiel.

Despite the potential of biomanipulation as a wetland rehabilitation tool, several patterns emerge from the studies summarised in Table 9.1, that highlight potential limitations which may affect restorative interventions in a context-dependant way. Such limitations must be considered if biomanipulation is applied at the ecosystem scale of Las Tablas de Daimiel.

Angeler et al. (2002) and Potthoff et al. (2008) have discussed the importance of fish life history traits in biomanipulations. Potthoff and colleagues found that additions of young-of-the-year (YOY) walleye (*Sander vitreus* Mitchell) was most effective in controlling planktivorous fathead minnows (*Pimephales promelas* Cope) in wetland lakes of the Prairie Pothole Region of North America, resulting in much lower densities of minnows, higher densities of cladocerans and some macroinvertebrates and decreased phytoplankton standing crop relative to sites that were not stocked with piscivores. Few changes in plankton and benthos communities were found when larger size classes of predatory walleye were added. These differences were attributed to the rapid diet shift of YOY walleye and their ability to consume and suppress all life stages of minnows. Consistent with observations made in lakes (Perrow et al. 1997; Hansson et al. 1998), a further limitation of this study was that stocking of piscivores was not efficient in the long term, suggesting that repeated stocking schemes are required for controlling the deleterious effects of minnows.

Angeler et al. (2002) suggested that biomanipulation schemes focusing on mosquito-fish may differ from those of other fish. So far, planktivorous and benthivorous fish removal in temperate lakes has considered species that produce off-spring once a year (e.g., roach (*Rutilus rutilus* L.), bream (*Abramis brama* L.), bleak (*Alburnus alburnus* L.) and perch (*Perca fluviatilis* L.)). Mosquitofish is a highly reproductive species which can have more than three generations per year (Vargas and de Sostoa 1996). Hence, the life history traits of mosquitofish may be of importance in the consideration of large scale fish manipulation designs, if long-lasting effects are desired. Recommendations based on observations from lakes include a reduction of planktivorous fish by at least 75%, if long term effects are to be attained (Perrow et al. 1997; Hansson et al. 1998). In regard particularly to Las Tablas de Daimiel, this number may be well suitable for common carp and pumpkinseed sunfish, but effective biomanipulation in mosquitofish dominated systems can only be attained by a 100% reduction (a seemingly impossible task), otherwise, the pre-manipulation abundance will soon return. However, extermination plans of mosquitofish could even encounter social rejection because these fish are considered to act as a biological control against nuisance mosquitoes.

The re-establishment of submerged vegetation is a desired secondary effect of biomanipulations in shallow aquatic ecosystems. However, several factors, including water colour and wind activity, have been shown to constrain the restoration of submerged macrophytes to extents prior to degradation (Angeler et al. 2003a). The enclosure study in Las Tablas de Daimiel (Angeler et al. 2002) showed that turbidity caused by high water colour remained very high whether or not fish biomass was manipulated. M. Alvarez-Cobelas (2009 unpublished data) found that high humic levels arise from the decomposition of the common reed (*Phragmites australis* Trin. ex Steud.), an emergent plant that has widely replaced sawgrass (*Cladium mariscus* (L.) Pohl), which generates less humic compounds, as a result of hydrological alterations and eutrophication of the wetland (Alvarez-Cobelas et al. 2008). Thus, while Shapiro (1990) suggested that light limitation resulting from high humic levels may enhance biomanipulation potential, because 'low light' refugia reduce fish predation on large-bodied zooplankton, the "facilitation effect" of water colour may work in deep lakes rather than in shallow aquatic ecosystems. Also the effects of wind-induced sediment re-suspension have been frequently considered to be a limiting factor for successful biomanipulations in shallow lakes and wetlands (e.g., Lammens 1988; Lougheed and Chow-Fraser 1998). These examples suggest that additional remedial actions, preferentially in sediments and vegetation, would be required to restore submerged aquatic vegetation, as has been previously suggested (Wilcox and Whillans 1999; Angeler et al. 2003a).

It is important to highlight that the usefulness of fish manipulations as a test of trophic cascade theory and alternative stable state concepts depends on landscape contexts (Angeler et al. 2003a; Reed 2006). The hydrogeomorphic settings and connectivity of wetlands, their flood frequencies and durations, land use characteristics in their catchments and climatic conditions, ultimately regulate wetland communities and ecosystem processes (Mitsch and Gosselink 2000). Thus, interactions among different biotic and abiotic parameters in wetlands add complexity to our understanding of ecosystem ecology, beyond levels known for shallow lakes. Global warming may further increase this complexity and complicate predictions on ecosystem responses to fish manipulations. Jeppesen et al. (2007) recently highlighted climate-related aspects that may limit biomanipulations. Interacting abiotic and biotic characteristics will certainly need thorough consideration in future wetland biomanipulation studies in Las Tablas de Daimiel and other wetlands. The following section will highlight potentials and limitations of an extended biomanipulation paradigm.

