Freshwater Biology (2003) **48**, 2203–2213

OPINION
APPLIED ISSUES

Biomanipulation: a useful tool for freshwater wetland mitigation?

DAVID G. ANGELER*, PATRICIA CHOW-FRASER†, MARK A. HANSON‡, SALVADOR SÁNCHEZ-CARRILLO§ AND KYLE D. ZIMMER¶

**Department of Environmental Sciences, University of Castilla – La Mancha, Toledo, Spain*
†Department of Biology, McMaster University, Hamilton, Ontario, Canada
‡Wetland Wildlife and Populations Research Group, Minnesota Department of Natural Resources, Bemidji, Minnesota, U.S.A.
§Department of Water Sciences, Instituto Tecnológico de Sonora, Ciudad Obregón, Mexico
¶Department of Biology, University of St Thomas, St Paul, Minnesota, U.S.A.

SUMMARY

1. Natural wetlands have traditionally been considered as efficient 'ecological engineers' for waste water treatment. However, the structure and function of many natural wetlands have been severely altered by the chronic exposure to pollutants, especially nutrients.
2. Despite the similarity of symptoms of eutrophied shallow lakes and wetlands, restoration strategies differ distinctly between these rather similar aquatic systems. Many of the tools applied in shallow lake restoration programs, for example biomanipulation, have received little attention in wetland management and restoration.
3. Although a strong conceptual basis for food web management exists, biotic interactions as influences on wetland communities have been largely neglected by wetland scientists and managers.
4. In this paper we show that biomanipulation may have a strong potential for wetland eutrophication abatement. This potential will be demonstrated by reviewing studies carried out in different wetland types in contrasting climatic regions.
5. We propose four different scenarios for when, where and why biomanipulation may be used to rehabilitate freshwater wetlands. These scenarios reflect different settings of hydrological variability, eutrophication sources and gradients of wind exposure and water colour.

Keywords: eutrophication abatement, hydrology, management, restoration, wetlands

Introduction

Natural wetlands have often been considered as waste water treatment areas because they function as filters, sinks and transformation sites for chemicals of many kinds (Johnston, 1991). However, this view conflicts with biological conservation, because the structure and function of many natural wetlands have been severely altered by eutrophication, which has often been intensified by disruptions of the natural hydrological cycle (Middleton, 1999). The symptoms of wetlands degraded by eutrophication differ little from those observed in temperate shallow lakes (cf. Jeppesen, 1998; Jeppesen *et al.*, 1998; Schutten & Davy, 2000). Increased nutrient and turbidity levels, shifts from submerged macrophyte dominance to phytoplankton dominance, decreased biomass of large-bodied zooplankton, elevated biomass of planktivorous and benthivorous fish and losses of

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Correspondence: David G. Angeler, Department of Environmental Sciences, University of Castilla – La Mancha, Avda. Carlos III s/n, E-45071 Toledo, Spain.
E-mail: dangeler@amb-to.uclm.es

piscivores have been frequently reported (e.g. Whillans, 1996; Chow-Fraser *et al.*, 1998; Alvarez-Cobelas, Cirujano & Sánchez-Carrillo, 2001). In addition, alterations in emergent vegetation community structure are functionally coupled to eutrophication in wetlands (Mitsch & Gosselink, 2000; Sánchez-Carrillo & Alvarez-Cobelas, 2001).

Despite the similarity of symptoms, restoration strategies have been curiously different between eutrophied wetlands and shallow lakes. In shallow lakes, a step by step approach has generally been applied, starting with control of catchment nutrient inputs (e.g. waste water treatment facilities, regulatory policies to reduce runoff etc.), followed by *in situ* manipulations (biomanipulation, macrophyte implantation, sediment dredging, nutrient precipitation) (e.g. Annadotter *et al.*, 1999; Madgwick, 1999; Søndergaard *et al.*, 2000). However, little of the methodology found to be useful in shallow lake restoration has been applied to wetland management (Kusler & Kentula, 1990; Wilcox & Whillans, 1999).

