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CONTENT

CHAPTER 1

GENERAL INTRODUCTION

1.1. Macrophyte assemblages in artificial fish-rearing ponds

1.2. Francová, K., Šumberová, K., Janauer, G.A., Adámek, Z., 2019. Effects of fish farming on macrophytes in temperate carp ponds. Aquaculture International 27, 413–416.

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1.1. Macrophyte assemblages in artificial fish-rearing ponds

Natural wetlands are declining worldwide due to alterations in hydrodynamics, eutrophication, pollution, unsustainable use, climate change, and spread of invasive species. In contrast, the extent of artificial wetlands has been increasing, sometimes through conversion of natural wetlands. However, their combined area is still small in comparison to that of natural wetlands (Ramsar Convention on Wetlands, 2018). Artificial wetlands have been receiving increased attention recently as, along with economic benefits, they provide multiple ecosystem services and alternative habitats for wetland biota, including macrophytes (Sayer et al., 2008; Wezel et al., 2014).

Wetlands can have different vegetation zones and contain various functional groups of macrophytes, such as emergent, floating leaved, free-floating, and submerged species (Sculthorpe, 1967), depending on the complex of abiotic (e.g. light availability, water level fluctuation) and biotic interactions (e.g. competition, grazing, shading by phytoplankton). The importance of factors relies on their temporal and spatial effects (Lacoul and Freedman, 2006). Macrophytes themselves also exert considerable impact on wetland ecosystem character and function. They impact the physical environment by furnishing shade that affects light and water temperature, modifying water flow, and contributing to stabilisation of sediment and control of erosion and turbidity (Carpenter and Lodge, 1986; Madsen et al., 2001). Macrophytes may influence biogeochemical processes in water and sediment and improve water quality (Dhote and Dixit, 2009; Rejmánková, 2011). They are at the base of the food chain for some herbivores, omnivores and detritivores (Lauridsen et al., 1993; Rejmánková, 2011; Bakker et al., 2016). In addition, macrophytes provide complex habitat structure (e.g. shelter, spawning and nesting material and area) for various organisms such as periphyton, invertebrates, amhibians, fish, and birds (Carpenter and Lodge, 1986; Landi et al., 2014).

Fishponds are among the most important types of artificial water bodies in many parts of Europe. Fish-rearing ponds, the construction of which began in the 11th century, occupy an important position in the national heritage and traditions of many European countries, including the Czech Republic (Hoffmann, 1996). The most commonly cultured fish is the common carp *Cyprinus carpio*. Pond culture of fish changed little from the 11th through the end of the 19th century. Extensive farming with regular winter and summer draining was primarily based on the natural resources of the fishponds. At the close of the 19th and beginning of the 20th century, practices such as supplementary feeding, fertilisation, and liming were introduced, providing the basis for fish farming intensification in the second half of the 20th century, particularly after World War II. At the same time, agricultural use of land surrounding fishponds also intensified. High application of inorganic and organic fertilizers and supplemental feeding to support increased fish stocking density led to increased fishpond trophic status (Pechar, 2000). These practices, along with measures such as dredging, large-scale duck farming and decline in winter and summer drainage, govern the fishpond environment and macrophyte communities (Dykyjová and Květ, 1978; Francová et al., 2019). Over time, with culture intensification, the fishpond production cycle has been reduced from six years to three to four years. Fish are commonly reared in nursery ponds from fry to one- to two-year-old fish and subsequently transferred to usually larger and deeper main ponds for ongrowing to three- to four-years. Currently, the intensity of fish farming is lower than at the end of the 20th century, but production is similar or higher, 500–1000 kg.ha^{-1} annually (Pechar, 2000; Pokorný and Hauser, 2002). Most Czech fishponds represent eutrophic to hypertrophic systems (Pechar, 2000). The high nutrient availability supports development of phytoplankton, increased turbidity, and decrease the occurrence of submerged macrophytes (Sheffer et al., 1993). Additionally, the higher fish stock pressure suppresses zooplankton, which could partially limit phytoplakton, and increases turbidity via bioturbations and nutrient resuspension. These factors, apart from submerged macrophytes, limit also emergent plants (Vilizzi et al., 2015). Thus, the macrophyte assemblages in fishponds under high fish stock pressure exhibit much lower structural and species diversity compared to those in fishponds with medium disturbance level, e.g. nursery ponds (Falkowski and Nowicka-Falkowska, 2004; Francová et al., 2019; Francová et al., in preparation). On the other hand, the temperate eutrophic fishponds, in which the management has been entirely excluded, usually have a very low species and community diversity across the species groups and vegetation types, with the predominance of highly competitive species and their communities (particularly some common types of reed beds). This fact well complies with the intermediate disturbance hypothesis (Bornette and Amoros, 1996). Therefore, the management providing disturbance at medium level should be considered as a suitable tool for long-term maintenance of biota in temperate eutrophic fishponds.

Fishpond habitats may comprise an open water zone that can be colonized with free-floating and submerged plant species including *Lemna gibba, Potamogeton crispus, Myriophyllum spicatum,* and *Stuckenia pectinata;* an exposed bottom zone with annual wetland plants such as *Bidens radiatus, Carex bohemica,* and *Persicaria lapathifolia;* and a reed bed zone that usually contains emergent plants such as *Glyceria maxima, Phragmites australis* and *Typha* spp.

Information about macrophytes in fishponds prior to the 20th century is scarce. Ambrož (1939) and Jílek (1956) reported the occurrence of species that are now rare or threatened in South Bohemia (Czech Republic), among them *Illecebrum verticillatum, Tillaea aquatica,* and *Litorella uniflora* (Šumberová, 2003; Šumberová et al., 2012). Macrophytes and their ecological requirements and limitations in fishponds, including effects of disturbances, have been studied, usually with a focus on selected fishpond habitat zones, including reed beds (Hroudová et al., 1988; Hroudová and Zákravský, 1999) and exposed bottoms (Šumberová et al., 2005, 2006). Hejný studied all types of fishpond vegetation (Hejný and Husák, 1978; Hejný et al., 1981; Hejný, 1990), but conclusions were based chiefly on field observations and were not supported by a consistent data sampling and analyses. The research reported in this thesis extends the results of previous studies and fills the knowledge gap about relationships of macrophyte communities to fish farming practices, fishpond environment, and characteristics of the surrounding landscape.

Fishpond aquaculture in the Czech Republic faces challenges related to deterioration of the pond environment and should be directed to more sustainable use and adaptation to current conditions, particularly climate change. This cannot be accomplished without a thorough knowledge of interactions among biota, fish farming practices, and environmental factors. The research summarized herein contributes to awareness and knowledge of macrophyte diversity patterns within fishpond ecosystems.

Objectives of the thesis

The study was devoted to the comprehensive survey of macrophyte assemblages in artificial fish-rearing ponds and pursuing the following objectives:

1. To review available knowledge of interactions between macrophytes and farming practices in fishponds throughout their mutual development, including associations with socio-economic aspects and climate change.
2. To define fishpond habitat zones and compare diversity of macrophytes in fishponds with that of wetlands having similar characteristics.

3. To study effect of fish farming practices, environmental quality, and adjoining land use on macrophyte assemblages in fishpond open water zones.
4. To focus on the vegetation of reed bed and exposed bottom zones in fishponds and how it is affected by management type, zone width, shore slope, and adjoining land use.

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1.2. Effects of fish farming on macrophytes in temperate carp ponds

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Effects of fish farming on macrophytes in temperate carp ponds

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Abstract
Anthropogenic impacts on carp pond environments have increased over the last 100–150 years in Central Europe. Present semi-intensive carp pond management combines natural food resources, supplementary feeding and additional intensification measures such as manuring, liming, and winter and summer drainage. Despite increased eutrophication and fish stock pressure, many carp ponds still serve as habitats for threatened biota, including macrophytes. Both the ecologically essential role of aquatic macrophytes and the impacts that reared fish may have on them have been repeatedly reported in the literature; however, information is scattered and there exists no multidisciplinary synthesis of knowledge of fish farming and plant interactions for European carp ponds. In this review, we show that macrophytes from different ecological groups have specific demands regarding optimal ecological conditions (e.g. pH and trophy level); hence, they can act as indicators of a water body's ecological status. Nevertheless, the overall ecological ranges of many species (i.e. the limits enabling their survival) remain rather broad. Moreover, interactions between the different elements within carp pond ecosystems are complex and change rapidly, facilitating the co-existence of macrophytes with contradictory ecological demands. As the literature suggests, carp ponds may play a role in biodiversity protection that is just as important (or even more so) than that of natural wetlands. Sustainable, environmentally friendly carp pond management is undoubtedly the best means of preserving the unique natural and cultural value of these aquatic ecosystems for the future.

