Chapter 9

Freshwater Wetland Eutrophication

S. Sánchez-Carrillo, D.G. Angeler, M. Álvarez-Cobelas, and R. Sánchez-Andrés

Abstract The traditional perception of wetlands as nutrient sinks has led them to be used as wastewater disposal areas for a long time, resulting in a severe alteration of the structure and function by eutrophication. Nutrient loading is usually linked to hydrological alterations which encompass shifts in vegetation patterns and nutrient cycling. The eutrophication process in wetlands accelerates primary productivity and increases net accumulation of organic matter and nutrients but also enhances organic matter decomposition, microbial activity, and soluble nutrients in sediments. Internal loading becomes the main nutrient source to the wetland, even in the years of low external inputs, controlling the nutrient dynamics. Since soil phosphorus microbial biomass responds positively to phosphorus enrichment in wetlands, mineralized phosphorus in wetland soils appears as the most responsive microbial indicator to nutrient enrichment in wetlands. Therefore, phosphorus internal loading is the critical factor in regulating eutrophication status of wetlands. N_2O and N_2 emissions by wetlands can be enhanced in the future as nitrate availability in wetlands continues to be high due to increased pollution. The biological symptoms of wetlands degraded by eutrophication differ little from those observed in shallow lakes, these changes being consistent with predictions made by alternative state theory. The turbid state shows phytoplankton dominance and elevated biomass of planktivorous and benthivorous fish. Zooplanktivorous fish contribute to eutrophication chiefly via food web-mediated effects. Benthivorous fish increase the nutrient availability to phytoplankton chiefly by transferring sediment-bound nutrients to the water column during bottom foraging. Little of the methodology found to be useful in shallow lake restoration has been applied to wetland management. Whereas catchment nutrient management programs may be insufficient because of substantial storage of nutrients in wetland sediments, recent studies indicate that biomanipulation of fish standing stocks could contribute significantly to wetland eutrophication abatement. Therefore, biomanipulation, when appropriately timed in accordance with low water levels, combined with sediment dredging and other interventions, may be a low cost–high benefit tool for wetland eutrophication abatement.

Keywords Freshwater wetland · Eutrophication · Nutrient cycling · Alternative stable states · Biomanipulation

9.1 Introduction

Wetlands are known to function as filters in the landscape (Phillips 1996), retaining and transforming nitrogen and phosphorus and other compounds (Gunatilaka 1991, Sánchez-Carrillo and Álvarez-Cobelas 2001). Wetlands contribute as much as 40% to the earth's renewable ecosystem services, even though they cover only 1.5% of the planet's surface (Costanza et al. 1997). Biogeochemical processes in wetlands are so intensive to improve drastically the water quality of rivers, although the efficiency depends on landscape position and the wetland type (Whigham et al. 1988, Johnston 1991, Zedler 2003). Given this efficiency, many wetlands have been constructed,

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A.A. Ansari et al. (eds.), *Eutrophication: Causes, Consequences and Control*,
DOI 10.1007/978-90-481-9625-8_9, © Springer Science+Business Media B.V. 2011

planted, and hydraulically controlled for the purpose of removing nitrate and phosphorus from wastewaters (Kadlec and Knight 1996). However, because of the intrinsic efficiency of nutrient retention, also natural wetlands have been used as wastewater disposal areas for a long time, resulting in a severe alteration of the structure and function by eutrophication (Vaithiyanathan and Richardson 1999, Álvarez-Cobelas et al. 2001). The symptoms of eutrophication in wetlands appear similar to those in shallow lakes (Angeler et al. 2003), although the high variability of wetlands associated with the hydrological disturbance regime comprises a marked difference to shallow lakes (Middleton 1999). Since hydrology is recognized as the primary force influencing wetland ecology (Mitsch and Gosselink 2000), hydrological fluctuations induce changes in nutrient budgets (Sánchez-Carrillo and Álvarez-Cobelas 2001) and, by extension, in the ecological functioning of wetlands (e.g., Sánchez-Carrillo and Angeler 2010). Recent studies, however, are beginning to highlight disadvantages when natural wetlands are exposed to prolonged nutrient loading as they result, for example, in net emissions of greenhouse gases to the atmosphere (Verhoeven et al. 2006), contributing to enhance the negative effects associated with global climate change.

The traditional perception of wetlands as nutrient sinks resulted in a focus on the effects of inflowing nutrient-enriched waters on wetlands rather than the other way round (Lowe and Keenan 1997). Because of the diversity of wetland types, the responses of these systems to eutrophication are varied. Nutrient enrichment has been shown to influence all trophic levels within a wetland and effects include changes in species abundance, displacement, biodiversity loss, and shifts in community structure and composition (Piceno and Lovell 2000, Álvarez-Cobelas et al. 2001, Guntenspergen et al. 2002, Liston et al. 2008). Abiotic shifts induce biotic changes and these, in turn, lead to complex feedback effects on ecosystem metabolism. However, the quantitative effects of nutrient enrichment on biological communities and how nutrient cycling is altered have not been studied sufficiently yet in wetlands. These topics are very important in describing wetland eutrophication patterns. The purpose of this chapter is to provide a general description of the effects of eutrophication on wetlands, with regard to biogeochemical processes, biological responses, and wetland ecosystem functioning. The final sections are devoted to the biological and chemical indicators of eutrophication as well as how to cope with eutrophication.

