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APPLIED ISSUES

Conflicting demands on wetland ecosystem services: nutrient retention, biodiversity or both?

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SUMMARY

1. Wetland ecosystems may, besides having considerable economical value, increase landscape biodiversity and function as traps for nutrients from land to freshwater- and marine systems. As a result of these features, wetlands are nowadays often protected and restored, and many countries have even initiated wetland construction programmes.
2. In the present study, we aim at increasing the knowledge on how to improve the design of a wetland with respect to both biodiversity and nutrient retention, by analysing physical, chemical and biological features of a large set of constructed wetlands.
3. Our results show that a combination of the wetland features, namely shallow depth, large surface area and high shoreline complexity are likely to provide a high biodiversity of birds, benthic invertebrates and macrophytes and to have high nitrogen retention, whereas a small, deep wetland is likely to be more efficient in phosphorus retention, but less valuable in terms of biodiversity.
4. Hence, among the features used to design new wetlands, area, depth and shoreline complexity have fundamental, and sometimes conflicting, effects on nutrient retention and biodiversity. This means that there are, within limits, possibilities to direct the ecosystem function of a specific wetland in desired directions.

Keywords: biodiversity, nutrient retention, restoration, species richness, wetland

Introduction

Large areas in Europe and North America were until a century ago scattered with wetlands; a type of ecosystems that was considered less desirable when industrialisation, modern agriculture and the increase in human populations accelerated. When the demands for dry land increased, national, regional and local authorities, as well as private landowners, responded by draining and channalisation of diffuse water flows, thereby increasing the area available for agriculture and forestry. In some areas with intense agriculture almost all wetlands disappeared within a few decades (e.g. Findlay & Houlahan, 1997; Paludan *et al*., 2002; Shan, Yin & Li, 2002).

On a global scale, wetlands are one of the most valuable resources per unit area, providing a number of ecosystem services, including water supply, raw material, food and recreation (Costanza *et al*., 1997; Zedler, 2000). They are inhabited by many organisms that are specialised to live in these ecosystems, such as many amphibian species, but may also function as important refugia and subsidy for organisms spending most of their life cycle in terrestrial or purely aquatic ecosystems. Hence, wetland reduction affects not only pure wetland species, but also the biodiversity of whole regions (Findlay & Houlahan, 1997; Keddy, 2000). During the last decades, the interest in biodiversity has increased tremendously (Ehrlich &

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Ehrlich, 1981; Wilson, 1992; Tilman, 1999; Strayer, 2001; Brönmark & Hansson, 2002), not only because high biodiversity may increase a systems resistance to invasive species (Moss, 2000; Loreau *et al.*, 2001), but also because it has been suggested to have strong effects on ecosystem function (Naeem, 2002). Wetlands increase the retention time for nutrient rich run-off water in the landscape, thereby decreasing the amounts of nutrients reaching lakes and, eventually, the sea (Mitsch *et al.*, 1995; Paludan *et al.*, 2002). Reduction in wetland area and the increased use of fertilisers has led to severe eutrophication problems both in freshwaters and coastal waters. An obvious result of this common scenario is that the waters affected become less useful as a resource for humans and as a habitat for most organisms.