Here, we emphasise the potential usefulness of biomanipulation for wetland eutrophication abatement. In its original concept, biomanipulation encompassed manipulation of all lake biota and their habitats to improve water quality (Shapiro, Lamarra & Lynch, 1975). More recently, the term is typically applied to top-down manipulation of lake fish communities, i.e. enhancement of piscivores or reduction of zooplanktivores and/or benthivores (Lammens *et al.*, 1990) to achieve long-lasting improvements in water quality and shifts in plankton and benthos community dynamics (see reviews in Reynolds, 1994; Perrow *et al.*, 1997; Hansson *et al.*, 1998; Drenner & Hambright, 1999).

A strong conceptual basis for food web management exists, but related strategies have not melded well with other aspects of wetland ecology or management. Although the importance of biotic interactions as influences on wetland communities and ecosystem structure are becoming well documented (Zimmer, Hanson & Butler, 2002; Hanson *et al.*, unpublished data), they have been largely neglected by scientists and managers. As we show here, recent studies indicate that manipulation of fish standing stocks could contribute significantly to wetland eutrophication abatement (Chow-Fraser, 1998; Lougheed, Crosbie & Chow-Fraser, 1998; Angeler *et al.*, 2002). Our aim is to illustrate this potential using results of case studies of biomanipulation in freshwater wetlands. We will emphasise ecological mechanisms associated with interventions in food webs, and highlight how abiotic and biotic factors may influence fish manipulations, thereby contributing to wetland eutrophication abatement. We will also emphasise a need to consider features that are unique to wetland ecosystems, such as physical disturbance regimes and hydrological variability. Using four hypothetical scenarios we suggest a theoretical framework that reflects a potential gradient of effectiveness of wetland biomanipulation in relation to different environmental settings.

Shallow lakes versus wetlands: is there a difference?

Whether one considers wetlands and shallow lakes as similar ecosystems may depend on personal views and on choice of definitions. An international definition of a wetland adopted by the Ramsar convention is sufficiently broad that both wetlands and shallow lakes fall within the wetland definition. Several authors of wetland studies seem to adhere to this definition (e.g. Lund & Davis, 2000).

In contrast to the definition of the Ramsar convention the functional classification scheme of Brinson (1993) is more discriminatory as it classifies wetlands according to their geomorphologic settings, water sources and hydrodynamics. Many wetlands have a marked hydrologic variability (fluctuations of hydrolevel and hydroperiod which respond to flood duration and flood frequency) which contrasts with shallow lakes. For the purpose of this paper it is recommendable to take into account such functional aspects because they could help in suggesting a framework of potential outcomes of interventions in the food webs in relation to abiotic characteristics of wetlands.

Biomanipulation: theoretical background

Biomanipulation was originally based on the concept of cascading trophic interactions in aquatic food webs (Carpenter & Kitchell, 1993; Polis & Winemiller, 1996), although, more recently, it incorporates the notion of two alternative stable states in shallow lakes (Scheffer *et al.*, 1993). Considerable evidence indicates that both concepts are useful for understanding characteristics and responses of wetlands (Chow-Fraser, 1998; Alvarez-Cobelas *et al.*, 2001).

Many aquatic ecosystems affected by agricultural or urban activities remain eutrophic, despite considerable reduction in external nutrient loading. Large quantities of phosphorus may be retained in sediments and subsequently work to maintain hysteresis (Scheffer *et al.*, 1993). Under such high-nutrient conditions, wetlands remain in a turbid (degraded) phase; phytoplankton is abundant and zooplanktivores and/or benthivores dominate the fish community. In shallow lakes, zooplanktivorous fish contribute to eutrophication chiefly via food-web mediated effects, limiting zooplankton biomass and hence relieving phytoplankton from zooplankton grazing. The resulting high phytoplankton biomass contributes to high turbidity, which in turn constrains submerged macrophytes. Benthivorous fish, on the other hand, increase the nutrient availability to phytoplankton chiefly by transferring sediment-bound nutrients to the water column during bottom foraging (Meijer *et al.*, 1990). Benthivores also contribute to high non-algal turbidity via resuspension of sediment particles, and by causing mechanical damage to submerged macrophytes (Crivelli, 1983; Brabrand, Faafeng & Nillsen, 1990).