Keywords Aquatic plants · Biodiversity · Fishponds · Central Europe · Pond management

Introduction

Carp ponds are shallow, man-made freshwater bodies varying widely in size from hundreds of square metres to hundreds of hectares. They are designed specifically for

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Extended author information available on the last page of the article the rearing of fish (mainly common carp *Cyprinus carpio*) that serve as a food source for humans (Pechar et al. 2002). A system of channels feeds the ponds with river water, and dams with a drainage outlet allow the pond to be drained completely. Many of these carp ponds were built on the former sites of marshes, swamps or floodplains (Pokorný and Hauser 2002). To a certain extent, this predetermines their plant assemblage structure. Over the years, both the carp pond environment and fish farming management practices have developed in close relationship with human society. Even so, natural colonisation of newly constructed ponds by macrophytes originating from the preceding habitat and those dispersed from more remote wetlands, along with their subsequent vegetational succession (i.e. development and stabilisation of different plant communities), has been one of the most important driving forces shaping their overall biodiversity, functioning and appearance (particularly vegetation zonation; Fig. 1).

The term 'macrophyte', 'aquatic macrophyte' or simply 'aquatic plant' is rather ambiguous, as some authors refer to true aquatic plants only (i.e. hydrophytes; Landucci et al. 2015), while others include amphibious plants ('amphiphytes', i.e. species tolerating total immersion of their vegetative parts while sustaining a terrestrial phase; Den Hartog and Segal 1964). A broader definition of the term macrophyte also includes marshland and annual wetland plants (i.e. 'helophytes', 'emergent plants' or 'emergent macrophytes'; Lacoul and Freedman 2006), and sometimes even selected wet meadow species (particularly those growing in floodplains or fen meadows) that tolerate flooding (Hejný 1960). Moreover, some authors avoid the terms listed above, using the term 'wetland plant' in its broadest sense instead (Cronk and Fennessy 2016). For the purposes of this review, we follow the delimitation of the term 'macrophytes' by Lacoul and Freedman (2006).

Not only are macrophytes valuable as natural habitats providing refuge and food for other wetland organisms, including fish, they have also been highly valued by humans for a range of purposes, including roofing, medicine and food. Nevertheless, elimination of excessive plant cover and prevention of natural succession has always been an important

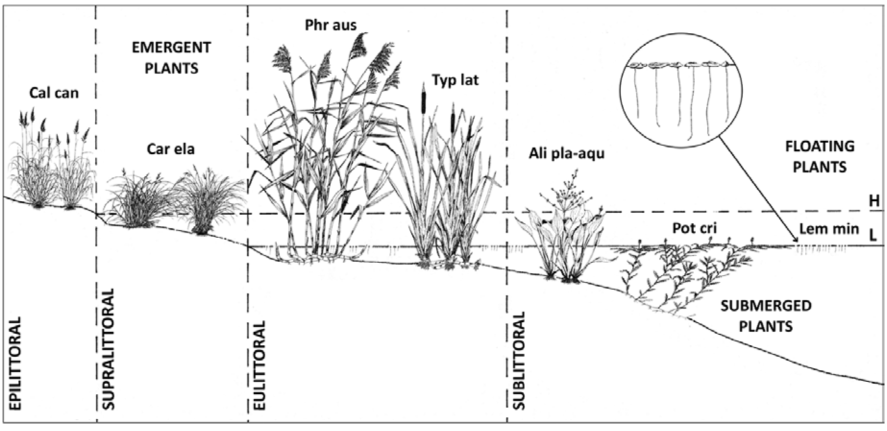

Fig. 1 Littoral zonation, indicating the different macrophyte forms in carp ponds. *H* high water level, *L* low water level. Macrophyte species abbreviations: Cal can *Calamagrostis canescens*, Car ela *Carex elata*, Phr aus *Phragmites australis*, Typ lat *Typha latifolia*, Ali pla-aqu *Alisma plantago-aquatica*, Pot cri *Potamogeton crispus*, Lem min *Lemna minor*

task in carp pond aquaculture (Dubravius 1953; Šusta 1898), without which it would have been impossible to maintain such shallow carp ponds (unlike the majority of natural lakes, the average depth of a carp pond rarely exceeds 1.5 m; Dykyjová and Květ 1978) in the landscape for centuries.

Nowadays, the importance of carp ponds is increasing as, in addition to traditional fish farming, they are now also recognised for providing a broad range of other ecosystem services, including water and nutrient retention, flood protection, nature conservation, biodiversity maintenance and recreation, as well as having a positive influence on local climate. Surprisingly, despite their many positive effects on biodiversity and human society, the relationships between pond biota, the environment and pond management methods are still poorly understood. On the one hand, this may lead to over- or underutilisation of pond resources by fish farmers, while on the other, it may lead to unrealistic expectations as regards carp pond habitat quality by nature conservation authorities.

In this review, we aim to step beyond the usual, narrow understanding of carp pond ecosystems and move toward a more holistic approach. Firstly, we summarise and evaluate available knowledge on interactions between carp pond management and macrophytes, including the direct and indirect impacts of fish. Secondly, we reconsider the role of important factors that have often been neglected, such as climate change, invasive species, pathogen spread, and political and economic impacts.

Historical development of carp ponds and their biota

Historical development has been an important factor influencing recent biodiversity in forest and grassland habitats (Rackham 1980; Hájková et al. 2011). This is almost certainly true for pond habitats (Kořínek et al. 1987); hence, the historical development of ponds should not be omitted in any study of pond habitats. Carp ponds have been constructed in Central Europe since the eleventh century, with the most intense period of establishment taking place between the fourteenth and the beginning of the sixteenth century (Hoffmann 1996). The methods employed in carp aquaculture greatly improved during this period, including a more systematic approach to carp rearing, based on categorisation and separation of individual age groups of carp within specific types of ponds (Hartman et al. 2015). During this period, biota probably varied between pond types, with any differences increasing in relation to increasing management intensity. Information on macrophytes remained scarce, however, until the beginning of the twentieth century. Šusta (1898) stressed the importance of both emergent and submergent macrophytes along the littoral zone, and annual plants growing on carp pond bottoms certainly occurred during the summer drainage period (for more information, see the section 'Summer and/or winter drainage' below). Nevertheless, annual plants were usually omitted from fish farming literature due to their low biomass and negligible economic importance. Macrophyte development at this time was thought to be limited only by nutrients, mechanical disturbance by wave action and water level fluctuation.

The level of nutrient loading at this time resulted in carp ponds of oligotrophic or mesotrophic status, which was reflected in a rather high macrophyte diversity but low overall biomass (Pokorný et al. 1990). A substantial part of the species spectrum in most ponds is likely to have shown a broad range in relation to nutrients, allowing growth in oligo-mesotrophic to hypertrophic waters (e.g. *Typha latifolia*, *Potamogeton crispus*), or was represented by species specifically related to nutrient poor habitats (e.g. *Littorella uniflora*, *Carex rostrata*). Owing to the low trophic status of such ponds, species with high nutrient demands and high biomass (e.g. *Glyceria maxima*) were most likely rare (Fig. 2).