9.2 The Wetland Hydroperiod and Nutrient Transformations

Wetlands are unique hydrosystems where water level varies seasonally, sometimes interannually. This annual fluctuation of water level is known as wetland hydroperiod which depicts the length of time and portion of year the wetland holds water. Hydroperiod integrates all aspects of wetland water budget (rainfall, evapotranspiration, runoff from adjacent areas, flooding, net seepage of ground water) and is probably the main signature of a wetland ecosystem which impinges on functional (biogeochemical transformations) and structural (biota) characteristics (Brinson 1993). The duration and frequency of inundation of a wetland site vary according to its hydrodynamic setting, depending on regional differences in physiography and climate and on antecedent soil moisture conditions (Winter 1988, Skaggs et al. 1991, Brinson 1993, Mausbach and Richardson 1994). Since the wetland hydroperiod controls nutrient cycling through changes on soil redox transformations (oxygen availability as electron acceptor), fluctuations of water level are crucial for understanding wetland eutrophication processes.

In a general scope, wetlands can be grouped into three major hydroperiod categories: short, intermediate, and long-time inundation duration. Short hydroperiods have ephemeral or temporary wetlands (including vernal pools) that hold water for less than 4 months a year. These wetlands tend to dry during summer months (Fig. 9.1a). Intermediate hydroperiods have also ephemeral wetlands that hold water for at least 4 months and tend to dry in late summer or later, drying completely only in years with low precipitation. Therefore, these wetlands in some years may hold water year-round (Fig. 9.1b). Finally, long hydroperiods are those wetlands that never dry up; they always hold water (Fig. 9.1c). They are also called "permanent" wetlands such as lakes and some ponds.

Wetlands can be also discerned hydrodynamically as a function of its degree of ecosystem closure (Hopkinson 1992). It shows the wetland connectivity

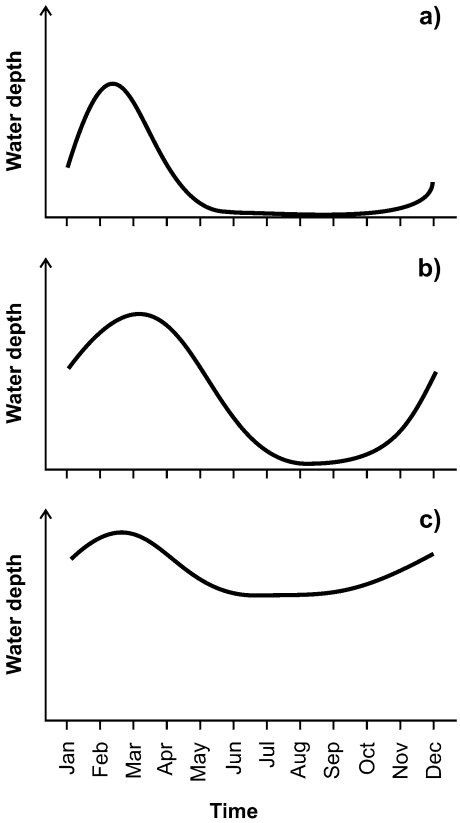

Fig. 9.1 Major wetland hydroperiod categories: short (**a**), intermediate (**b**), and long-time inundation duration (**c**)

to downstream and exerts strong influence on ecosystem dynamics as wetland exports water and chemical substances downstream, affecting retention and some chemical processes. The degree of closure of a wetland system is strongly related to its rate of water turnover (or water renewal time), which is strongly related to wetland nutrient loading (Mitsch and Gosselink 2000). In general, the openness of a wetland to hydrological fluxes determines nutrient loading, and it is an important determinant of wetland productivity, organic matter decomposition, and nutrient cycling.

9.2.1 Biogeochemical Transformations in Wetlands Under Anaerobic Conditions

The diverse hydrologic conditions in wetlands markedly influence nutrient biogeochemical processes (changes in the chemical forms and spatial movement of nutrients within wetlands, as water-sediment exchanges and plant uptake, and with surrounding ecosystems; Mitsch and Gosselink 2000). Because of the shallowness of wetlands, most nutrient transformations occur in wetland soils. While oxygen governs most of the biogeochemical reactions in upland soils, in wetlands during inundation, oxygen in soils is curtailed because soil pores are filled with water (oxygen diffusion in water is around 10,000 times slower than diffusion in air; Reddy and DeLaune 2008). The rate at which the oxygen is depleted depends on the ambient temperature, the availability of organic substrates for microbial respiration, and sometimes the chemical oxygen demand from reducing compounds such as ferrous iron. Under anaerobic conditions reduction of inorganic electron acceptors, accumulation of reduced compounds, accumulation of organic matter as a source of electron donor occur.