9.4 Biomanipulation in Wetlands: Extending the Paradigm

Fish occupy a key position in lake food webs, and it may not be surprising that the biomanipulation paradigm is mainly based on the notion that interventions in fish community structure have cascading effects towards lower trophic levels, ultimately improving water quality. The complexity of wetland food webs and the strong influence of abiotic factors require a focus on different communities and habitats, as initially proposed by Shapiro et al. (1975). In fact, recent studies suggest that the introduction of bivalves (e.g., *Dreissena polymorpha* Pallas) could be used to control cyanobacterial blooms (Gulati et al. 2008); however, the introduction of these species could cause more ecological damage than benefits; therefore, a thorough assessment of impacts is needed. The following examples highlight that targeting multiple communities could extend the usefulness of biomanipulations beyond water quality improvements to control key abiotic wetland processes.

A striking difference between many shallow lakes and riparian wetlands, such as Las Tablas de Daimiel, is the low ratio of open water area to space covered by emergent vegetation in marshes. With the exception of, for example, Lake Neusiedlersee (Austria/Hungary), emergent vegetation in shallow lakes is frequently limited to a littoral fringe. By contrast, vast areas of Las Tablas de Daimiel are covered by large extents of emergent plants (Chapter 7), where they play important roles in many biological (primary production, decomposition, nesting ground for birds, refuge for fish and other wildlife), and abiotic processes (sedimentation patterns (Sánchez-Carrillo et al. 2000, 2001), wetland hydrology (Sanchez-Carrillo et al. 2004)). Thus, emergent vegetation clearly represents a key biotic component in this wetland.

Before large-scale degradation took place during the second half of last century, the emergent macrophyte community of Las Tablas de Daimiel was dominated by the evergreen *Cladium mariscus.* Nowadays, *Cladium* has largely been replaced by annual *Phragmites australis,* which better tolerates the hypertrophic conditions and irregular flooding patterns in the wetland (Alvarez-Cobelas and Cirujano 2007; Alvarez-Cobelas et al. 2008; Chapter 7). Sánchez-Carrillo et al. (2000) demonstrated that internal primary production, mainly through emergent vegetation, accounts for the considerable variability in sedimentation patterns of Las Tablas de Daimiel. The rates determined were substantial (max. 2.88 ± 1.2 cm year^{-1}), suggesting that, if current sedimentation patterns are maintained, the wetland will silt up and convert to a terrestrial ecosystem by the end of this century (Sánchez-Carrillo et al. 2000).

This provides a strong argument in favour of intervention in the vegetation community structure, which could help to decrease the present sedimentation rates and extend the lifespan of Las Tablas de Daimiel. Specifically designed plant harvesting schemes should focus chiefly on controlling *Phragmites*, which contributes with a high detritus biomass after plant senescence. These plant biomanipulation designs must be balanced, to continue providing “vegetation services” to the wildlife of Las Tablas de Daimiel, and to counteract the negative impacts which arise as a result of large amounts of biomass generation.

Biomanipulations of components of the benthic food web of lakes and wetlands have often focused on common carp. Las Tablas de Daimiel has become infested with the invasive American red swamp crayfish (*Procambarus clarkii* Girard) which had a profound effect on benthic ecology. A large body of scientific evidence has accumulated about the negative impacts of *P. clarkii* in invaded ecosystem (Geiger et al. 2005; Rodríguez et al. 2005). These negative impacts include the eradication of submerged aquatic vegetation and the alteration of sediment and water quality which have been also experimentally demonstrated in Las Tablas de Daimiel (Angeler et al. 2001, 2003b). The broad tolerance to a wide range of ecological conditions, the ability to survive droughts by burrowing into the sediment, and its capacity to profoundly alter abiotic and biotic wetland characteristics, confer this species the status of an ecosystem engineer (Jones et al. 1994).

Biomanipulation of crayfish populations could hold potential to lessen the ecological damage caused to the wetland. However, it is currently hard to evaluate which management strategy can be most efficient in controlling crayfish populations in Las Tablas de Daimiel. Control of crayfish biomass emphasizes that extending the biomanipulation paradigm undoubtedly increases the spectrum of potential limitations. Several examples highlight these limitations.