From the seventeenth to the middle of the nineteenth century, progress in European fish farming was interrupted by wars and subsequent economic crises. While recovery took place across Central Europe between the end of the nineteenth and the beginning of the twentieth century, the total area of ponds has never reached the same extent as in the fourteenth–sixteenth century (Pavelková et al. 2016). Since the nineteenth century, carp pond management practices aimed at increasing productivity have either been rediscovered, e.g. summer drainage, or newly introduced, e.g. supplementary feeding, fertilisation and liming (Šusta 1898). Knowledge gained during this period served as a baseline for the next significant period of intensification and diversification in pond management over the second half of the twentieth century. At the beginning of this process, management included high levels of supplementary feeding (mainly cereals, as used to this day), addition of solid and liquid manure and inorganic fertilisers, liming and use of heavy machinery for carp pond amelioration. In the 1960s, herbivorous (Chinese) carp were introduced from South-East Asia, and duck farms were established at many Central European ponds to diversify production. All such management measures led to large-scale changes in carp pond biota during the second half of the twentieth century (Hejný 1990), diminishing the former extent of a number of vegetation types and leading to the retreat of sensitive plants, particularly those dependent on oligotrophic or mesotrophic habitats (for examples see Fig. 2).

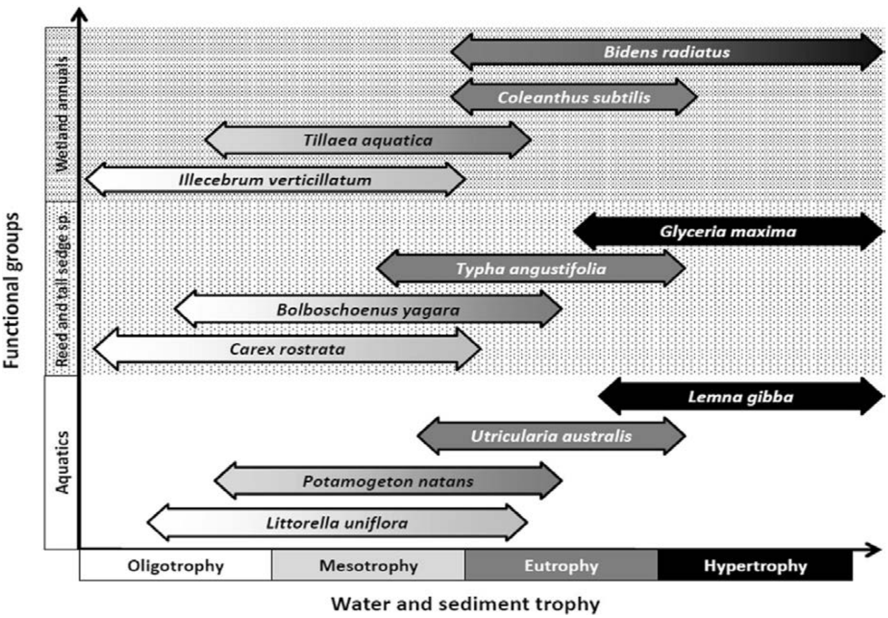

Fig. 2 Relationship between macrophyte species and water and/or sediment trophic level in carp ponds. The length and position of each arrow indicate the width of a species' range in relation to trophy (i.e. the conditions where the species is still able to grow). The shaded area represents the species' trophic optimum. Only those species with a specific relationship to trophy were selected, species with broad trophic ranges being omitted. All examples are based on our own field experience supplemented by published information (Hejný 1960; Hejný et al. 1982; Chytrý 2011; Kaplan et al. 2016; Kaplan et al. 2017)

Today, as in the past, fish farming management is subject to outside forces, including political impacts and global market fluctuations. While these are indirect forces, they can still have a strong impact on overall fish farming success. For example, state fishery organisations managing carp ponds in former socialist European countries were transformed into numerous private companies after 1990, all managing different numbers and total areas of carp ponds. Carp pond management today tends to be less intensive than at the end of the twentieth century, and large-scale 'carp-cum-duck' farming and application of inorganic fertilisers have effectively ceased in most parts of Central Europe. New ventures, such as organic carp farming, have been launched in Germany, Austria and Hungary, though its contribution to total European carp production remains low. Nevertheless, such changes are indicative of a move to a more environmentally friendly approach to carp pond aquaculture (Adámek et al. 2015). Many of the changes inherent in this new approach, e.g. limiting stocking density, reduced feed and fertiliser usage, a ban on chemical treatment, have undoubtedly had positive impacts on pond macrophyte communities.

Despite the overall modernisation of pond management, individual countries still display differences in pond management practice related to local fish farming traditions, policies and other factors. Further, while management in some fish farming companies may be adjusted to reflect such traditions and to suit local environmental conditions, the personal views of company managers can also play an important role. As such, similar pond habitats may still display differences in habitat quality and biodiversity, both regionally and nationally.

Fish stock composition as a driving factor in the development of macrophyte communities

Temperate European carp ponds are usually stocked with common carp (~ 90%), often reared in polyculture with Chinese carp (i.e. grass carp *Ctenopharyngodon idella*, bighead carp *Aristichthys nobilis* and silver carp *Hypophthalmichthys molitrix*), traditional supplemental fish such as tench *Tinca tinca*, and predatory species such as pike *Esox lucius*, zander *Stizostedion lucioperca* and European catfish *Silurus glanis*. While whitefish (*Coregonus lavaretus* and *C. peled*) and rainbow trout *Oncorhynchus mykiss* are cultured in specialised highland carp ponds, their contribution to overall production is negligible (Adámek et al. 2012). Overall, fish production in ponds has doubled in some Central and Eastern European countries over the last 50 years, despite turning to more semi-intensive management. On the other hand, polyculture stock composition has remained more-or-less stable since the widespread introduction of Chinese carp 50 years ago. At the same time, production of tench has dropped due to its inability to compete with increased carp stocking densities (Adámek et al. 2003) and whitefish production has dropped due to deterioration of environmental conditions and increased cormorant predation. In the case of predatory fish, production has increased somewhat since the early 1990s due to increasing demand from local and foreign markets (Adámek et al. 2012). Most of these species are highly sensitive to unfavourable environmental conditions, with the youngest stages particularly sensitive to changes in temperature and pH. Hence, while natural reproduction is often possible in carp ponds, most is artificially controlled in fish hatcheries to reduce losses as much as possible. Other fish, not intentionally stocked but naturally reproducing in carp ponds (so called coarse fish), may also play an important role in the functioning of carp pond ecosystems, with species such as roach *Rutilus rutilus* and rudd *Scardinius erythrophthalmus* serving as prey fish for high value predatory species. On the other hand, expanding populations of native species, such as bream *Abramis brama*, or invasive non-native species, such as topmouth gudgeon *Pseudorasbora parva* and gibel carp *Carassius gibelio*, sometimes occur at high enough densities to impair the ecosystem through overexploitation of zooplankton and/or zoobenthos, thereby competing with commercial fish for natural food resources (Musil et al. 2014). Where fish grazing pressure has been reduced (e.g. in nature reserves), the influence of non-commercial coarse fish usually increases (Pechar et al. 2017). Some of these species (topmouth gudgeon and gibel carp in particular) are very difficult to control as they can survive short-term pond drainage in refuge pools in bottom depressions. As both qualitative and quantitative fish stock composition has an impact on the pond macrophyte community, it is essential that fish stock is addressed when considering such issues.

Macrophyte habitats within carp ponds and a comparison with similar types of wetlands

Broadly speaking, carp pond habitats comprise open water occasionally colonised with aquatic plants (e.g. *Potamogeton crispus*, *Myriophyllum spicatum* and *Lemna minor*), exposed bottoms with annual wetland plants (e.g. *Carex bohemica*, *Bidens radiatus* and *Cyperus fuscus*), and littoral zones with reeds and tall sedge beds (e.g. *Typha* spp., *Phragmites australis* or *Carex acuta*; Fig. 1). In addition, there may be wet sites along the banks that are under the direct influence of pond water levels and/or established during succession in shallow littoral zones and pond inundation areas. Finally, the pond dam itself offers habitat for a range of plant species, including wetland species growing along the lower, partly flooded part of the dam (e.g. *Lycopus europaeus*, *Rorippa palustris*; Hejný et al. 2002).