In contrast, community structure in shallow lakes differs at lower nutrient concentrations, typical of the clear water state. Submerged macrophytes dominate because of an improved light climate. Plants provide predation refugia for large daphnids, thus contributing to more control of phytoplankton via zooplankton grazing. Submerged plants also control phytoplankton via competition for light and nutrients (Balls, Moss & Irvine, 1989; Ozimek, Gulati & van Donk, 1990; Van Donk *et al.*, 1993) and/or by allelopathy (Wium-Andersson *et al.*, 1982; Jasser, 1995). Here, fish communities tend toward higher piscivore to planktivore ratios, ultimately relieving large daphnids from predation by zooplanktivores.

At intermediate nutrient concentrations (50–150 $\mu g\ L^{-1}$ total phosphorus (TP); Jeppesen *et al.*, 1997), either alternative state (clear or turbid) may persist and system shifts are possible. Shifts are resisted by internal stabilising mechanisms, such as the activities of planktivorous and benthivorous fish. Biomanipulation has management potential because, in at least some cases, it disrupts equilibrium conditions and favours shifts to the clear-water state (Scheffer *et al.*, 1993; Hanson & Butler, 1994; Scheffer, 1998).

Can biomanipulation be effective in wetland eutrophication abatement?

Catchment attempts to achieve eutrophication abatement should have primacy for restoring degraded aquatic ecosystems. However, studies of shallow lakes have shown that catchment nutrient management programs may be insufficient because of substantial storage of nutrients in sediments (Havens *et al.*, 2001). Hence, lake internal management may be more useful to reduce eutrophication effects.

By definition, wetlands are shallow ecosystems (<2 m), and this has important implications for management. Jeppesen *et al.* (1990) suggested that effects of planktivorous and benthivorous fish increase with decreasing water depth in shallow lakes, and similar assertions have been made for wetlands (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 likely, (2) the limitation of zooplankton refugia in shallow, turbid systems, especially when macrophytes are absent, (3) fish ingestion of sediment with high nutritive value because of 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 resuspension by benthic-dwelling fish in shallower systems, because turbidity may affect the entire water column.

Considerable evidence indicates that fish reduction schemes should have potential positive effects in many deteriorated wetlands, and that fish catch per unit effort should increase with decreasing water column depth. Thus, it is reasonable to suggest that biomanipulation, when appropriately timed in accordance with low water levels, may be a low cost–high benefit tool for wetland eutrophication abatement. However, vegetation characteristics and other inherent features of many wetlands may complicate intervention.

Biomanipulation: case studies from wetlands

Here, we describe wetland case studies that demonstrate potential mechanisms associated with biomanipulation in wetlands (changes in water quality and plankton communities, i.e. primary effects of biomanipulation). We also identify factors that may constrain the responses and secondary processes (macrophyte recolonisation) resulting from manipulation.

Results reported here are from different wetland types and from contrasting climatic regions. They cover a range from whole system manipulations to small-scale enclosure studies. Controversy exists regarding the relevance of biomanipulation and even small-scale manipulations in ecosystem ecology (De Melo, France & McQueen, 1992). Nonetheless, we believe that both small-scale experiments and whole-system manipulations are useful for addressing specific hypotheses along gradients of processes and spatiotemporal scales (Huston, 1999), and demonstrate successful biomanipulation across a wide size-range of aquatic ecosystems (De Melo *et al.*, 1992; Hansson *et al.*, 1998; Drenner & Hambright, 1999).

Wetlands of the Prairie Pothole Region (U.S.A.)

Many wetlands in the Prairie Pothole Region (PPR) of North America are semipermanently to permanently flooded (sensu Stewart & Kantrud, 1971) and dry only occasionally, depending on climate and local landscape configuration. Fathead minnows (*Pimephales promelas* Rafinesque, hereafter minnows) are common residents of these wetlands (Peterka, 1989). Food webs here are comprised largely of aquatic invertebrates that form important links between primary producers and vertebrate consumers, especially birds and amphibians known to rely on these habitats for foraging (Euliss, Wrubleski & Mushet, 1999).

Zimmer, Hanson & Butler (2001) assessed the ecological responses to colonisation and subsequent extinction of a population of minnows in a whole-system experiment in a prairie wetland (4.1 ha; maximum depth 2.1 m) in Minnesota, U.S.A., near the eastern margin of the PPR. Using a Before-After Control-Impact (BACI) approach, data from the colonised (Impact) wetland were paired with data from a similar fishless site. Comparisons were made when both wetlands were fishless (1996), when minnow populations reached moderate densities in the colonised site (1998) and, finally, when the colonised site became fishless following fall treatment with rotenone (1999).