Oxygen is the preferred electron acceptor for microorganisms and, therefore, is always used first by them when it is available in the substrate. In the absence of oxygen, facultative anaerobes and obligate anaerobic microorganisms predominate in the substrate (Schlesinger 1997). These specialized microorganisms have the capacity to switch to other oxidants that replace oxygen in supporting biological oxidation of organic substances. The sequential thermodynamic reduction of inorganic electron acceptors according to changes in oxygen availability (as measured by the redox potential) occurs in a predictable sequence (Table 9.1). The reduction on the metabolic free energy (ΔG) determines the order of microbial processes under anaerobic conditions. The order of reductions in wetland soils starts with oxygen followed by oxides of nitrogen as nitrate (denitrification), oxides of iron and manganese, sulfate (sulfate reduction) and elemental sulfur, and carbon dioxide (methanogenesis). The rate at which these compounds are consumed in the wetland soil depends on their concentration, readily biodegradable organic compounds, and the microbial population involved in the process (Reddy and DeLaune 2008). The oxygen depletion (reduced conditions) in wetland soils appears quickly on the order of several hours to a few days after inundation (Turner and Patrick 1968, Fig. 9.2). Denitrification process develops during first aerobic stages but the rate increases strongly after oxygen is curtailed. Contrarily, reduction of iron does not begin until fully anaerobic conditions are achieved (Fig. 9.2).

Table 9.1 Thermodynamic sequence of reactions for reduction of inorganic substances by hydrogen (pH=7 and 25°C)

Reaction	Eh (V)	ΔG (kcal mol^{-1}/e^{-})[a]
Reduction (disappearance) of O_2	0.812	−29.9
Reduction of NO_3^-	0.747	−8.4
Reduction of Mn^{4+} to Mn^{2+}	0.526	−23.3
Reduction of Fe^{3+} to Fe^{2+}	−0.047	−10.1
Reduction of SO_4^{2-} to H_2S	−0.221	−5.9
Reduction of CO_2 to CH_4	−0.244	−5.6

Eh: redox potential, ΔG: free energy of reaction

[a] Assuming coupling to the oxidation reaction: $\frac{1}{4}CH_2O + \frac{1}{4}H_2O \quad \frac{1}{4}CO_2 + H^+ + e^-$ and $\Delta G = -RT\ln(K)$

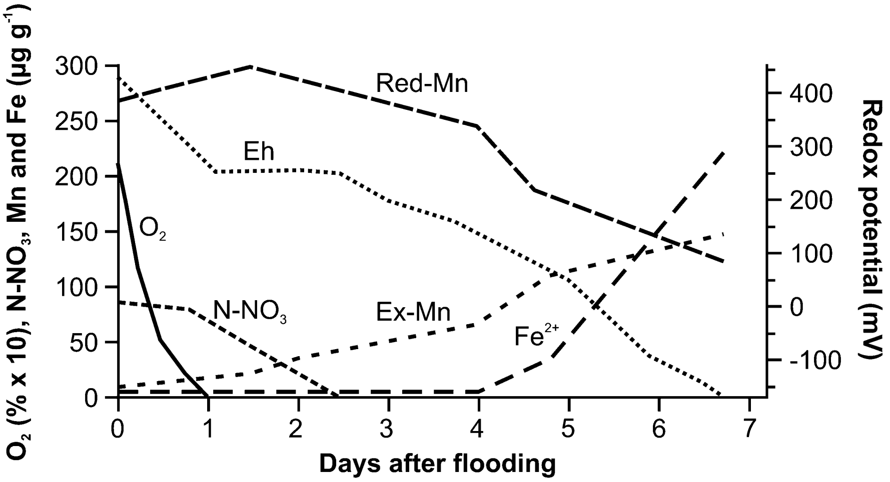

Fig. 9.2 Effects of flooding on the water chemical composition overlying a flooded soil. Redox potential (Eh) is expressed at pH 7. Red-Mn is the easily reducible Mn and Ex-Mn is the exchangeable Mn (modified from Turner and Patrick 1968)

Although the oxygen supply to the wetland soil is restricted during inundation, the oxygen demand continues to be high. These conditions result in the development of a thin layer of oxidized surface soil which has a significant effect on regulating nitrogen reactions and phosphorus sorption. It also functions as a sink for reduced compounds which diffuse from the underlying anaerobic soil layer (Reddy and DeLaune 2008).