Over the centuries, a range of different fish farming pond types have been developed and, as each requires a different form of management, there will be differences in the structure and species composition of the associated vegetation (for details, see the section ‘Farming technologies and their links with macrophytes development’ below). Furthermore, while many thousands of carp ponds and other waterbodies (e.g. natural lakes or farmland ponds) are to be found throughout Europe, species lists are only available for a limited number and, as such, the overall biodiversity of these habitats remains largely unknown, or at best poorly known. As an example, a study of 51 ponds (mainly marl pits) in north-west England by Hassall et al. (2012) documented the occurrence of 167 plant species (including charophytes and bryophytes). While aquatic macrophytes dominated in the species list, there were also several species with optimum habitats outside wetlands, such as *Poa annua*, *Lychnis flos-cuculi* and *Carex hirta*. In a second English study, also based on 51 ponds, 94 vascular plant and macroalgae taxa were recorded, including hydrophytes, helophytes and a few species typical of exposed pond bottoms (Jeffries 2012). These figures appear extremely low when compared to data available for Czech carp ponds, with Juříček (2012), for example, reporting 254 vascular plant species from 46 ponds in the Bohemian-Moravian Highlands, a number that included typical wetland taxa along with a high number of terrestrial species, mainly ruderal weeds and wet meadow species. Our own data from a single large (> 200 ha) South-Bohemian carp pond revealed 278 vascular plant species, including wetland trees and shrubs (Šumberová et al., unpublished data). Such high species numbers were due, in part, to the common occurrence of accidental terrestrial species (e.g. *Calamagrostis epigejos* and *Poa annua*) and, especially, species typical of exposed pond bottoms (e.g. *Elatine hydropiper*, *Coleanthus subtilis* or *Eleocharis ovata*). Just a few species in this group were also recorded in the English papers cited above. A similarly high species richness was recorded in small, mainly natural (glacial) ponds (≤ 1 ha) in north-western Poland, where a total of 576 vascular plant taxa were reported from 450 ponds (Waldon 2012). As in the case of Czech carp ponds, however, a large part of the species spectrum was represented by terrestrial species from surrounding habitats. Despite this, these ponds have been designated as important for the protection of wetland plant species and communities. Although actual data on total species richness was not provided, ponds in the Franche-Comté region of France have also been highlighted as having a high plant diversity supporting numerous rare vascular plant and charophyte communities (Schäfer-Guignier 1994). These ponds, which harbour numerous species sensitive to intensive management, now represent one of the best-preserved pond complexes in Europe. Wezel et al. (2014) reported 63 aquatic plants for a set of 59 ponds in the Dombes Region of France; however, the authors did not provide a species list, nor did they specify whether charophytes and bryophytes were included.

From this short summary, it is clear that carp ponds represent high value wetland and aquatic habitats as regards plant biodiversity protection, in most cases comparable with natural water bodies.

Plant–fish interactions

Macrophytes create complex structures that provide spawning areas for adult fish, refuges for small fish hiding from predators and sources of fish food, either in the form of periphyton and phytophilous invertebrates or as food sources in themselves (Petr 2000; Thomaz and Cunha 2010). On the other hand, dense macrophyte stands can negatively affect fish survival by causing strong diurnal shifts in oxygen and pH concentration (Pedersen et al. 2013). This has been observed both in dense stands of submerged plants and under free floating species of *Lemnaceae* or floating-leaved species such as *Nymphaea* (Bican et al. 1986; Sayer et al. 2012). Critically low oxygen concentrations may also occur at the end of the growing season as the macrophyte biomass decays (Ficke et al. 2007). Some macrophytes can also negatively affect fish by acting as mechanical barriers, with fish fry quickly dying if caught in the fine nets formed by the interconnected cells of the green alga *Hydrodictyon reticulosum* (Podubský 1948) or when trapped in dense beds of submerged plants (e.g. *Elodea* spp., *Ceratophyllum* spp.) following the rapid drop in water levels before pond harvesting. Finally, some littoral plants, such as *Cicuta virosa*, can even be toxic to fish (Hejný 2000).

Different macrophyte groups exhibit varying sensitivity to stocking pressure and fish production management measures (Broyer and Curtet 2012). In general, carp ponds suit species that tolerate regular mechanical, fish-mediated disturbances contributing to plant damaging and/or uprooting, and increased water turbidity (Sidorkewicj et al. 1998). The pressures acting on plants differ markedly between the different types of carp ponds, and even sensitive species may occur in some pond types (e.g. fry and nursery ponds; see next section). Species with submerged and floating leaves (e.g. some *Batrachium* spp. such as *Batrachium peltatum*) or those tolerant to turbid conditions (e.g. *Myriophyllum spicatum*, *Potamogeton crispus*) have an advantage over species that only have submerged leaves and demand clear water (e.g. *Potamogeton lucens*, *P. acutifolius*). A specific vegetation type commonly found in fish-farming ponds is that associated with summer drainage (Šumberová et al. 2006), i.e. short-lived plant species that are able to survive for a long time in the soil seed bank (Thompson et al. 1997; Bernhardt et al. 2008), though these depend on regular water level fluctuations. As these plants do not germinate until the bottom has been exposed to air, they do not suffer directly from fish stock pressure. A second vegetation type typically associated with carp ponds is reed beds, which tend to form species-poor stands that spread out from the shore. The area colonised by reeds tends to trap organic sediment, thereby contributing to terrestrialisation of the pond. As such, reed bed succession is either intentionally eliminated as part of the pond's normal management regime or (especially in main ponds) is restricted by the fish stock, though part of the stand may be protected against fish mediated disturbance by shallow water (Zákravský and Hroudová 2007).

Both common carp and grass carp are known to disturb macrophytes in carp ponds and other water bodies, though both act on them in different ways. The benthivorous common carp, for example, uproots submerged vegetation during spawning and while searching for benthic invertebrates as food (Zambrano and Hinojosa 1999; Badiou and Goldsborough 2015). Such activities, particularly under high stocking densities, also increase turbidity through sediment resuspension (Breukelaar et al. 1994; Kloskowski 2011). These impacts are particularly strong in the presence of larger carp, which are capable of penetrating deeper into the substrate (Panek 1987). Both sediment resuspension and excretion increase nutrient concentration in the water column, thereby supporting phytoplankton blooms that can shade macrophytes and further suppress growth, creating an ecological feedback mechanism that perpetuates a persistent turbid state (Adámek and Maršálek 2013). Numerous studies have documented large-scale habitat deterioration in aquatic ecosystems with common carp (Hejný 1990; Scheffer et al. 1993; Matsuzaki et al. 2007). On the positive side, common carp may also consume macrophyte seeds (Anton-Pardo et al. 2014) and disperse them over large distances, possibly even improving the germination rate of some species (Pollux 2011). Seed's survival success, and subsequent storage in the sediment seed bank, will depend on the seed's size, shape and surface structure, all of which determine whether the seed is destroyed, damaged but still able to germinate or remains more-or-less untouched during gut passage (Pollux 2011). It remains unclear whether carp consume seeds accidentally alongside vegetation and zoobenthos collected from the pond bottom, or whether they are ingested intentionally. Should carp select seeds of specific plant species only, this may have important implications for the species' population dynamics (Pollux 2011). While common carp can feed on aquatic plants directly, the proportion of plant matter in the diet tends to be relatively low (Adámek et al. 2003; Rahman et al. 2008; Anton-Pardo et al. 2014).