Fish colonisation in this wetland was associated with dramatic increases in turbidity, total phosphorus and chlorophyll *a* in the water column; significant decreases in abundance of aquatic insects and large cladocerans were also evident (Table 1). Elimination of minnows largely reversed the effects of minnow colonisation, indicating that the wetland's ecological properties changed rapidly in response to fish colonisation or elimination. Unfortunately, responses of macrophytes, as a measure of secondary processes related to the manipulation, were not reported in this study.

In a similar study, Walker & Applegate (1976) added 25 000 young-of-the-year (0+) walleye (*Stizostedion vitreum vitreum* Mitchill) to a single semipermanent wetland in east-central South Dakota, U.S.A. (mean and maximum depths of 1.4 and 1.8 m, respectively, surface area: 12.5 ha, and specific conductance ranging from 1680 to 2000 μmho). This wetland also supported a dense population of minnows prior to walleye addition. These age 0+ walleyes initially consumed zooplankton, macroinvertebrates and young fish; later in the growing season, walleyes >106 mm in length consumed primarily minnows. Fathead minnows disappeared when walleye became piscivorous. *Daphnia* was either absent or occured at very low density (<10 animals L^{-1}) in zooplankton samples in the presence of minnows and 0+ walleyes. However, following the decline of minnows by piscivorous walleyes, *Daphnia* increased sharply, at times exceeding 200–300 animals L^{-1}. Mean Secchi disk transparency increased from approximately 20 to 70 cm, apparently in response to increased herbivory because of elevated densities of *Daphnia*. Unfortunately, data are available for only a single year and reports on phytoplankton and submerged macrophytes are unavailable.

The Cootes Paradise marsh (Canada)

This wetland is a coastal marsh of Lake Ontario, which was profoundly altered because of anthropogenic activities (Chow-Fraser *et al.*, 1998). Lougheed *et al.* (1998) studied the relationship between the exotic benthivorous common carp (*Cyprinus carpio* L.), which now dominates the marsh fish community, and water quality, zooplankton and submerged macrophytes. Effects of carp were assessed using 50 m^2 *in situ* experimental enclosures during the spawning season in 1995. Turbidity, total phosphorus

Table 1 Comparison of selected water quality and biotic parameters in response to fish manipulations in selected wetlands

Site	Secchi transparency	Chlorophyll *a*	Total phosphorus	Total nitrogen	Turbidity	Cladocerans	Intervention	Type of study/ duration	Source
Prairie wetland (U.S.A.)	n.d.	− 6.1*	−1.5*	−2.0*	−4.7* as NTU	+176.8*	Planktivore elimination with rotenone	Whole-ecosystem study; 4 years	Zimmer *et al.* (2001)
Cootes Paradise Marsh (Canada)	n.d.	n.s.†	−1.6†	n.d.	−2† as NTU	n.s.	Carp exclusion	Enclosure study; 15 days	Lougheed, Crosbie & Chow-Fraser (1998)
Tablas de Daimiel floodplain (Spain)	n.s.	−2.6 †,‡	−2.3†,‡	−1.4†,‡	−3†,‡ as total suspended solids	+ ca. 250†,‡	Carp, sunfish, and mosquitofish exclusion	Enclosure study; 6 weeks	Angeler *et al.* (2002)

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.
*Changes observed between a treatment and a reference wetland.
†Values calculated by comparing enclosures with highest fish stock and fishless control enclosures.
‡Shown are only data for carp because its effect was the most deleterious for water quality.

and total ammonia levels increased with total carp biomass (Table 1). Carp did not directly affect the zooplankton community. However, reduced zooplankton biomass was observed and likely resulted from indirect effects of carp associated with high non-algal turbidity and nutrient loading.

During spring 1997, the Royal Botanical Gardens (owner and manager of the wetland) implemented a plan to exclude carp from the entire marsh (Wilcox & Whillans, 1999). Lougheed & Chow-Fraser (2001) were able to test predictions based on the 1995 enclosure study by comparing data before and after the biomanipulation. Effects of carp exclusion were noted in the first year at three different sites in terms of decreased turbidity (49–80%), accompanied by increased growth of submerged plants. At the most degraded open water site, no significant difference between turbidity levels was found in the second year after carp exclusion, and no notable changes in community structure were observed compared with pre-exclusion values. Only the least degraded vegetated site showed a prolonged positive response to the carp exclusion; manifested as an increase in water clarity, decrease of edible algae, increase of large zooplankton grazers and substrate-associated cladocerans and increase in biomass of submerged vegetation. The differential response of sites to the biomanipulation was attributed to site characteristics. The open water site and sewage lagoon are kept in a turbid state by wind and wave action, and high sediment loading and may hence not be susceptible to carp exclusions (Chow-Fraser, 1998).