Wetland ecosystems may serve as economically important resources, increase biodiversity and function as nutrient traps. These multiple functions have lead to an increasing interest in restoring, or even constructing wetlands, especially in agricultural areas. This option has recently been made more possible as the demand for agricultural areas has decreased. However, a major problem is that wetlands with high nutrient retention may not necessarily have a high potential for increasing biodiversity and vice versa (e.g. Zedler, 2003). Another problem is that present-day focus is usually on nutrient dynamics or biodiversity, but both are seldom treated simultaneously. Hence, although wetland construction programmes are being implemented in many countries, our knowledge on how to design a wetland, taking both nutrient reduction and biodiversity into account, is surprisingly scarce. In the present study, we aim at identifying features of wetland design, addressing both biodiversity and nutrient retention by analysing physical, chemical and biological features of a large set of constructed wetlands. Most studies regarding wetland function have focused on mass balances of nutrients or on biodiversity of different taxa in wetlands, whereas a 'helicopter perspective' including chemical, physical and biological variables is rarely taken. Our study aims at taking such a perspective by screening for general patterns in a large set of variables potentially important for wetland ecosystem functioning. Although this approach inevitably leads to simplification, it may be an efficient tool for the advancement of ecological knowledge and, in combination with previously published studies, it may create a basis for predictions (Rigler, 1982; Keddy, 1992; Rigler & Peters, 1995). Such predictions include, for example, a positive relation between the species richness of macrophytes and phosphorus retention (Engelhardt & Ritchie, 2001). For example, based on a study of 30 wetlands in Canada (Findlay & Houlahan, 1997), a positive relation between wetland area and species richness of most taxa may be predicted, as well as that wetlands with low nutrient concentrations should have a higher species richness (Moore *et al.*, 1989). Besides validating predictions from previous studies using our data set, the main aim of this study was to identify features that define a 'good' wetland; that is, a wetland providing high biodiversity, as well as high nitrogen and phosphorus retention.

Methods

Our study was focused on 32 recently constructed wetlands situated in two adjacent catchment areas in southern Sweden, the rivers Kävlinge (18 wetlands) and Höje (14 wetlands; Ekologgruppen, 2001a,b). The Höje river catchment covers an area of 315 km^2, whereas the Kävlinge river catchment is 1185 km^2. The catchments are both used for intense agriculture leading to yearly mean nitrogen concentrations (total nitrogen) in streams and rivers of 5–10 mg L^{-1}, but with peaks above 20 mg L^{-1}. Yearly mean values for total phosphorus in running waters of the catchments are generally between 70 and 150 $\mu g\ L^{-1}$, with peaks above 500 $\mu g\ L^{-1}$. The wetlands used in our study were constructed within a regional project aimed at improving biodiversity and nutrient retention within the catchments (Ekologgruppen, 2001a,b). Criteria used in wetland selection consisted of age and morphometry, as well as having been well surveyed with respect to flora and fauna. All data used in the analyses are from 2000, except for macrophyte cover and measures of nitrogen and phosphorous which were sampled in July and November 2001. The species richness of several taxonomical or functional groups was surveyed; benthic invertebrates, birds, vegetation, amphibians and fish and the proportional coverage of macrophytes were estimated. Species richness of benthic invertebrates was surveyed by kick-sampling during 15 s along each of four 1-m stretches in each wetland (Ekologgruppen, 2002). The net used was 0.25 m in diameter and had flat bottom.

The invertebrates were caught by sweeping the net (0.5 mm mesh size) above the bottom and through vegetation on each 1-m stretch during kicking. In addition to kick-samples, qualitative samples were taken in the wetland vegetation and water column and pooled before analysis. The samples were preserved in 70% ethanol (final concentration) and identified to species in the laboratory using a microscope.

Vegetation surveys were conducted during the period 4–29 September 2000 by walking along the shoreline (0–5 m above the shore), and all plants found were identified to species (Ekologgruppen, 2001a). Submersed vegetation was surveyed by throwing a small anchor (120 mm hook length) 15 m out into the water and retrieving aquatic plants upon hauling. This sampling was performed at regular distances around the whole wetland. Depending on wetland area, the anchor was thrown between five and 15 times in each wetland. As the wetlands included in our study are rather small (0.3–6.1 ha), visual inspection was used to estimate the percentage of wetland vertical projection area covered by macrophytes. Plant or invertebrate species that were not dependent on the wetland habitats for at least part of their life history were excluded from further analysis.

Bird species richness for each wetland was obtained by surveys on two occasions during the breeding season, mid-May and beginning of June 2000 (Ekologgruppen, 2001b). The wetlands were surveyed in a standardised way for breeding species with telescope and binoculars, and directly by eye and hearing, first from a distance and then during a walk around the wetland. Bird species that were considered not connected to the wetland habitat were excluded from analysis. In total, 33 wetland bird species were recorded in the area.