In comparison, grass carp are typical phytophagous fish, feeding almost exclusively on macrophytes after reaching a length of 5 cm (Adámek and Sanh 1981; Watkins et al. 1981). In polyculture ponds where supplementary feeding is provided for common carp, grass carp usually prefer the supplementary feed to macrophytes (Adámek 2014). In waterbodies without supplementary feeding, however, grass carp represent an important biomeliorative agent. The optimal stocking density will depend on a range of factors, including climatic conditions, fish size, extent of macrophytes beds, required level of control and biotic and abiotic environmental conditions. This makes any assessment of appropriate stock biomass difficult; however, Van Zon (1977) has stated that good results can be achieved by stocking 150–250 kg of 1 to 2-year-old fish per hectare. Grass carp are non-specialist feeders, and over 170 different macrophyte species have been recorded in their diet (Redding and Midlen 1991). In general, they tend to avoid plants with rough and/or sharp leaves (like *Stratiotes aloides*), large floating leaves (e.g. *Nymphaea* and *Nuphar* spp.) and plants with a strong taste (as *Persicaria hydropiper* and *Batrachium* spp.), particularly if other, preferred macrophyte species are available (Van Zon 1977). Food preferences will also differ depending on age cohort and ambient temperature. Softer tissues of submerged vegetation (e.g. *Elodea* spp. and

Potamogeton spp.) tend to be preferred by younger grass carp and by all age groups when water temperatures drop below 12–15 °C (Redding and Midlen 1991). Depending on the specific conditions prevalent at each pond (e.g. temperature regime, macrophyte species composition and fish stock age structure), grass carp feeding may cause selective pressures encouraging some macrophyte species and restricting others, resulting in significant changes to the pond's vegetation cover over just a few growing seasons.

Other cyprinid species are also known to ingest plant matter, with roach and rudd, for example, tending to take a higher percentage than bream or tench (Niederholzer and Hofer 1979; Adámek et al. 2003). As with grass carp, roach and rudd, the main plant consumers native to Central Europe consume the majority of submerged macrophytes but avoid plants that are difficult to utilise as food (Prejs 1984). Even predatory species, such as perch *Perca fluviatilis*, may take plant matter sporadically, though this usually occurs while taking other (animal) food items (Zapletal et al. 2016).

Farming technologies and their links with macrophyte development

Carp pond farming in Central Europe is presently undertaken at two levels, i.e. low-intensity and semi-intensive. Both the intensity and type of pond management employed have important consequences impacting qualitative and quantitative features of aquatic macrophyte communities. In general, any management measure will usually lead to an enhancement or restriction of some macrophyte species. Interactions within the carp pond ecosystem are complex, and the response of macrophytes may vary depending on a wide range of influences, including management-related factors, period of the year, weather or pond location.

Low-intensity (extensive) management is characterised by low stocking densities and no supplementary feeding or fertilisation, the food base relying on the natural productivity of the pond. Fish production tends to be low, ranging usually from 150 to 300 kg ha^{-1} (Kestemont 1995). Ponds in France, for example, have natural fish production < 200 kg ha^{-1} (Lazartigues et al. 2013).

In comparison, semi-intensive management is characterised by relatively high stocking densities and application of supplementary feed, manure and liming. Fish yields generally range between several hundreds and 1000 kg ha^{-1} (Kestemont 1995). In Germany, for example, yields average 855–1140 kg ha^{-1}, while 600–1000 kg ha^{-1} is more typical for Austria (Adámek et al., unpublished data). In comparison, average yields in the Czech Republic are 800–1000 kg ha^{-1} (Adámek et al. 2012).

Fish are usually harvested as 3 to 4 years old, utilising two to four main pond types: (i) pre-nursery ponds (optional) for production of advanced fry, (ii) nursery ponds for production of 1-year-old fish, (iii) on-growing ponds for production of 2-year-old fish, and (iv) main ponds for production of 3- to 4-year-old marketable fish (Horváth et al. 1992). The majority of marketable fish are not sold during or directly after the pond harvest (Appendix Fig. 4) but are usually kept in storage ponds (Appendix Fig. 5) until transported or sold (Šumberová et al. 2006). In recent years, fish farmers have tended to simplify this system by using pond types i, ii and/or iii as nursery ponds.

Pre-nursery ponds (fry ponds) are filled and stocked with sack fry for approximately 4 to 6 weeks during May and June (nursing period). Successive flooding of the bottom littoral vegetation is considered important for supporting the development of phytophilous invertebrates, which serve as an important, highly nutritious (Sychra et al. 2010) food item for the fry. Some marshland grasses, such as *Poa palustris*, *Alopecurus pratensis*, *Glyceria fluitans* and *G. maxima*, withstand medium- to long-term flooding and are considered suitable for this type of pond (Hejný et al. 2002). Nowadays, fish farmers often stock fry into nursery ponds straight from the hatchery, omitting the pre-nursery phase, though successive flooding is usually still applied during the first 2 to 3 months.

Nursery ponds (Appendix Fig. 6), used to grow fish from fry (~ 3 cm) to fingerling size (10–15 cm), are usually completely flooded between May and July (Šumberová et al. 2006). Most aquatic plants and helophytes thrive in nursery ponds, especially those with a life cycle extending over the whole growing season, e.g. *Potamogeton natans*, *Alisma plantago-aquatica*, *Sparganium emersum* and, occasionally, rare species such as *Potamogeton lucens* and *P. acutifolius* (Hejný et al. 2002). Annual wetland plant species are also typical for nursery ponds, as the ponds are usually left dry for several weeks (or months) after harvesting before being slowly flooded, i.e. after the seeds of these species ripen (e.g. *Coleanthus subtilis*) or plants develop enough to survive flooding (e.g. *Elatine triandra* and *Limosella aquatica*).

Submerged and floating-leaved macrophytes in main and on-growing ponds tend to suffer due to management practices aimed at increasing fish production (Hejný et al. 2002). While they are only in use for a relatively short period (a few weeks to a few months) each year, extensive stands of submerged or floating-leaved macrophytes also tend to be absent in fish storage ponds. While the fish have ceased feeding at this time, plant damage, or even eradication, occurs due to high fish stocking densities. Consequently, storage ponds tend to be dominated by either short-lived or perennial wetland herbs, grasses and *Cyperaceae* (Hejný 1978b). These macrophytes only occur during the summer drainage period, however, and species composition will largely depend on any additional management measures undertaken (Šumberová et al. 2006). Some storage ponds may also be in use during the growing season, e.g. for early fry culture, for spawning of zander or catfish, and/or storage of marketable fish from the summer fish harvest. Vegetation cover in such cases will depend on direct pressure by fish stock, which will vary in age, species, density and length of storage. Frequent water level fluctuations, occurring over days, will be repeated several times during the storage period in order to remove fish for marketing. This may have important implications for some annual wetland plant populations, resulting in selection of genotypes for short life cycles and/or resistance to short-term flooding (Böckelmann et al. 2017).

Management measures

Summer and/or winter drainage

The summer and/or winter drainage was introduced as a pond management technique in the sixteenth century, when carp ponds were regularly drained over a 3- to 4-year rotation. Following drainage, grain, clover and grass would be cultivated on the bottom sediment over the summer season (Pokorný and Pechar 2000), after which it was either mown or grazed by livestock (Šusta 1898). Nowadays, cultivated crops are no longer planted; rather, natural development of plant species is encouraged as a ‘green fertiliser’, which acts as direct source of nutrients and as an important substrate for phytophilous aquatic organisms. Drainage also reduces fish diseases and parasites, prevents sediment build up and supports the decomposition (mineralisation) of organic matter in bottom sediments.

Drainage may be partial (i.e. exposing the pond littoral zone) or complete (i.e. the pond is left empty). Partial drainage is the more frequently applied approach in carp ponds, and especially main ponds. In this case, the water level is kept low during the first year of the 2-

year management cycle (i.e. the period between stocking and fish stock harvesting). On occasions, partial drainage may also occur naturally due to high evaporation rates in extremely dry springs or summers (Appendix Fig. 7). Drainage can last over the whole season (i.e. full summer or winter drainage) or may only take place over a short period (i.e. short summer or winter drainage; Hejný 1978b). Nowadays, the short summer drainage is mainly applied to nursery ponds and lasts from the spring (March–April) fish harvest to the end of May–June (sometimes July), depending on the local climate (Richert et al. 2016). In case that nursery ponds are harvested in autumn, the drainage may continue to winter (full winter drainage) and to spring or early summer of the subsequent year (short summer drainage). While the full winter drainage (lasting from the autumn fish harvest to early spring) is also frequently applied today, the full summer drainage is only used during repair work or in special pond types (e.g. storage ponds). The economic costs entailed during full summer drainage (1-year potential production lost) make it undesirable, especially in large main ponds for marketable fish. Consequently, the full summer drainage has been replaced in larger production ponds by other techniques aimed at increasing productivity (see below), though these do not provide many of the beneficial effects of summer drainage, such as sediment mineralisation. The full summer drainage favours plant species with a relatively long life cycle, i.e. plants with life cycle continuing throughout the single growing season (annual species) or partially also to the second growing season (biennial species), with their seeds being subsequently stored in the soil seed bank, e.g. *Tillaea aquatica* and *Pseudognaphalium luteo-album* (Šumberová et al. 2012). Today, these species have been replaced by fast growing perennial littoral species (especially *Typha* spp.) or wetland trees and shrubs, such as willows *Salix* spp. (Hejný 1978b). The seeds of these taxa usually originate from the surrounding landscape, having been dispersed by wind or water. The seedlings can then rapidly colonise the entire pond bottom due to the absence of competition from other species. This situation frequently occurs in ponds drained after 20+ years, during which time the seeds of many annual wetland plants will have become deeply buried in sediment and/or lost viability.