Las Tablas de Daimiel floodplain wetland (Spain)

Las Tablas de Daimiel, a Ramsar site and National Park, is situated within the Mediterranean, semi-arid climatic setting. As in the previous example, this wetland was dramatically altered by human action during the second half of the last century (Alvarez-Cobelas & Cirujano, 1996; Cirujano *et al.*, 1996; Alvarez-Cobelas *et al.*, 2000, 2001).

Using enclosures, Angeler *et al.* (2002) assessed impacts of three exotic fishes that comprise the dominant species of the degraded wetland's fish community. 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, pumpkinseed sunfish (*Lepomis gibbosus* L.) and mosquitofish (*Gambusia holbrooki* Girard) on water quality and zooplankton.

With addition of either 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 compared with a fishless control (Table 1). Zooplankton biomass was significantly lower in the carp treatment. However, no direct negative effects (predation) of carp were observed. 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.

Beneficial effects of fish exclusion on water quality and plankton communities were also evident in this study. However, turbidity caused by high water colour remained very high whether or not fish biomass was manipulated, indicating a possible constraint for submerged macrophyte re-colonisation.

An ecosystem perspective of biomanipulation in wetlands: potential influence of physical factors on biomanipulation

These case studies indicate that fish contribute to wetland water quality and food web characteristics in a manner consistent with the trophic cascade theory (Carpenter & Kitchell, 1993) and recent models describing community dynamics within shallow lakes (Scheffer *et al.*, 1993; Scheffer, 1998). They also indicate that physical factors may mediate outcomes of wetland food web interventions. This merits a more detailed consideration.

The influence of hydrology and landscape setting

We acknowledge that hydrogeomorphic setting and interactions with groundwater ultimately establish the boundaries for most wetland features (Winter, 1989) including characteristics of biological communities (Euliss *et al.*, unpublished data). However, even in the PPR of North America where groundwater interactions are widely believed to regulate major wetland features, biotic influences may account for more variability in the structure of biological communities than do abiotic constraints (Hanson *et al.*, unpublished data). We suggest that when and where hydrogeomorphic setting and ground water interactions are conducive for fish communities, biomanipulation may be a useful tool.

Before discussing further the value of biomanipulation for wetland rehabilitation, we need to examine two points in more detail. First, the importance of two hydrological variables (flood duration and flood frequency) and secondly, the source of eutrophication, which is intimately associated with hydrology (Sánchez-Carrillo & Alvarez-Cobelas, 2001).

Flood duration and flood frequency typically establish the disturbance regime of a wetland (Mitsch & Gosselink, 2000). We emphasise that frequency and duration of flooding, interacting with wetland type, geomorphology and climate, ultimately regulate biological processes and communities (Mitsch & Gosselink, 2000). Below, we suggest four hypothetical scenarios of biomanipulation in freshwater wetlands, highlighting potential responses to fish community interventions, and which are listed after their success potential (Fig. 1). However, long-term stability is another matter. Although guidelines favouring long-term stability have been suggested [for example, the critical phosphorus concentration threshold theory of Benndorf (1995), refined by Jeppesen *et al.* (1999), or perhaps critical fish biomass levels], we believe this is beyond the scope of our paper. For further related discussion see reviews in Perrow *et al.* (1997) and Hansson *et al.* (1998).