While some studies suggest that piscivorous fish readily feed on *P. clarkii* (Elvira et al. 1996), it is unlikely that management based on piscivore introductions is fruitful in the long term. The environmental harshness in the wetland (frequent hypoxia, poor conditions for reproduction) may inflict high mortality to piscivorous fish, requiring costly and periodic restocking. Furthermore, the ability to seek refuge in sediment burrows could provide a means for *P. clarkii* to, at least temporarily, escape piscivore predation, thereby reducing efficiency of fish stocking. More importantly, the history of Las Tablas de Daimiel, and the Iberian Peninsula in general, shows a lack of large fish predators, suggesting that negative impacts of piscivore introductions on other components of the wetland food web could outweigh beneficial effects.

The efficiency of periodic and selective harvesting of crayfish as a management tool is also difficult to evaluate from a cost-benefit perspective. Crayfish commerce is an important socioeconomic factor in many areas (Avault 1992), and, therefore, it may be feasible to assess whether commercialization of crayfish can compensate the costs resulting from periodic harvesting. A best-case scenario would be profitable crayfish commerce, raising crayfish harvests to levels able to lessen the ecological damage of this species.

Hydroperiod is an important abiotic constraint of *Procambarus clarkii* populations (Gutiérrez-Yurrita and Montes 1999), suggesting that reducing hydroperiods could have management potential. Water levels can be artificially regulated through the terminal dam at Las Tablas de Daimiel (Chapter 1), helping to inflict drought-induced mortality to crayfish and fish. However, artificial management of hydroperiods as a tool to manage *P. clarkii* populations must be balanced in ways that avoid negative impacts on other biotic components of the wetland and its whole ecological integrity.

Procambarus clarkii has a wide tolerance to a range of environmental conditions, and this should be highlighted, as it may currently impede its eradication from the wetland. However, future advances in pest species science and management could provide insight to effective control/extirpation of this species from the wetland, through the development of highly taxon-specific biocontrol agents.

9.5 Biomanipulation: A Model for Las Tablas de Daimiel

As has been noted by Angeler et al. (2003a), the complex nature of abiotic and biotic parameters complicates the predictability of ecosystem responses to biomanipulations in wetland ecosystems. Therefore, the usefulness of biomanipulation as a wetland rehabilitation tool is complicated by this uncertainty. It is apparent, however, that biomanipulation has been a useful tool to improve wetland quality in certain circumstances (overview in Table 9.1), particularly when focusing on benthivorous carp (Lougheed and Chow-Fraser 1998) or YOY walleye (Potthoff et al. 2008). Likewise, targeting emergent vegetation biomass seems promising to counteract excessive sedimentation rates and to avoid the conversion of Las Tablas de Daimiel into a terrestrial ecosystem during this century.

Further exploration on the usefulness of biomanipulations as a wetland rehabilitation tool seems warranted. It may be that the integral restoration of Las Tablas de Daimiel is impossible, due to the inability of restoring the natural disturbance regime and wetland geomorphology to conditions existing before large-scale degradation. New constraints arising from climate change will further complicate restoration at local and catchment scale. Under such limitations, the conceptual model presented in Fig. 9.1 could serve managers as a useful guide for improving the environmental quality of Las Tablas de Daimiel.

The model will focus on primary and secondary effects, extensively studied in lakes as a result of fish manipulations. Primary effects are associated to cascading effects in lake food webs that may lead to improved water quality. In the context of Las Tablas de Daimiel, fish manipulations should focus primarily on benthivorous carp which has been shown to have the most deleterious effects on water quality (Angeler et al. 2002). It will be necessary to evaluate whether the 75% biomass reduction threshold suggested for lakes will be also suitable to achieve the desired long-term improvements in this wetland (Perrow et al. 1997; Hansson et al. 1998). Effective management of crayfish populations will, presumably, also result in improved water quality, in terms of reduced sediment re-suspension and nutrient recycling from sediments to the water column, and relief submerged vegetation from herbivorous pressure (Angeler et al. 2001). Artificial and prolonged reduction of hydroperiods could increase the effectiveness of fish and crayfish reduction schemes.