Drainage that continues for more than one growing season can represent a serious threat to carp pond habitats (especially in warm regions) due to the rapid succession of perennial species that form large quantities of biomass. Such conditions are particularly unsuitable for hydrophytes and annual wetland herbs, along with their soil seed bank. Interestingly, reduction of submerged and floating-leaved macrophytes at high stock densities can facilitate germination of species growing on the pond bottom during the summer drainage (Hejný 1960), as seedling recruitment from the seed bank is not prevented by dense stands of aquatic plants. When such dense stands do occur, they usually die back and decay over a period of several weeks after bottom exposure. At the same time, the sediment will begin to desiccate and, by the time the plants have decomposed completely, it is usually too dry for a broad range of wetland species to germinate. Consequently, high aquatic macrophyte species richness during the flooding phase is often negatively correlated with annual wetland plant species richness during the summer drainage.

Fertilisation

Aquatic macrophyte growth is directly linked to the trophic status of a water body (Barko and Smart 1981, 1983), which in turn is affected by climatic, geographic and hydrological conditions and by human intervention (Přikryl 1996). Carp pond manuring was first practised around the end of the nineteenth century; however, systematic application of organic manure and mineral fertilisers (particularly superphosphate) as part of carp pond management started in earnest from the 1930s (Pokorný and Hauser 2002). The gradual intensification of fish production (e.g. through carp pond fertilisation) and changes in agricultural land use since the second half of the twentieth century have dramatically increased pond nutrient loading, leading to highly eutrophic or even hypertrophic conditions in many carp ponds (Pechar 2000). This, in turn, has had a highly detrimental impact on pond macrophyte communities. Though macrophytes can thrive under high nutrient loading, growth usually collapses as turbidity increases due to excessive phytoplankton development and/or fish activity. While many macrophytes are able to produce allelopatic compounds that inhibit phytoplankton, these only become effective later in the growing season when macrophytes form large stands (Gross 2003). Once the ecosystem switches to a turbid state, nutrients need to be drastically reduced before macrophytes, and especially submerged macrophytes, are able to recover (Scheffer et al. 1993).

Mineral fertilisation has not been used in the majority of carp-producing countries since the 1970s, as present nutrient levels in carp ponds greatly exceed the requirements for semi-intensive carp farming, due, in part, to the excessive levels of phosphorus remaining in the sediment (Potužák et al. 2016). Animal manure is occasionally applied at low levels in spring or early summer; however, most manuring is now considered excessive as it tends not to be reflected by any increase in fish production (Potužák et al. 2007).

Manuring favours macrophytes with a high nutrient demand and tolerance to low water transparency, e.g. hydrophytes such as *Lemna gibba* and *Spirodela polyrhiza* or semi-aquatic plants such as *Bidens radiatus*, *Ranunculus sceleratus* and *Rumex maritimus* (Fig. 2). These species produce high biomass and are all strong competitors, preventing development of relatively slow growing and sensitive macrophytes such as *Potamogeton natans* or *Nymphaea candida* in the water or *Tillea aquatica* and *Pseudognaphalium luteo-album* along the exposed margins (Šumberová et al. 2006, 2012). Similarly, *Glyceria maxima* is able to spread rapidly and outcompete *Phragmites australis* in manured carp ponds, as it is better able to cope with the increased levels of organic matter (Pokorný et al. 2002).

Supplemental feed components

The benefits of supplemental feeding were first recognised in the nineteenth century. At that time, lupin was the predominant supplement used; however, since the 1930s, supplemental feeding has been applied systematically and in higher amounts, mainly using cereals. It has been noted, however, that components of such supplemental feeds could represent possible sources of alien plants (Chytrý et al. 2005), including species such as *Echinochloa crus-galli*, *Chenopodium album* agg. or *Tripleurospermum inodorum* (Pyšek et al. 2012). Such species are not only spread directly in fish and duck food but also in solid organic manure, on equipment (e.g. fishing nets) and on vehicles used for fish or material transport (Šumberová and Ducháček 2017). Vehicle transportation, for example, was directly implicated in the spread of *Bidens frondosa*, a North-American alien species currently invading wetland habitats throughout Europe, including carp ponds in the Czech Republic (Kaplan et al. 2016). Seeds of many alien species can easily be spread from one carp pond to another in the same pond system or to watercourses situated downstream of the affected pond. Colonisation of ponds by alien species can vary greatly, with some species becoming established in other habitats first (e.g. arable fields or waste land) and later invading the pond, while others may be introduced directly from distant regions, e.g. *Lythrum hyssopifolia* (Kaplan et al. 2017). Whatever their origin, alien species can either show a marked impact on native flora, e.g. *Epilobium ciliatum*, or become established as part of the native vegetation without additional changes (Hejný et al. 2002).

Carp pond liming

Liming was also first applied in a systematic manner in the 1930s (Pokorný and Hauser 2002). Since then, liming has remained an important management practice for adjusting pond water alkalinity. Liming provides calcium (Ca^{2+}) for the bony structures of many aquatic organisms, including fish, participates in the bicarbonate buffer system, and acts as a strong disinfectant (Hartman et al. 2016). In carp ponds with high assimilatory pH, liming supports macrophyte 'bicarbonate users', such as *Myriophyllum spicatum* or narrow leaved species of the *Potamogeton* genus, mainly *P. crispus* (Kirk 2011). At the same time, liming inhibits the growth of plants that use free carbon dioxide, e.g. soft-water vascular plants such as *Aldrovanda vesiculosa* or *Utricularia* spp., as photosynthesis in such species stops at pH 8–9 (Adamec 1997). As such species can only occur in waters with low calcium content, their occurrence has decreased in carp ponds subject to liming (Hejný 1978a). The relationship between selected plant species and water and sediment pH is displayed in Fig. 3.

Duck farming

The historical combination of 'carp-cum-duck' farming has probably had the most destructive impact on carp pond macrophytes. Grazing ducks affect all macrophytes, from open water species to those along the littoral zone, as both are used as foraging areas and the banks serve as resting sites. Other carp pond biotopes are also affected as duck faeces alter the trophic status of the carp pond (Hejný et al. 2002). Long-term duck farming results in significant changes to the sediment chemistry of carp ponds, particularly those occurring in areas with acidic, calcium-poor bedrock. Such ponds show an increase in pH, excessive levels of nitrogen