Scenario 1 (low disturbance regime – high internal nutrient loading). Given a wetland with limited physical disturbance and high internal nutrient loading as the principal cause of eutrophication, biomanipulation may be a useful tool for wetland mitigation. Here, a single, extreme manipulation of the fish standing crop has high potential to shift plankton community structure and biomass (cascading trophic effects), and induce water quality improvement, in a manner consistent with trophic cascade theory and

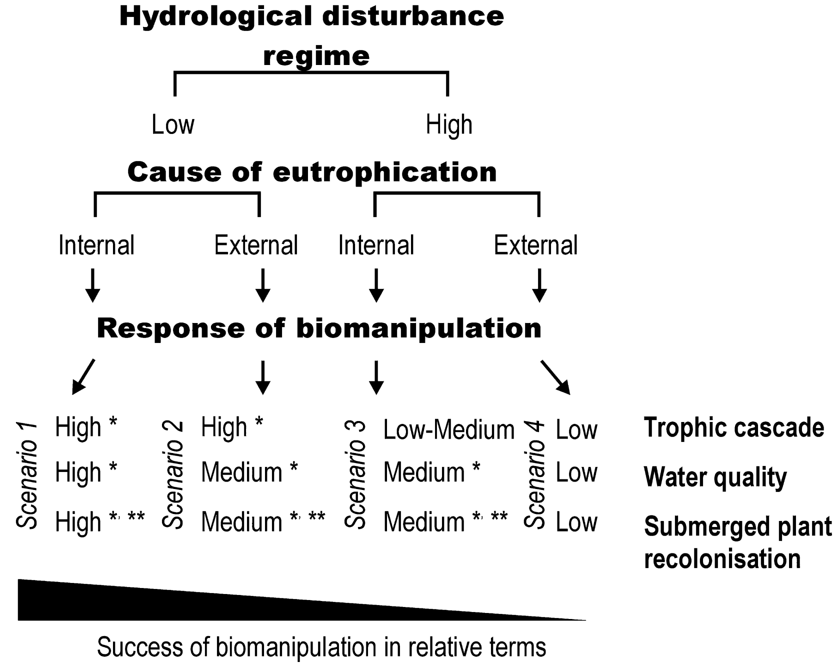

Fig. 1 Hypothetical scenarios of biomanipulations under different environmental settings and along a success gradient. *Potential benefit of biomanipulation may be counteracted if a given wetland has a high fetch. **Intensive water colour may constrain submerged macrophyte recolonisation.

alternative stable state concepts. Potential for submerged macrophyte recolonisation is also high and may begin within 1 year after fish manipulation. Such results are likely, provided that influences of water colour and wind resuspension are limited following fish removal. This scenario is nicely illustrated by the vegetated area of Cootes Paradise Marsh (Lougheed & Chow-Fraser, 2001).

Scenario 2 (low disturbance regime-high external nutrient loading). In contrast to the former example, consider a situation in which external nutrient loading to the wetland is considerable because of ineffective water treatment or other problems in the catchment. As above, assume high internal nutrient loading and little physical disturbance. *In situ* symptoms of eutrophication may be drastically reduced for some time following interventions in the fish community, even if external phosphorus loading can not be reduced to such a level that the future equilibrium concentration would be <100 μg L^{-1} (Hansson *et al.*, 1998). However, reduction in phosphorus loading levels to achieve concentrations <100 μg L^{-1} prior to biomanipulation has been recommended (Hansson *et al.*, 1998). Without abatement of external nutrient loading, characteristics of the turbid equilibrium (high phytoplankton biomass, low cladoceran and submerged macrophyte biomass, non-algal turbidity) may be extremely resilient and there is a high risk that biomanipulation may need to be repeated to maintain water quality improvements over time.

Scenario 3 (high disturbance regime – internal nutrient loading). Consider that high disturbance may result in intermittent fish transfer from adjacent aquatic ecosystems to biomanipulated wetlands during high-water flow. This may lead to increased fish predation on zooplankton, thereby relieving phytoplankton from grazing pressure. In addition, pronounced fish-induced sediment resuspension, especially under periodically low water level situations, may limit plant recolonisation, and work to maintain the turbid state. Sustaining water quality improvements and changes in community structure will likely require frequent interventions in the fish community and effective barriers to fish migration; these measures will significantly increase costs of wetland management programs.

Scenario 4 (high disturbance regime – external nutrient loading). This scenario might reflect a situation where biomanipulation is simply not useful for ameliorating eutrophication symptoms. As in Scenario 3, it is plausible that food web-mediated influences may be insufficient to control phytoplankton. Also, when high nutrient inputs are associated with frequent or prolonged water inputs to the wetland, phytoplankton may never become nutrient limited, even if benthic pelagic interactions are reduced by fish manipulations. This may lead to the maintenance of high turbidity, low light penetration, thereby perpetually limiting growth of submerged macrophytes.