9.2.2 Nitrogen and Phosphorus Cycling in Wetlands

Although very recent findings demonstrate some controversy about the role of N and P in limiting the productivity of aquatic ecosystems (Lewis and Wurtsbaugh 2008, Schindler et al. 2008), nitrogen is often but not only the most limiting nutrient in flooded soils. Because of the presence of anoxic conditions in wetlands, microbial denitrification of nitrates to gaseous forms of nitrogen in wetlands and their subsequent release to the atmosphere remain one of the main nutrient transformations occurring in wetlands. In addition, nitrates serve as one of the first terminal electron acceptor in wetland soils after oxygen disappearance, making them an important chemical in the oxidation of organic matter in wetlands. Nitrogen transformations in wetlands involve several microbiological processes. The presence of an oxidized zone in the soil over the anaerobic zone is critical for several of the nitrogen pathways (Mitsch and Gosselink 2000). Nitrogen retention is of particular interest in wetlands because they retain almost twice the amount of nitrogen than lakes (mean 64% of N inputs, Sanders and Kalff 2001). It has been shown that nitrogen retention depends mainly on both the nitrogen loading and the water residence time (Sanders and Kalff 2001). Water renewal rate in wetlands is lower depending on hydrodynamic openness, density and cover of macrophyte stands and those related to human intervention (damming, channelization, etc). Although nitrogen sedimentation could often be considered as the primary mechanism of nitrogen retention in wetlands, denitrification has been observed to be one order of magnitude larger than sedimentation. In an experimental wetland measured denitrification rates were 3.0–3.3 g N m^{-2} day^{-1} whereas sedimentation achieved values were 0.16–0.27 g N m^{-2} day^{-1} (Van Oostrom 1995). In a natural floodplain wetland, Saunders and Kalff (2001) also cited the same pattern between denitrification (1.3 g N m^{-2} day^{-1}) and sedimentation (0.6 g N m^{-2} day^{-1}). Denitrifying bacteria play an important role in the carbon cycle of wetlands as they contribute significantly to the carbon mineralization budget (up to 50% of the carbon mineralized in eutrophic freshwaters has been attributed to denitrifier activity, Andersen 1977, Christensen et al. 1990). The relative importance of macrophyte uptake as a nitrogen retention mechanism appears to be small compared to denitrification or sedimentation (Van Oostrom 1995). Despite the relatively small weight of plant uptake in total nitrogen retention, aquatic plants affect nitrogen cycling indirectly by retaining N during the growing season. It can influence the growth of phytoplankton by sequestering nitrogen during the highest algal demand period (Sanders and Kalff 2001). Also nutrient assimilation by plant wetlands impinges on nutrient sedimentation rates by contributing particulate matter to sediments during their senescence (Sánchez-Carrillo et al. 2001). Wetland vegetation contributes to create suitable environment for denitrification by increasing the supply of potentially limiting organic carbon and nitrate to denitrifying bacteria (Reddy et al. 1989, Brix 1997). Finally, as retention, nitrogen export downstream in open wetlands is recognized to depend on N loading and water renewal time. N export downstream in wetlands appears to be lower oscillating 10–40% of the N inputs (Kadlec and Knight 1996, Saunders and Kalff 2001).

Phosphorus is not a limiting factor in wetlands, although there are few exceptions (Reddy and DeLaune 2008). Phosphorus requirements of biota are usually much lower than that of nitrogen (mean N:P ratio of 16:1), as compared to available nitrogen in wetlands. Several wetland communities can assimilate phosphorus beyond their requirements through a process called “luxury uptake” and store phosphorus in their tissues as polyphosphates. It has been observed in sediment bacteria (Khoshmanesh et al. 2002) as well as in some wetland plants such as *Leersia oryzoides* (Kröger et al. 2007). Depending on water retention capability wetlands can operate as both a source and a sink for phosphorus. Usually, phosphorus-rich wetlands function as source of phosphorus to adjacent ecosystems. Phosphorus retention in wetlands has been cited to be regulated by macrophytes, periphyton and plankton, plant litter and detrital accumulation, soil physicochemical properties, water flow velocity, water depth, hydraulic retention time, length-to-width ratio of the wetland, phosphorus loading, and hydrologic fluctuations (Reddy and DeLaune 2008). Phosphorus retention mechanisms include uptake and release by aquatic vegetation, periphyton, and microorganisms; sorption and exchange reactions with soils and sediments; chemical precipitation in the water column; and sedimentation and entrainment (Reddy et al. 1999). Since the wetland environment provides nearly all of these favorable conditions, the ability of wetlands to accumulate phosphorus in soils is considered to be high, retaining between 40 and 90% of total phosphorus inputs, depending on the wetland hydrology, substrate composition, and redox conditions (Reddy et al. 1999). Water entering wetlands is not well mixed, resulting in typically high concentrations near the inflows, decreasing with the distance from the source (Reddy et al. 1993). Natural and constructed wetlands receiving inflows enriched in phosphorus exhibit same gradients. The reason for this spatial pattern is that phosphorus is carried in a plug flow fashion through the wetland (Reddy and DeLaune 2008), with high phosphorus sedimentation in wetland soil near to the inflow (Fig. 9.3, Sánchez-Carrillo et al. 2001). Seasonal retention rates of phosphorus usually peak at the end of summer and in fall, which match the senescent stage of macrophytes (Johnston et al. 1984, Sánchez-Carrillo et al. 2001), although higher rates have been also reported during the initial vegetation growth periods (Meeker 1996). One of the most controversial aspects of the buffer function of wetlands has focused on their ability to retain phosphorus in the long term. Wetland substrates can only hold a limited quantity of phosphorus. Since natural wetlands are also sites where sediment accretes, if the rate of sediment accretion is greater than the rate of phosphorus absorption, then wetlands can store phosphorus. In fact, wetlands tested as wastewater treatment systems became

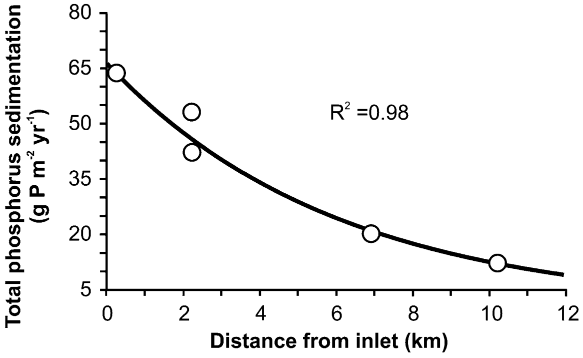

Fig. 9.3 Relationship between distance from the inlet and total annual phosphorus sedimentation in Las Tablas de Daimiel wetland during 1997–1998 (data source from Sánchez-Carrillo et al. 2001)

phosphorus-saturated in a few years, with the export of excessive quantities of phosphate (Richardson 1985).