Amphibian (larvae) species richness was surveyed by netting and ocular inspection of the littoral zone during daytime. At least 100 m, or the complete littoral zone for smaller wetlands, was inspected and special attention was paid to microhabitats suitable for larval amphibians. Fish species richness was surveyed by electrofishing in the shallow, littoral zone. At least 50 m stretches of the littoral zone were fished, or the complete volume in small wetlands.

Water samples for nitrogen (N) and phosphorus (P) analyses were taken in acid washed 100 mL glass bottles from the inflow and outflow of each wetland in July and November 2001 (i.e. summer and winter conditions, respectively). The samples were stored at 5 °C for a maximum of 4 days. Total phosphorus was analysed as soluble reactive phosphorus after digestion with potassium persulphate and total nitrogen was analysed as nitrite after digestion with potassium persulphate and sodium hydroxide after nitrate reduction by a copper-cadmium reductor column. The analyses were carried out with a Technicon autoanalyser II (Pulse Instrumentation, Saskatoon, SK, Canada) according to Technicon protocols. The relative nitrogen and phosphorus retention of the wetlands was calculated as the difference between inflow and outflow concentrations. Mean nutrient concentrations (July and November) from the inflow of each wetland was used as an estimate of nutrient inflow.

The physical characters used to describe and characterise wetlands were age, area, shoreline complexity and maximum depth. Area (ha) and shore length (m) were measured from detailed drawings produced for the wetland construction. Shoreline complexity was calculated as the ratio between wetland shore length and the circumference of a circle of the same area as the wetland.

Statistical analysis. Variables were examined for normal distribution and all data, except nutrient concentrations, were $\log_{10}$ transformed. Area, shoreline complexity, maximum depth and age of each wetland were used as independent variables. Variables associated with features of wetland biodiversity, including species richness of benthic invertebrates, wetland birds, macrophytes and the cover of macrophytes were used as dependent variables in a stepwise regression model (Sokal & Rohlf, 1995). Fish and amphibian species richness were not possible to include in the analysis as the variances were not large enough (range 0–6 and 0–2 species, respectively). Age, area, shoreline complexity and maximum depth were categorised as independent variables potentially affecting nutrient retention (P and N retention in July and November). Probability values ≥ 0.10 are presented for the regression models.

Results

All wetlands included in our study were young, ranging in age between 1 and 8 years. The wetland area ranged from 0.3 to 6.1 ha (mean ± SD = 1.4 ± 1.5 ha), and maximum depths ranged from 0.2 to 3.5 m during summer.

Table 1 Ranges and mean values (±1 SD) of selected biological and chemical features of 32 wetlands. The ranges in inflow concentrations of total nitrogen (TN; mg L^{-1}) and total phosphorus (TP; μg L^{-1}) to each wetland are given for July and November 2001.

	Range	Mean	SD
Benthic invertebrates	15–54	34	9
Wetland birds	0–12	5	3
Macrophytes	18–51	34	8
Macrophyte cover	0–100	35	30
Nitrogen			
July	1.2–12.0	3.7	2.6
November	2.1–16.9	7.9	3.5
Phosphorus			
July	39–387	125	84
November	50–332	108	57

Inflow concentrations ('load') of nitrogen were generally lower in July than in November (Table 1); only nine of the 32 wetlands (28%) had inflows >4 mg L^{-1} in July, compared with 26 wetlands (81%) in November. The relative retention of nitrogen was linearly related to inflow concentrations in July (r^2 = 0.82; Fig. 1), suggesting that outflow concentrations were relatively constant at approximately 2 mg L^{-1} irrespective of inflow concentration. No such relation was recorded in November. At winter inflow concentrations >8 mg L^{-1} nitrogen retention decreased (Fig. 1). Phosphorus inflow concentrations ranged from 39 to 387 μg L^{-1} in July and from 50 to 332 μg L^{-1} in November (Table 1). Relative phosphorus retention showed a less clear pattern compared with nitrogen retention, with a tendency to a linear relation between inflow and retention in winter, whereas in July retention increased with inflows up to about 150 μg L^{-1}, but then levelled off (Fig. 1).