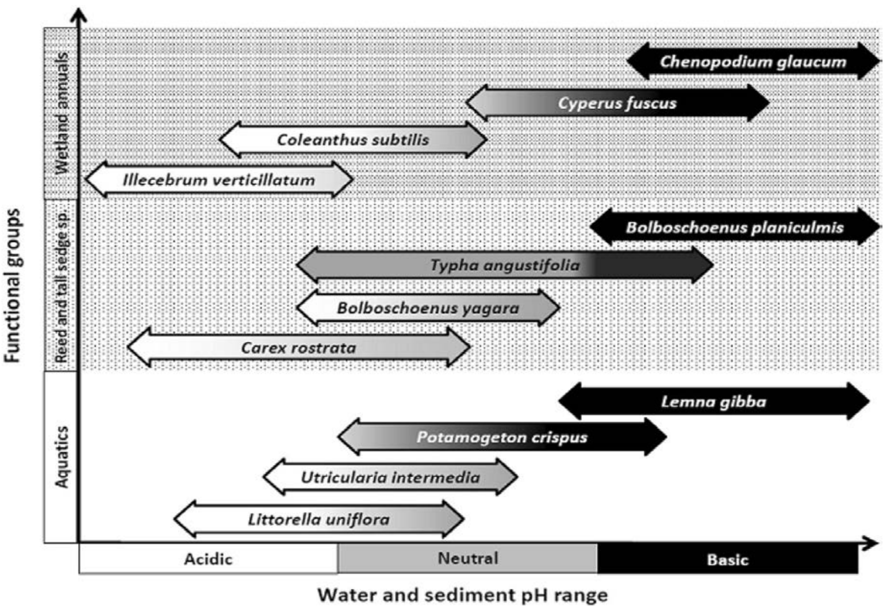

Fig. 3 Relationship between macrophyte species and water and/or sediment pH in carp ponds. For further explanations, see caption in Fig. 2

and phosphorus and elevated levels of calcium (Hejný et al. 1982). These effects are even more pronounced than those induced by liming and/or fertilisation. Alongside these changes, the annual wetland vegetation assemblage (mainly acidophytes), including species growing on muddy substrates such as *Coleanthus subtilis* or *Elatine hydropiper*, is transformed into one dominated by calcitolerant or calciphilous species, such as *Cyperus fuscus*, *Plantago uliginosa*, *Chenopodium glaucum* or *Ch. rubrum* (Hejný et al. 2002; Šumberová et al. 2006; Fig. 3). To this day, some of these species can still be used to indicate the sites of duck farms decades after their abandonment. Recently, 'ranching' of mallards (*Anas platyrhynchos*) has been put into practice at some carp ponds. In such cases, the impact is not as dramatic as with large-scale domestic duck farming as the numbers kept are not so high.

Vegetation control

Approaches used to control macrophytes in carp ponds depend on many factors, including the options available (e.g. mechanical, biological and/or chemical), the species present, site characteristics, management objectives and legal restrictions (Hofstra and Clayto 2012). Currently, mechanical harvesting is the most commonly used method for controlling unwanted or invasive macrophyte species, though the method is labour intensive and relatively low in effectiveness (Appendix Fig. 8). Mechanical harvesting usually results in short-term benefits or, as in the case of *Elodea* spp., can even cause unintentional spread of sprouting plant fragments (Hoffmann et al. 2013). Amelioration of the pond bottom and littoral zone using heavy machinery can also result in large-scale, and often permanent, changes to the macrophyte assemblage (Hejný et al. 2002), affecting not only the above-ground parts but the sediment seed bank also (Hilt et al. 2006). Bottom material deposited on the pond banks creates new habitat for a range of plant species, including ruderal plants in the early stages of succession or reed bed species and annual wetland species under conditions of high moisture (Hejný 1960; Hejný et al. 2002). Slow-growing species typically found on the exposed pond bottom, along with macrophytes with low nutrient demands, may be found on newly cleared pond bottoms. One relatively new approach that has been little used to date is that of the 'benthic barrier', which utilises shading of the bottom of a water body to prevent macrophyte growth. A range of different materials has been used to provide shading, including everything from plastic sheeting to biodegradable materials. Biodegradable materials, however, do not have such a long lifespan, though they are easier to manipulate and are less harmful to other organisms (Peterson et al. 1974; Mayer 1978; Caffrey et al. 2010).

Methods used to control vegetation in fish storage ponds vary greatly between individual fish farms. While some still prefer traditional mowing to eliminate excessive stands of aquatic and wetland plants (Appendix Fig. 5), others use chemical treatment, usually based on glyphosate herbicides. In many areas, it is still common to use animal grazing (e.g. by sheep) to control vegetation on the exposed bottoms of storage ponds (Richert et al. 2016). Both use of herbicides and grazing can have strong selective effects on macrophytes, mainly related to interactions between herbicide compounds or the nutritional preferences of the animal on the one side and the morphology and physiology of specific plant species on the other side (Šumberová et al. 2012). As an alternative, flooding for a substantial part of the growing season is now more frequently used to restrict vigorous vegetation growth in summer drained fish storage ponds. In such cases, grass carp may also be stocked to control macrophyte growth. In some cases, the different vegetation control approaches may be combined (Richert et al. 2016).

Indirect interactions between macrophytes and fish

Pond macrophytes serve not only as food sources for herbivorous fish and water birds, but they also provide environments for the developmental stages of fish parasites, their intermediate- and final hosts and/or dispersal organisms, e.g. water birds. On the other hand, a lack of macrophytes is likely to result in poor herbivore vitality, increased sensitivity to parasites and subsequent mortality (Morley 2007). Interactions between aquatic macrophytes, their consumers and parasites can be highly complex. Brönmark and Vermaat (1998), for example, recorded tench in a small reservoir as significantly reducing the biomass of both submerged vegetation (*Elodea* spp.) and an associated snail (*Lymnaea* spp.), and this also led to a reduction in fish parasite numbers (e.g. eye fluke *Diplostomum spathaceum*).

Macrophytes may benefit from factors leading to the reduction of fish stock density and biomass, such as excessive predation by the Eurasian otter *Lutra lutra* or great cormorant *Phalacrocorax carbo*. Where aquatic birds occur in large numbers, they can have direct effects on organisms used as food (whether fish, macrophytes or aquatic invertebrates) as well as important indirect effects, e.g. by increasing interspecific competition for food or by causing changes in the pond's chemical balance (Hejný et al 1982; Klimaszyk and Rzymski 2016).

Surprisingly, the creation of bottom depressions by carp searching for food or during overwintering aggregations, or zander during the reproduction period can also have a positive impact on plant assemblages. For example, such depressions can increase habitat diversity, especially in hard substrates such as clay or sand where newly formed depressions may remain wet far longer than the surrounding bottom after drainage (Appendix Fig. 9). Such sites are particularly important for annual wetland plant reproduction (Šumberová et al. 2005). Furthermore, this type of disturbance can release deeply buried seeds from the sediment seed bank and enable their germination.

Climate change and carp pond ecosystem instability

The last two decades have been characterised by the increasing frequency of extreme climate events, such as flooding, summer droughts and exceptionally high summer and winter temperatures. Such climatic extremes have had important consequences as regards abiotic and biotic conditions in wetland habitats, including carp ponds.

As water level in carp pond vegetation zones can drop more frequently, phytophilous fish recruitment could suffer due to a decline in plant availability (Ficke et al. 2007). On the other hand, species tolerant to disturbance, and particularly those tolerant to frequent and severe fluctuations in water level, could be favoured and spread. The rapid desiccation of exposed pond substrates may also restrict species preferring high substrate moisture, e.g. *Coleanthus subtilis*, *Spergularia echinosperma* or *Elatine* spp. (Šumberová et al. 2006; Kaplan et al. 2016; Richert et al. 2016). Moreover, water level drawdown and subsequent re-flooding increases the pond's trophic level by enhancing phosphorus release from the sediment (Klotz and Linn 2001; Lu et al. 2018), resulting in more frequent algal blooms that go on to compete with submerged aquatic macrophytes. This effect may be even more profound under continuing pond fertilisation.

Some highly thermophilous macrophytes, such as *Najas minor* (native to warmer parts of Europe, though recently appearing in colder regions) or *Lindernia dubia* (introduced to Europe from North America), have already become established in carp ponds and/or fish storage ponds in some regions of the Czech Republic, and further spread is expected in the future

(Kaplan et al. 2016, 2018). Other aquatic neophytes, such as *Vallisneria spiralis*, have occasionally been found in Czech and German water bodies, though not yet in carp ponds, though this situation could soon change. Many wetland species, until now only known from garden ponds or aquaria, also have the potential to become established in carp ponds (Husák et al. 2010). At the same time, the probability of new diseases and parasites being introduced and spreading is also increasing (Spikmans et al. 2013), with subsequent impacts on the functioning of the carp pond ecosystem, including relationships between fish and macrophytes.