Abiotic phosphorus retention by wetland soils is controlled by pH, iron, aluminum, and calcium content of soils, organic matter, phosphorus loading, and phosphorus concentration in soils (Reddy and DeLaune 2008). Changes in redox potential affect phosphorus solubility in wetland soils and therefore their retention. Ann et al. (1999) found that under reduced conditions, dissolved P concentrations increased in soils, which decreased with increasing redox potential. Several studies suggested that phosphorus sorption in wetland soils is related with amorphous and poorly crystalline forms of iron and aluminum (Richardson 1985, Gale et al. 1994, Reddy et al. 1998). Furthermore, total organic matter complexed with iron and aluminum also exerts an indirect effect on phosphorus sorption by wetland soils (Reddy et al. 1998). Because phosphorus retention (adsorption) in soils occurs at low concentrations, if concentration in soil pore water increases beyond the capacity of soil to adsorb phosphorus, it can precipitate some solid phases (e.g., under alkaline conditions: dicalcium phosphate, octacalcium phosphate, and hydroxyapatite; Reddy and DeLaune 2008). Similarly, continuous accretion of phosphorus in soils increases the dissolved phosphorus concentrations of soil pore waters, which results in flux from soil to the overlying water column (Reddy et al. 1999). Although periphyton and some macrophytes (e.g., submerged, floating, and some emergents as cattail and cut-sedge) have demonstrated statistically significant relationships with phosphorus concentration in the water column (McCormick et al. 1998, Sánchez-Carrillo and Álvarez-Cobelas 2001, Álvarez-Cobelas et al. 2010), plant uptake of phosphorus and incorporation into detrital tissues only must be considered as short-term storage as phosphorus is released after plants die off. Contrarily, the abiotic retention of inorganic phosphorus in soils can be considered as long-term storage of phosphorus by wetland ecosystems. Total phosphorus content in wetland soils varies from 30 to 500 mg P kg^{-1} in wetlands not impacted by anthropogenic phosphorus loading, until more than 10,000 mg P kg^{-1} in severely eutrophied wetlands receiving large discharges of phosphorus from urban wastewater and agricultural and animal operations (Reddy and DeLaune 2008). In spite of phosphorus not being a limiting nutrient in wetlands, phosphorus export downstream in open wetlands is generally low (10–60% of the total P inputs). Long-time exposition of wetlands to high nutrient loading has resulted in an increase of phosphorus concentration at the outflow during high inundation periods (Sánchez-Carrillo and Álvarez-Cobelas 2001).

9.3 Main Nutrient Sources to Wetlands: External Load vs. Internal Load

Since wetlands are hydrologically variable, nutrient inputs to the ecosystem come from various sources which can change seasonally or annually. Fluctuations in hydrological conditions induce large quantitative changes in nutrient inputs to the wetland (Sánchez-Carrillo and Álvarez-Cobelas 2001). However, the weight of the external vs. internal nutrient sources in the nutrient budget of the wetland often does not depend on the hydrologic regime. This is a distinctive feature between lakes and wetlands. While plankton controls nutrient cycling in lakes which mainly depend on external sources (Harper 1992), macrophytes and microbial communities usually control nutrients in wetlands through sedimentation and recycling (Mitsch and Gosselink 2000). Therefore, internal loading (i.e., release of accumulated nutrients to the water column) comprises the biggest nutrient fraction in wetlands as a result of continuous recycling by bacteria (Sánchez-Carrillo et al. 2001). External nutrient loading increases net accumulation of organic matter and associated nutrients in wetlands through accelerated primary productivity (Craft and Richardson

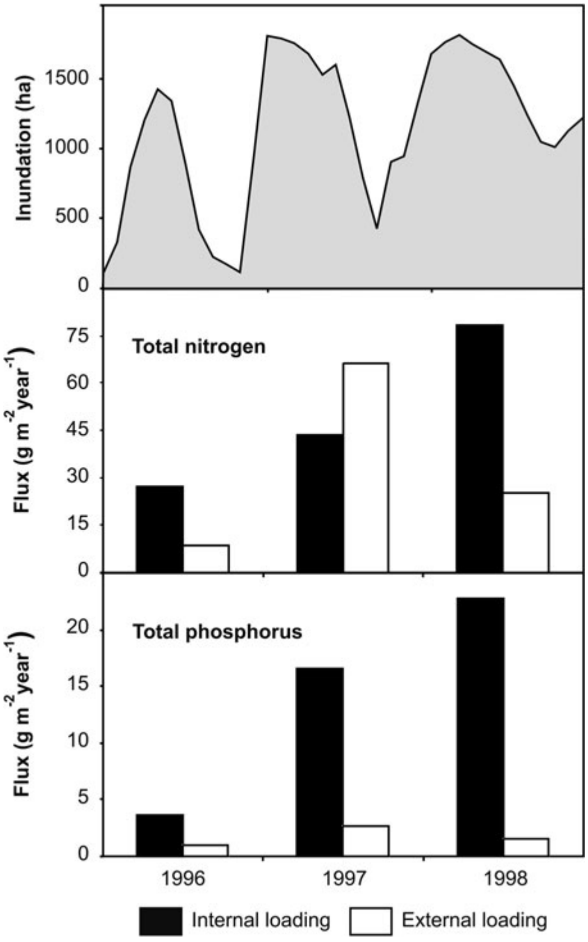

Fig. 9.4 Annual external and internal loadings of nitrogen and phosphorus and inundation in Las Tablas de Daimiel from 1996 to 1998 (data source from Sánchez-Carrillo and Álvarez-Cobelas 2001)