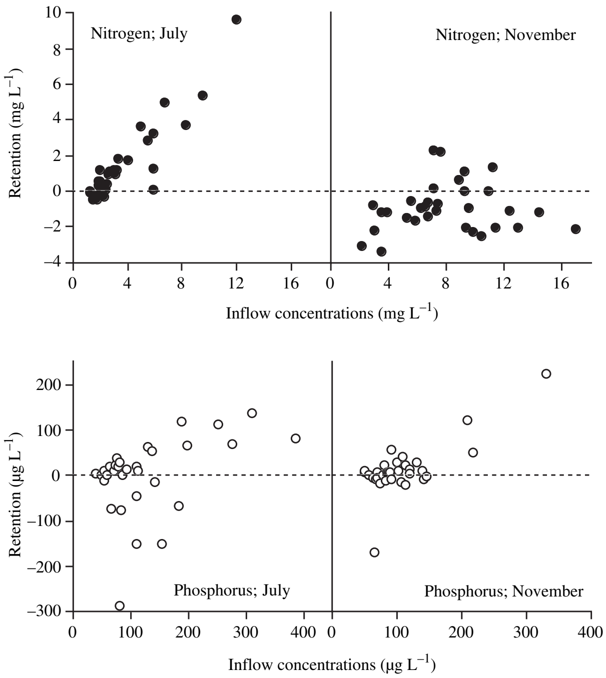

Fig. 1 The relation between inflow and relative retention of nitrogen (filled symbols) and phosphorus (open symbols) in summer (July) and winter (November). Data points below and above the dashed zero line indicate leakage and retention, respectively.

Retention, estimated as percent reduction in concentration through the wetlands, of both phosphorus and nitrogen varied widely in the wetlands investigated (Table 2). Some wetlands even leaked nutrients downstream (i.e. negative retention), whereas others were highly efficient (retention >80%), especially during summer (Table 2). Of the 32 wetlands investigated, 50% had lower total phosphorus concentrations in the outflowing than in the inflowing water in July as well as in November (Fig. 2). On the contrary, six wetlands (19%) released phosphorus downstream on both sampling occasions, whereas the remaining 31% had either positive or negative retention on one sampling occasion (Fig. 2). With respect to nitrogen, the proportion of wetlands that had a positive retention both in July and November was somewhat higher than for phosphorus (63%), whereas the proportion with either positive or negative retention was similar to phosphorus (28%). Only three wetlands (9%) always leaked nitrogen downstream. Relative nitrogen retention tended to be positively, although not significantly, affected by wetland area both in summer and winter, whereas shoreline complexity tended to have a negative effect on nitrogen retention in summer (Table 3). In contrast, retention of phosphorus during winter was negatively affected by wetland age and surface area, whereas retention during summer was positively affected by large maximum depths (Table 3).

Benthic invertebrate species richness ranged from 15 to 54 species among the 32 wetlands, and the macrophyte species richness showed a similar range (18–51 species; Table 1). The number of wetland bird species was lower, ranging from 0 to 12, with a mean of five species per wetland (Table 1). Species richness of benthic invertebrates showed an increase with wetland age up to about 5 years and then levelled off

Table 2 Ranges in retention (%) of total nitrogen (TN) and total phosphorus (TP) in natural, constructed and simulated wetlands. *n* indicates number of wetlands included.

Wetland type	TP (%)	TN (%)	*n*	Reference
Constructed (U.S.A.)	11–49	26–78	5	Sakadevan & Bavor, 1999
Constructed (China)	83	–	1	Shan *et al.*, 2002
Natural (U.S.A.)	59	80	1	Kao & Wu, 2001
Constructed (U.S.A.)	53–92	–	4	Mitsch *et al.*, 1995
Constructed (U.S.A.)	75	–	1	Nungesser & Chimney, 2001
Constructed (Spain)	–	84–98	4	Comín *et al.*, 1997
Simulation (Sweden)	–	1–40	40	Arheimer & Wittgren, 2002
Constructed (Sweden)				
July	−136–97	−37–80	32	This study
November	−27–67	−57–48	32	This study

Note that the minimum retention in the wetlands included in this study was negative as some of the wetlands leaked nutrients downstreams.