Empirical support for this scenario is also given by the Cootes Paradise Marsh in that neither open-water nor wind-exposed sites (sites one and five in Fig. 1 of Lougheed & Chow-Fraser, 1998) responded dramatically to carp exclusion (see Lougheed & Chow-Fraser, 2001). The only exception was that for a brief period in 1997, site one experienced a clear-water phase that lasted about 2–3 weeks and allowed considerable increases in submerged vegetation. The clear-water phase was brought about by the delayed migration of the alewife (*Alosa pseudoharengus* Wilson), the main planktivore in the system, because of an exceptionally cool spring. This resulted in an extreme increase of *Daphnia* which consequently grazed down the phytoplankton standing crop. Once the alewife migrated into the marsh, the *Daphnia* was sharply reduced and small bosminids, rotifers and phytoplankton increased. These conditions persisted for the remainder of the season and were observed in subsequent years (Lougheed *et al.*, unpublished data). Although climatic conditions may have had confounding effects on the biomanipulation outcomes, these results suggest that benthivore or planktivore reductions may have unexpected outcomes in wetlands.

The influence of water colour

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. However, water colour may constrain secondary processes (macrophyte establishement) triggered by biomanipulations (Portielje & van der Molen, 1999). If managers were to restore submerged vegetation, such as in the Tablas de Daimiel marsh, additional remedial actions would be required and should focus on sediments and vegetation.

The influence of wind

Wind often has been considered a limiting factor for successful biomanipulation in shallow eutrophic lakes (Lammens, 1988; Hosper & Meijer, 1993; Van Donk *et al.*, 1994; Benndorf, 1995), and wetlands with a large fetch will be no exception. In the Cootes Paradise marsh, large-scale loss of emergent vegetation made this wetland susceptible to wind-induced sediment resuspension (Lougheed *et al.*, 1998). Such action can only be interrupted if artificial barriers to fetch are constructed and revegetation attempts undertaken. Unfortunately, such interventions are costly and are currently faced with several limitations (Whillans, 1996).

Additional measures to improve top-down control of algae

French, Wilcox & Nichols (1999) tested experimental barriers to fish migration to prevent benthivorous common carp from entering Metzger marsh, a coastal Laurentian Great Lakes wetland, while potentially permitting access of piscivorous northern pike. Such migration barriers may have high potential for wetland restoration in cases where recolonisation of fish from lotic and lentic aquatic systems adjacent to biomanipulated wetlands may be effectively limited.

As in shallow lake management, and where possible, remedial measures including other hydrological, sedimentological and biological actions (Wilcox & Whillans, 1999), should be used to bolster effects of biomanipulation in wetlands. There exists a growing literature on potential benefits and limitations of such approaches (see e.g. Moss *et al.*, 1996; Madgwick, 1999; Murphy & Munawar, 1999; Søndergaard *et al.*, 2000), and we encourage researchers to consider wetland application of such strategies.

Conclusion and perspectives

Biotic interactions often play important roles in structuring wetland communities (Hanson *et al.*, unpublished data). Even more than in most shallow lakes, biotic interactions in wetlands are tightly coupled with, and mediated by, abiotic factors such as the physical disturbance regime. Interactions among biotic and abiotic influences need thorough consideration in future wetland studies. Related research on basic wetland ecology has been neglected but may hold potential for development of powerful management and restoration strategies, including tools to improve wetlands degraded by severe anthropogenic stress. Biomanipulation, as the application of food web and alternative state concepts, may be very useful in wetlands. However, the complexity of interacting abiotic and biotic parameters complicates predictions on ecosystem responses to fish manipulations and limits potential usefulness of this tool for wetland mitigation. Future research should address this information need to the benefit of wetland science and future mitigation strategies.

Acknowledgments

Financial support of this study was provided by a Training and Mobility of Researchers grant (European Commission, ERBFM-BICT983001) to DGA during a postdoctoral stay at the Centre for Environmental Sciences (CSIC), Madrid, Spain. KDZ acknowledges financial support from the Department of Ecology, Evolution and Behaviour at the University of Minnesota. We acknowledge M. Alvarez-Cobelas for insightful discussions on this topic.

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(Manuscript accepted 11 September 2003)