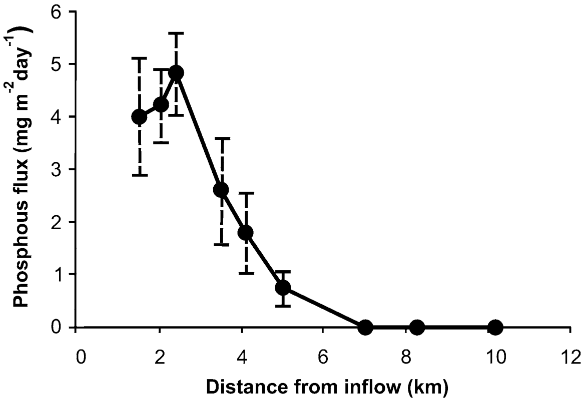

Fig. 9.5 Mean soluble phosphorus flux (±standard error) from the wetland soil to the water column measured in the Water Conservation Area 2A at the northern Florida Everglades (USA) (data source from Fisher and Reddy 2001)

1993, Reddy et al. 1993). However, increased loading not only increases total nutrient content of soils but also increases soluble forms, which can potentially be released into the water column (Reddy et al. 1998). Mechanisms involved in phosphorus mobilization between soil and overlying water column are advection, dispersion, diffusion, seepage, resuspension, and bioturbation (see Reddy and DeLaune 2008 for further information).

Several studies have demonstrated the importance of internal loading of P in the nutrient dynamics of wetlands affected by long-term nutrient loading. In semiarid fluctuating wetlands such as Las Tablas de Daimiel (Central Spain), internal loading becomes the main phosphorus source to the wetland, even in the years of high external inputs (Fig. 9.4, Sánchez-Carrillo and Álvarez-Cobelas 2001). At this site, the ratio of internal vs external phosphorus loading experienced a roughly yearly doubling as humid conditions were imposed (3.93, 6.19, and 14.26, respectively). Also, in the Water Conservation Area 2A (WCA-2A) of the northern Florida Everglades (USA), Fisher and Reddy (2001) reported that these soils function as a source of P to the overlying water column (Fig. 9.5). These authors estimated that the measured P flux (2 mg P m^{-2} day^{-1}) would be sustained for a period of approximately 5 years, assuming that approximately 25% of the total P in the top 30 cm of soil is potentially mobile and can diffuse. Phosphorus internal loading is a critical factor in regulating eutrophication status of the wetland once external loads are curtailed.

9.4 Biogeochemical Responses of Wetlands to Nutrient Enrichment

As nutrient loading increases, biogeochemical processes in wetlands are altered, changing concentrations in water and soil and, therefore, nutrient fluxes. These ecosystem-wide changes modify conditions within the wetland and alter physical and chemical environment. The addition of limiting nutrients to ecosystems increases primary productivity and stimulates microbial processes. Organic matter decomposition and nutrient cycling in wetlands depend on the chemical and physical composition of soil, microbial activity, and nutrient availability (Wright et al. 2009). Therefore, changes affecting soil characteristics through increase of organic matter and accretion rates can result in severe physical and hydrological changes to wetlands, including disappearance by siltation to short term (Sánchez-Carrillo et al. 2001).