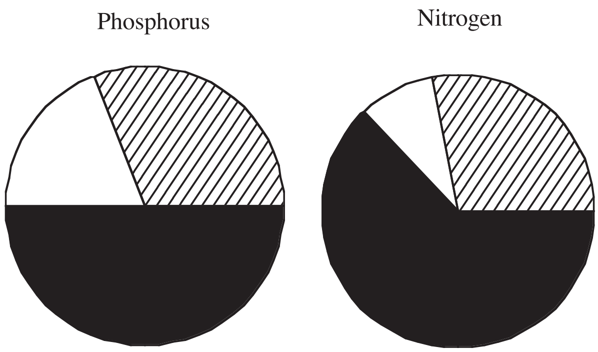

Fig. 2 Proportion of the wetlands included in our study showing relative phosphorus and nitrogen retention on both sampling occasions (black), none of the sampling occasions (white) and either in winter or summer (striped).

(Fig. 3; $r^2 = 0.35$; $P < 0.001$; $y = -0.97x^2 + 9.96x + 16.03$). Bird species richness increased with wetland area up to about 4 ha where it reached a maximum richness at about 12 species (Fig. 3; $r^2 = 0.72$; $P < 0.001$; $y = -0.56x^2 + 4.90x + 0.11$). Wetland plant species richness was linearly related to shoreline complexity throughout the range of wetlands included in our study (Fig. 3; $r^2 = 0.50$; $P < 0.001$; $y = 14.27x + 13.19$). The species richness of fish ranged from zero to three, except for two wetlands that had four and five species, respectively (mean = 1.2 species per wetland, Fig. 4a). In natural wetlands (age > 100 years), situated in the same region as our wetlands, fish species richness is considerably higher (mean = 4.2 species per wetland; Fig. 4b). The number of

Table 3 Partial correlation coefficients from a stepwise multiple regression of wetland features [age, area, shoreline complexity, maximum depth and phosphorus (P) and nitrogen (N) inflows] on biodiversity variables (species richness of wetland birds, benthic invertebrates and plants, as well as macrophyte cover) and N and P retention (summer and winter)

	N-summer	N-winter	P-summer	P-winter
Effects on nutrient retention				
Age	–	–	–	−0.53 (0.001)
Area	0.20 (NS)	0.19 (NS)	−0.24 (NS)	−0.56 (0.001)
Complexity	−0.21 (NS)	–	–	–
Max Depth	–	–	0.37 (0.040)	–
	Invertebrates	**Birds**	**Plants**	**Macrophyte cover**
Effects on biological variables				
Age	0.65 (0.001)	NS	0.22 (NS)	0.43 (0.008)
Area	0.28 (0.100)	0.53 (0.001)	–	–
Complexity	–	–	0.69 (0.001)	0.39 (0.015)
Max. Depth	–	0.28 (0.070)	–	−0.28 (0.070)
N load	–	0.25 (0.100)	–	–
P load	−0.51 (0.003)	–	–	–

All correlation coefficients larger than ±0.15 (*P*-values within brackets) are included whereas coefficients smaller than 0.15 are illustrated by a hyphen. Significance levels up to 10% are shown and non-significant correlations at this level are denoted NS. As none of the biological variables in our study affected nutrient retention significantly they are not shown in the table.