According to the alternative state theory, secondary effects are based on the notion that fish manipulations disrupt equilibrium conditions in shallow lakes, ultimately allowing re-colonisation of submerged macrophytes. It is reasonable to assume that submerged macrophyte re-colonization will be facilitated at Las Tablas

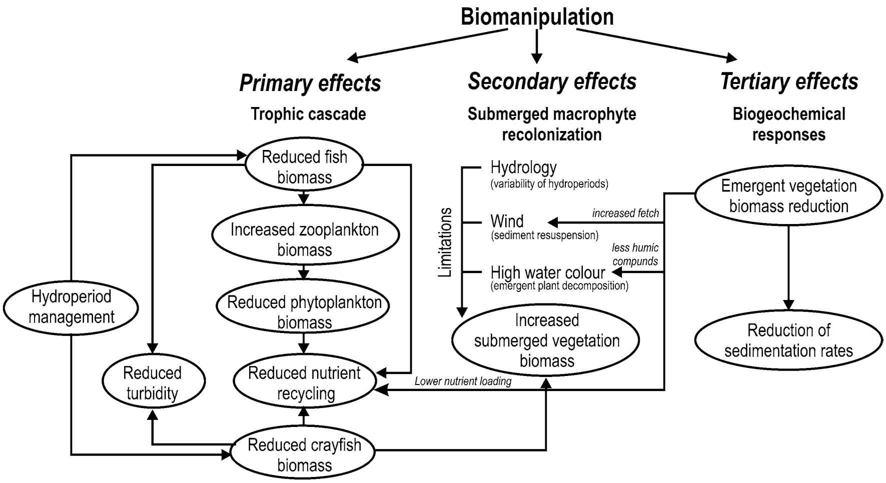

Fig. 9.1 Conceptual model showing potential effects of biomanipulations in the abiotic and biotic environment of Las Tablas de Daimiel (for details see text)

de Daimiel by manipulating benthic species (carp, crayfish), favored by the storage effects (re-growth from seed banks). However, several other factors may limit the establishment and persistence of submerged plants. Jeppesen (1998) suggested that significant changes in the biological community structure cannot be expected to occur until phosphorus concentrations in lakes are reduced to levels below 0.1–0.15 mg L^{-1}. If these thresholds are also applicable to wetlands, then, theoretically, stability in submerged macrophyte reestablishment is not to be expected in the hypereutrophic Las Tablas de Daimiel (Angeler et al. 2002). Furthermore, the high water colour, arising chiefly from emergent plant decomposition, may constrain macrophyte re-colonisation by deteriorating the aquatic light field, even if phytoplankton biomass and turbidity are significantly reduced. A further point to consider is the wetland hydrology. Based on the high seasonal variability of hydroperiods, large-scale submerged macrophyte re-colonization and persistence may be constrained and restricted to species adapted to disturbance (e.g., charophytes, Wade 1990).

The model in Fig. 9.1 will include a novel category representing ecosystem processes that are especially relevant in riparian wetlands. Effects that may arise from manipulation of other wetland communities (e.g., emergent vegetation) are considered tertiary. On one hand, tertiary effects negatively feedback factors that maintain degraded conditions (poor water quality, low submerged macrophyte biomass), and may therefore reinforce effects of manipulations on fish communities. For example, by retrieving high biomass of *Phragmites*, the decomposition of plant litter may generate fewer amounts of humic substances, leading to clearer waters, which could favour submerged plant re-colonisation. Retrieval of emergent plant litter also reduces the autochthonous nutrient load to the system, and may counteract eutrophication phenomena related to nutrient recycling from the sediments to the water column. Conversely, decreasing the area of emergent vegetation cover increases fetch and may favour wind-induced sediment re-suspension. Tertiary effects also contemplate processes that are uncoupled from changes in communities and water quality. Geomorphological and other biogeochemical processes affected by sedimentation fall within this category.

9.6 Conclusions and Perspectives

There exists increasing evidence that the application of theories related to trophic cascading interaction and alternative stable states holds potential to rehabilitate degraded wetlands. Even more than in most shallow lakes, riparian wetland are characterised by a high food web complexity in which many communities play a key role (emergent vegetation, crayfish). This suggests that interventions in other wetland communities, in addition to those of fish, could improve ecological conditions beyond water quality in wetlands, thereby broadening the biomanipulation paradigm.

Biological processes in wetlands are tightly coupled with, and mediated by, abiotic factors such as the hydrological disturbance regime. Although the complexity of interacting abiotic and biotic parameters complicates predictions on ecosystem responses to biomanipulations, ultimately limiting its potential usefulness for wetland rehabilitation, interactions between biotic and abiotic influences need thorough consideration in future wetland studies. Future research in Las Tablas de Daimiel could address this need for information, to the benefit of wetland science and future rehabilitation strategies.

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