The first step of nutrient enrichment in wetlands is a productivity increase of wetland plants. High primary productivity associated with nutrient-rich areas has been observed in numerous wetlands (Davis 1991, Childers et al. 2003, Álvarez-Cobelas et al. 2010). It promotes increases of autochthonous organic matter accumulation in wetland soils (Sánchez-Carrillo et al. 2001). Usually, an increase of nutrient loading is linked to hydrological alterations and shifts in vegetation patterns can be expected (i.e., plant species replacement, Green and Galatowitsch 2002, Childers et al. 2003, Álvarez-Cobelas et al. 2008). Therefore, changes in organic supply and litter quality can be expected in high-nutrient scenarios (Engelhardt and Ritchie 2002). Because microbial activity responds to nutrient loading and hydrology (Wright and Reddy 2001), strong shifts in decomposition rates and nutrient cycling can also be expected as wetlands become eutrophic. We have previously commented that after prolonged exposure to high nutrient loading an increase of the wetland internal loading can be expected and hence a reduction in nutrient retention. Because sediment releases into the water column tend to increase the nutrient soluble forms during eutrophication (Reddy et al. 1998), more available nutrients promote more productivity, resulting in a positive feedback process which can last years. Thus, nutrient loading into these wetlands enhances organic matter decomposition and microbial activity which increase nutrient concentrations in water (Wright et al. 2008). Although decomposition in these wetlands appears to be dominated by anaerobic pathways (denitrification, sulfate reduction, and methanogenesis; Wright and Reddy 2001), some studies have shown that also aerobic heterotrophic microbial activity is often enhanced by nutrient loading (Aers and Toet 1997, Qualls and Richardson 2000). In the Everglades it has been observed that heterotrophic microorganisms are limited by the high C/P ratios of organic matter but external P loading removes this limitation and induces changes in microbial activity (DeBusk and Reddy 1998). However, aerobic CO_2 production could not be related to the content of dissolved nutrients in soils (Wright et al. 2009) whilst microbial biomass appeared positively related to nutrient loading (D'Angelo and Reddy 1999). While heterotrophic microbial activity is immediately enhanced after addition of oxygen in nutrient-rich wetland experiments, net soil organic carbon mineralization did not demonstrate significant differences using other electron acceptors as NO_3^-, SO_4^{2-}, or CO_2 under anaerobic conditions (D'Angelo and Reddy 1999). Soil phosphorus microbial biomass responds positively to phosphorus enrichment in wetlands (Qualls and Richardson 2000, Newman et al. 2003). Labile phosphorus (the most available P fraction to vegetation and microbial communities, Ivanoff et al. 1998) has been cited as the most responsive P fraction and sensitive to eutrophication in wetland soils and suspended sediments (consisted of algae, periphyton, and particulate organic matter; White et al. 2006). Carbon and nitrogen microbial biomass did not consistently respond to nutrient loading (Wright et al. 2008, 2009). Microbial C and N are linked to C and N cycles but cannot be considered as sensitive to nutrient loading. Although eutrophication promotes mineralization rates of both nitrogen and phosphorus, the latter has been cited as the most responsive microbial indicator to nutrient enrichment in wetlands (Wright et al. 2009). Mineralized phosphorus in wetland soils appears to be significantly related to soil total phosphorus and phosphorus microbial biomass.

Increased availability of sulfate in wetlands is known to cause serious eutrophication problems, as S^{2-} produced by SO_4^{2-} reduction interacts with Fe-PO_4^{3-} complexes in the sediment to produce FeS_2 and FeS, resulting in mobilization of phosphate (Smolders and Roelofs 1993, Lamers et al. 1998). High nitrate concentrations in groundwaters have been cited to inhibit eutrophication of sulfate-rich freshwater wetlands (Lucassen et al. 2004). Since NO_3^- is an energetically more favorable electron acceptor in anaerobic wetland soils than Fe and SO_4^{2-} (Table 9.1), high NO_3^- loads function as a redox buffer, preventing reduction of Fe and SO_4^{2-}. Therefore, limited SO_4^{2-} reduction prevents S^2-mediated mobilization of PO_4^{3-} from Fe–PO_4^{3-} complexes. At higher redox potential, reduced Fe is oxidized, increasing the content of Fe (III) capable of binding PO_4^{3-}. While the typical loading rates of nitrogen and phosphorus in natural and constructed freshwater wetlands exceed proposed critical loads to prevent eutrophication (total phosphorus: 10 kg P ha^{-1} $year^{-1}$, total nitrogen: 25 kg N ha^{-1} $year^{-1}$), wetlands continue to have serious problems preserving its structure (species composition) and functioning (nutrient cycling and retention; Verhoeven et al. 2006). The potential impact of climate change on wetlands shows that they will be significantly altered because temperature and precipitation are strong determinants of freshwater wetland ecosystem structure and function (Mitsch and Gosselink 2000). Lower water availability will reduce the flushing rate of wetlands as water renewal time increases. It probably will contribute to increase the high nutrient state of wetlands as biogeochemical processes will be promoted. In the same way, because wetlands are a major natural source of greenhouse gases to the atmosphere we could expect changes on the emissions of N_2O and N_2 as a consequence of eutrophication. Nitrogen emissions, which have a global warming potential 310 times that of CO_2 (IPCC 1996), can be enhanced in the future as nitrate availability in wetlands continues to be high due to increased pollution. When nitrate availability is high, reduction of nitrate instead of N_2O is energetically favorable for denitrifiers (Barnard et al. 2005). This potential negative consequence of nitrate-rich wetlands is often ignored or downplayed. Thus, there is a great need for additional information about the risk of nitrogen emissions from nitrogen-loaded wetlands (Verhoeven et al. 2006).

9.5 The Biological Effects of Wetland Eutrophication: Community Structure, Alternative Stable States, and Trophic Cascades