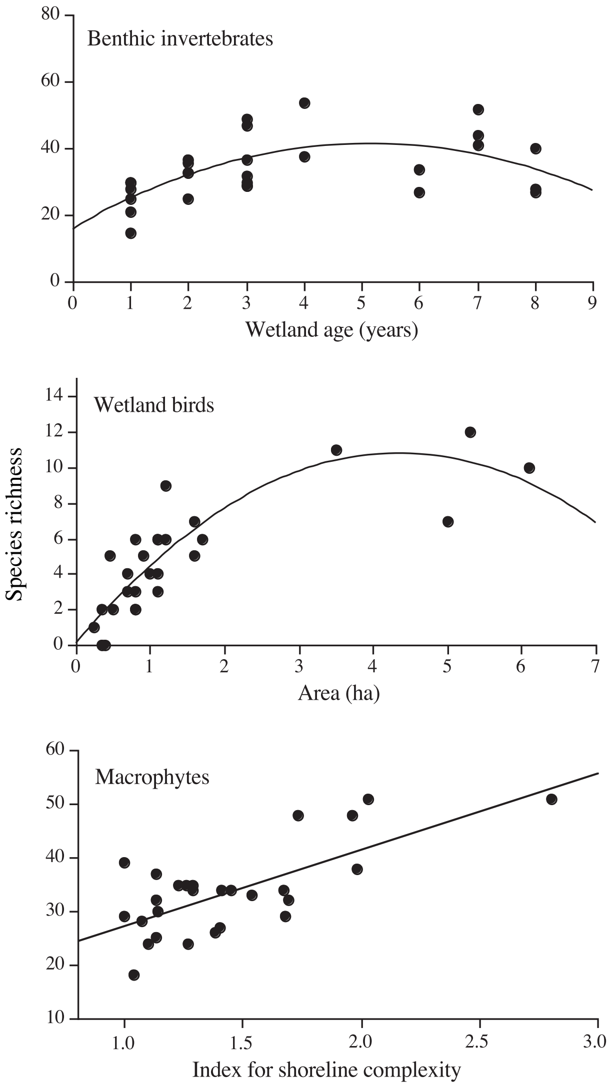

Fig. 3 Relation between wetland age (years) and species richness of benthic invertebrates ($r^2 = 0.35$; $P < 0.001$; $y = -0.97x^2 + 9.96x + 16.03$); between wetland area (ha) and species richness of wetland birds ($r^2 = 0.72$; $P < 0.001$; $y = -0.56x^2 + 4.90x + 0.11$); and between the shoreline complexity and wetland plant species richness ($r^2 = 0.50$; $P < 0.001$; $y = 14.27x + 13.19$).

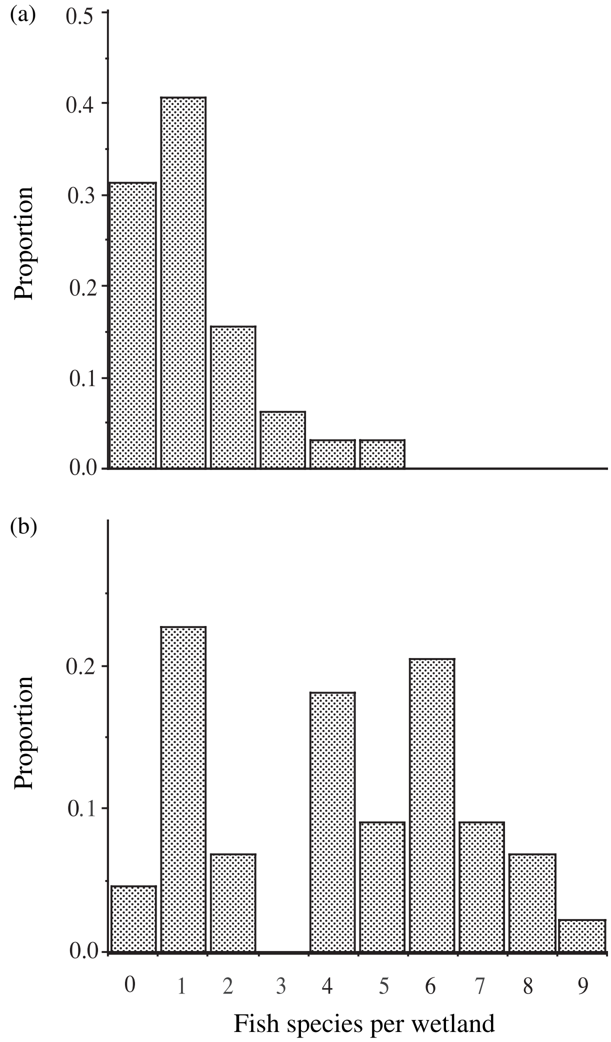

Fig. 4 The frequency of wetlands and fish species for (a) 32 constructed wetland ecosystems included in our study and (b) old, natural wetlands in the same region. Data in (b) are from Brönmark & Edenhamn (1994, 1996); and C. Brönmark (unpublished data).

amphibian species recorded was lower than for fish, ranging from zero to two species per wetland.

Stepwise multiple regression showed that benthic invertebrate species richness was positively related to age and surface area of wetlands and negatively related to phosphorus load (Table 3). Wetland bird species richness was strongly positively related to surface area up to an area of about 4–5 ha (Fig. 3). Shoreline complexity was the main factor affecting the number of macrophyte plant species. High shoreline complexity, together with age, improved conditions for the establishment of high macrophyte cover, whereas greater maximum depth affected macrophyte cover negatively (Table 3).

Discussion

One of the measures undertaken to counteract negative effects from nutrient run-off and biodiversity loss caused by agricultural and urban activities is the construction of wetlands (e.g. Paludan *et al.*, 2002). Wetlands are often used to reduce nutrient transport from land to the sea, mainly through denitrification of nitrogen and sedimentation of phosphorus rich particles (Cooper & Gilliam, 1987; Craft, 1997; Keddy, 2000), and to increase the biodiversity and the recreational value of the cultural landscape.

The technical knowledge on how to maximise nutrient retention is relatively well developed (Leonardson, 1994; Kadlec & Knight, 1996), whereas knowledge on how to increase wetland biodiversity is, in comparison, negligible. Generally, the construction of wetlands should increase biological richness through the increase of habitat complexity, although this could be true to different extents, depending on the design of the wetlands. Thus, a wetland designed to improve nutrient retention may not necessarily increase biodiversity and vice versa. One way to handle this problem is to design some wetlands for nutrient reduction and others for improving biodiversity. Such 'diversified use' (Hansson, Lundqvist & Drake, 2000; Brönmark & Hansson, 2002) may be applicable when planning at a catchment scale. Another alternative would be to design a specific wetland by taking into account both biodiversity and nutrient reduction. In the present study, we focus on the latter approach.

Our results show that some wetland features are important for nutrient retention or biodiversity, whereas others have only a negligible impact, suggesting that there are, within limits, possibilities to direct the function of a specific wetland. This notion is further strengthened by the considerable ranges in nutrient retention recorded in different wetlands throughout the world (Table 2), suggesting that wetland design may be important for nutrient retention. For example, inflow concentrations, hydraulic loadings, area, shape and retention time of the wetland (Arheimer & Wittgren, 2002), as well as biological variables, such as macrophyte cover have been shown to influence nutrient retention (Saunders & Kalff, 2001). As several of these variables and processes can be manipulated it may be possible to construct wetlands to maximise retention. With respect to biodiversity, previous studies have demonstrated a positive relation between wetland area and species richness of several organism groups, including birds, amphibians, benthic invertebrates and plants (Brönmark, 1985; Møller & Rørdam, 1985; Findlay & Houlahan, 1997; Keddy & Fraser, 2000; Zedler, 2003). This is in accordance with our findings, with respect to both birds and benthic invertebrates. Moreover, a high shoreline complexity increases biodiversity of macrophyte plants (Table 3). Hence, a wetland created with the aim to increase biodiversity should have a large surface area and a complex shoreline. According to our study at least 4 years are needed to reach maximum species richness of benthic invertebrates. Moreover, macrophyte species richness showed a tendency to increase with time, which agrees with the findings of Galatowitsch & van der Valk (1996). In our study, the fish biodiversity was low in the young (<8 years) wetlands, suggesting that it may take even longer time for fish than for benthic invertebrates to become established in constructed wetlands. This notion is supported by data from natural wetlands (>100 years old), showing a less skewed frequency distribution than the constructed wetlands with respect to fish biodiversity. Further, high nutrient inflow may result in low biodiversity of wetland birds and invertebrates. For example, high nutrient loads have been shown to reduce the biodiversity of macrophytes in North American wetlands (Keddy & Fraser, 2000). In our study we found no relation between nutrient load and species richness or cover of macrophytes. On the contrary, a high biodiversity of macrophytes has been predicted to improve the nutrient retention of wetlands (Engelhardt & Ritchie, 2001), although our data provide no support for such a relation either. Similarly, we found no significant effects of macrophyte cover on nutrient retention or indeed on any of the biological variables. A possible reason for this may be the relatively low age of our wetlands (i.e. the macrophyte stands are not fully developed).