The biological symptoms of wetlands degraded by eutrophication differ little from those observed in temperate shallow lakes (Jeppesen 1998, Schutten and Davy 2000). Increased nutrient and water 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 piscivores have been frequently reported in wetlands (e.g., Whillans 1996, Chow-Fraser et al. 1998, Álvarez-Cobelas et al. 2001). These changes are consistent with predictions made by alternative state (ASS) theory (Scheffer et al. 1993) and the trophic cascade concept (Carpenter and Kitchell 1993). The ASS concept posits that ecological systems may shift between contrasting states, the shifts being triggered either by altered community structure in similar abiotic environments (Chase 2003a, 2003b) or by changing abiotic environmental settings that cause major community shifts (e.g., Scheffer et al. 2001, Dent et al. 2002). In aquatic ecology, the ASS paradigm is based on research results from north-temperate, shallow lakes where cultural eutrophication is the main driver causing lakes to shift from the clear-water, submerged macrophyte-dominated state to the degraded, turbid, phytoplankton-dominated state (e.g., Scheffer et al. 1993, Jeppesen et al. 1997). This classic example from shallow lakes is an ideal starting point from which to reflect on the current status of the ASS concept in aquatic ecology and its particular application to wetlands. Our most pressing environmental problems demand consideration of diverse anthropogenic impacts that act in concert with global climate change, potentially pushing ecosystems irreversibly to other alternative states (Falk et al. 2006). This raises major challenges in managing novel ecosystems in ways that go beyond the simple control of nutrient loading and algal blooms and includes maintaining sustainability that guarantees the provision of ecosystem services to humans (Kremen 2005). Given the many ecosystem services which wetlands provide to humans and wildlife, understanding the processes that contribute to shift wetland ecosystems between ASS is relevant with regard to impact assessment and management interventions. In addition to alternative state theory, considerable evidence indicates that also concepts related to trophic cascading interaction are useful for understanding characteristics and responses of ASS in wetlands (Chow-Fraser 1998, Álvarez-Cobelas et al. 2001). As has been pointed out previously, the trophic status of aquatic ecosystems seems to mediate in the configuration of food webs and thus trophic cascading interactions from fish to plankton. 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 wetlands in the degraded state (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. Under such conditions planktivorous and benthivorous fish can affect food web structure and ecosystem characteristics in different ways.

In shallow lakes and wetlands, 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). Benthivorous fish, like for example common carp, also contribute to high non-algal turbidity via resuspension of sediment particles and by causing mechanical damage to submerged macrophytes (Crivelli 1983, Brabrand et al. 1990).

In contrast, community structure in shallow lakes and wetlands 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 et al. 1989, Ozimek et al. 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 μg L^{-1} total phosphorus (TP); Jeppesen et al. 1997), either alternative state (clear or turbid) may persist and system shifts are possible, although shifts may be resisted by internal stabilizing mechanisms, such as the activities of crayfish and planktivorous and benthivorous fish. It is not yet clear which factors contribute to the prevalence of either state during different years under intermediate nutrient concentrations; however, climatic factors (mild or harsh winters) may play an important role (Piet Verdonschot, Wageningen University and Research, The Netherlands, personal communication).

9.6 Biomanipulation of Wetlands as a Tool for Eutrophication Mitigation

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., wastewater treatment facilities, regulatory policies to reduce runoff), 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 and Kentula 1990, Wilcox and Whillans 1999). Angeler et al. (2003) emphasized 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 et al. 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 benthic community dynamics (see reviews in Reynolds 1994, Perrow et al. 1997, Hansson et al. 1998, Drenner and Hambright 1999, Gulati et al. 2008). 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 is becoming well documented (Zimmer et al. 2002), they have been largely neglected by scientists and managers. Recent studies, however, indicate that manipulation of fish standing stocks could contribute significantly to wetland eutrophication abatement (Chow-Fraser 1998, Lougheed et al. 1998, Angeler et al. 2002).

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 (Table 9.2), 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.

Fish occupy a key position in lake food webs, and it may not surprising that the biomanipulation paradigm is mainly based on the notion that interventions in fish community structure have cascading effects toward 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 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 riparian wetlands are covered by large extents of emergent plants (Mitsch and Gosselink 2000), 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 (Sánchez-Carrillo et al. 2004)). Thus, emergent vegetation clearly represents a key biotic component in this wetland, and the following example highlights that an extension of biomanipulations to cope also with other target communities than fish may be useful for wetland rehabilitation.

A case study is that of Las Tablas de Daimiel National Park, which is a semiarid floodplain wetland located in central Spain. Before large-scale degradation took place during the second half of last century, mainly in the form of wastewater discharge and groundwater abstraction, the emergent macrophyte community of this wetland was dominated by the evergreen *Cladium mariscus*. Nowadays, *Cladium* has largely been replaced by the 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). Sánchez-Carrillo et al. (2001) 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 favor of intervention in the vegetation community structure, which could help to decrease the present sedimentation rates and extend the life span of Las Tablas de Daimiel.

Table 9.2 Comparison of selected water quality and biotic variables in response to biomanipulation in selected wetlands. The table has been taken from Angeler (2010)

Site	Secchi depth	Phytoplankton biomass	Total P	Total nitrogen	Turbidity	Cladocerans	Submerged vegetation	Intervention	Type of study/duration	Sources
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 et al. (1998)
Tablas de Daimiel floodplain (Spain)	n.s.	–2.6[b,c]	–2.3[b,c]	–1.4[b,c]	–3[b,c] as total suspended solids	+ ca. 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]	–ca. 1.2[d]	n.d.	n.s.	+ ca. 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)
Prairie 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 tends to increase or decrease after the manipulations are indicted)

[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

9.7 Conclusion

In conclusion, even though wetlands are usually seen as efficient nutrient sinks, however, the prolonged exposition to high nutrient loading has demonstrated serious negative effects on wetland structure and functioning. Because the eutrophication symptoms in wetlands differ little from those observed in temperate shallow lakes, restoration strategies may be similar than those applied to shallow lakes. Sediment dredging and biomanipulation of fish standing stocks could contribute significantly to wetland eutrophication abatement, when appropriately timed in accordance with low water levels.

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