Our study showed that large surface area of wetlands is related to improved nitrogen retention, but not to phosphorus retention. Hence, it may be difficult to maximise both nitrogen and phosphorus retention in the same wetland. High phosphorus retention may also result in low species richness of benthic invertebrates, as invertebrate richness increased and relative phosphorus retention (winter) decreased with wetland age (Table 3; Craft, 1997). The wetlands included in our study were highly efficient with respect to nitrogen retention during summer, which was most probably because of enhanced denitrification (Craft, 1997). In winter this biological process becomes less efficient, which was reflected in the poor relation between nitrogen inflow concentration and relative retention. This is especially problematic as inflows are high during winter because of run-off from agriculture. Phosphorus showed the opposite response with relatively low retention during summer when a considerable proportion of the wetlands were leaking phosphorus. A possible reason for summer leakages of phosphorus is probably the combined effect of low oxygen concentrations and high temperatures resulting in the release of phosphorus from sediments ('internal loading'; Boström, Jansson & Forsberg, 1982; Craft, 1997). As a major part of the phosphorus is particle bound, the higher phosphorus retention during winter in some of the wetlands is most probably because of higher water levels and sedimentation of particles in the wetlands (Cooper & Gilliam, 1987; Craft, 1997). This conjecture is supported by the positive relation between maximum depth and phosphorus retention, as well as by the tendency towards a negative relation between phosphorus retention and wetland area, as the effect of wind-induced resuspension of sediment particles increases with surface area in these shallow systems (Table 3). Hence, to maximise phosphorus retention, the wetland should be small and deep to increase particle sedimentation, whereas, conversely, to maximise nitrogen retention the wetland should have a large surface area. Possibly, these conflicting requirements can be overcome by constructing large wetlands with deep parts where phosphorus rich particles can accumulate. Moreover, the wind exposure and thereby wave energy can be dampened, for example, by constructing islands in the wetland or allowing emergent and riparian vegetation to grow (Knutsson, 1988). It should be noted that the outcome of a multiple regression is affected by the variables included in the model; that is, variables interact with each other, which is, however, also the case in natural wetland ecosystems. Hence, the results presented here should not be viewed as guidelines, but should form the basis for further discussions and experimentation.

Our approach to apply a 'helicopter perspective' by including many variables and wetlands certainly has shortcomings, but has the strength of revealing that some of the desired features of wetlands in agricultural areas are indeed conflicting, whereas others may well be embraced in the same wetland design. Of the features that are possible to manipulate when creating new wetlands, surface area, depth and shoreline complexity were shown to affect both nutrient retention and biodiversity. Hence, shallow and large wetlands with high shoreline complexity are likely to have high bird and macrophyte species richness and high nitrogen retention, whereas small, deep wetlands are likely to be more efficient in phosphorus retention, but less valuable if high biodiversity is desired. Thus, our study shows that wetland ecosystem functioning to some extent is possible to govern; a possibility that should be considered in ongoing and planned projects creating new wetland ecosystems.

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