Currently, carp ponds can be considered highly unstable ecosystems in terms of hydrology, water level and sediment physico-chemical parameters (Potužák et al. 2007), and this is reflected in associated changes in biodiversity (Miklín and Macháček 2016). The instability inherent in these systems could even increase under continuing climate and environmental change (e.g. eutrophication and aquatic pollution), resulting in multiple pressures and threats to the whole Central European carp pond farming system. The challenge for the future, therefore, is to predict such changes and to come up with methods for mitigating their negative impacts. One possibility may be what has been termed ‘automated high frequency monitoring’ (AHFM) of environmental and biotic parameters (Marcé et al. 2016). This method, based on a network of sensors permanently installed in water bodies, enables identification of relationships between different elements within complex ecosystems, such as carp ponds. In fish farming practice, AHFM would facilitate the planning of fish feeding, particularly during periods of oxygen depletion or low temperature when feed consumption by fish is reduced. Oxygen concentrations in eutrophic carp ponds fluctuate to such an extent that measurement on a daily basis is insufficient using standard devices. In such cases, AHFM could prove a useful tool for exploring the role of specific macrophyte species as regards changes in oxygen and nutrient concentration in carp ponds (Jawecki et al. 2013; Lu et al. 2018). In extensive macrophyte stands, diurnal and seasonal oxygen concentrations and water chemistry can change rapidly (Pedersen et al. 2013); however, the extent and speed of these changes under different conditions, including temperature, hydrodynamics, water depth, type of bottom substrate and dominance of macrophytes, are still poorly understood, both in carp ponds and other types of water bodies. While present management tends toward eliminating large macrophyte stands to prevent fish kills, the knowledge offered by AHFM would provide guidelines as to which plants should be supported and which eliminated under specific conditions, thereby improving fish farming practice and biodiversity protection. Permanent monitoring using AHFM will be even more necessary under continuing global climate change, which is predicted to alter oxygen and nutrient cycling (Rahel and Olden 2008; Jeppesen et al. 2009) and contribute to the spread of non-native and invasive species (Rahel and Olden 2008; Duarte 2017) and loss of sensitive species (Markovic et al. 2014). While this could lead to significant changes in both abiotic and biotic pond conditions, carp ponds, unlike natural aquatic habitats, have yet to be considered in models predicting future development and possibilities in fish farming.

Socio-economic factors influencing pond ecosystems and their macrophytes

Throughout its historical development, Central European carp farming has shown itself sensitive to a range of socio-economic changes (Cooke et al. 2016). Intensification in carp farming following World War II, for example, proceeded hand-in-hand with changes in other areas of agriculture (Stoate et al. 2009). Today, free market trading poses serious threats to fish farms (e.g. through competition with seafood products and veterinary issues), with serious implications for the maintenance and sustainability of carp ponds and their associated macrophyte communities (Cooke et al. 2016). One potential way forward is enhancement of the supplementary roles carp ponds can play, though this cannot be performed without changes in the public's perception of the values provided by carp ponds (Lamine and Bellon 2009; Bacon et al. 2012). Increasing the awareness of local communities and fish farmers as regards the environmental and biodiversity protection roles of ponds is crucial and should be widely supported by local nature conservation authorities and policy makers (Siebert et al. 2006; Sterling et al. 2017). One of the most important issues is the need for improved communication between nature conservationists and scientists on the one side and fish farmers on the other. At present, there is a clear gap between these professional groups, with negative implications for carp pond habitat protection (Kloskowski 2011). Placing strict restrictions on how fish farmers can influence carp pond ecosystems is inadvisable, as they can provide unique knowledge on the features and dynamics of each pond and are best able to perform management measures supporting target plant species or communities (e.g. manipulating water levels during summer drainage). Close cooperation between all professional groups involved is essential for the successful maintenance and improved status of carp pond ecosystems.

Conclusions

Macrophytes are an integral part of carp pond ecosystems, and yet their natural development often suffers from measures associated with pond management, particularly as regards application of organic fertilisers and high carp stocking densities. Any reduction in the macrophyte community inevitably leads to a decline in the pond's natural production; hence, macrophytes must be considered within fish farming management practice if pond production is to be sustainable and biodiversity protected. What does this mean? In short, management measures would need to be tailored to each carp pond based on its nutrient status, proposed use and the biota present. Modifications to present fish farming practice should proceed gradually as profound shifts usually result in problems related to increases in trophic level. Even gradual change could prove difficult, however, considering the high levels of nutrient supplied to carp ponds from arable fields and sewage treatment plants. At this time, there is probably no one example of 'best carp pond practice', where the results of management changes would meet with the expectations of nature conservation authorities. Even in nature reserves where carp stocks have been deliberately reduced to improve the pond's ecological status, the ponds usually suffer from heavy algal blooms or growth of excessive species-poor macrophyte stands due to high nutrient inputs (Pechar et al. 2017). As such, lowering nutrient input into carp ponds should be a first step when low-intensity management is planned. This intervention would, at least in highly eutrophic ponds, favour both the fish stock (e.g. by eliminating the risk of oxygen depletion) and the macrophyte community (e.g. by restricting highly competitive nutrient-demanding species). Macrophytes preferring low nutrient conditions and a low level of mechanical disturbance, e.g. *Littorella uniflora*, *Potamogeton gramineus*, *Tillaea aquatica* and *Utricularia intermedia*, are particularly endangered under present carp farming practice. Shifting ponds to a purely recreational or other non-productive use could even increase the threat to pond biota. Many macrophytes require regular water level fluctuations, particularly those that spend all or part of their life cycle on exposed pond bottoms, e.g. annual wetland species such as *Coleanthus subtilis*, *Carex bohemica* and *Spergularia echinosperma* show a clear preference for the carp pond environment (Kaplan et al. 2016; Richert et al. 2016). These species are still frequent in Central European carp ponds but could be threatened by any dramatic management change or through interactions with other factors such as climate change.

We conclude that carp pond farming needs to be protected, both as a highly valued source of food fish and as an important part of European cultural heritage. Protecting carp ponds also protects European biodiversity, ensuring the survival of a wide range of macrophytes that are presently facing negative pressures. Greater cooperation and communication between fish-farming professionals, nature conservation authorities, scientists and local communities in relation to carp pond issues are essential, as many of the problems arising cannot be solved through the work of a narrow group of specialists.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement This article does not contain any studies with animals performed by any of the authors.

Appendix 1 Examples of fish farming practice in carp ponds

Fig. 4 Harvesting of a main carp pond in Bohemia (photo K. Šumberová)

Fig. 5 Fish storage pond in early summer. Note the freshly mowed perennial vegetation on the dry bottom (photo K. Šumberová)

Fig. 6 Nursery carp pond with rich floating-leaved, submerged and helophytic vegetation (photo K. Šumberová)

Fig. 7 Partial summer drainage (during an extreme summer drought) of a main carp pond with a 2-year management cycle (photo K. Šumberová)

Fig. 8 Mechanical elimination of submerged aquatic vegetation (photo K. Šumberová)

Fig. 9 Bottom depressions (nests) left by spawning zander (photo K. Šumberová)

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CHAPTER 2

MACROPHYTE ASSEMBLAGES IN FISHPONDS UNDER DIFFERENT FISH FARMING MANAGEMENT

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Macrophyte assemblages in fishponds under different fish farming management

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ABSTRACT

Seasonal and inter-annual macrophyte assemblage dynamics were surveyed in ten nursery and ten main fishponds stocked primarily with common carp *Cyprinus carpio* fry and with common carp being reared to market size, respectively. The results indicate a significant difference in macrophyte species number and abundance between the nursery and main fishponds, with up to 24.5% of the variation in macrophyte species distribution patterns explained by fishpond management type (nursery or main) and up to 6.7% by water transparency. Fish biomass used as a fish stock proxy explained up to 13.9% of variability. Although not significant, differences in species number and abundance were found (i) between spring and summer survey periods during the growing season with both species number and abundance usually decreasing in summer, and (ii) between years of the farming production cycle with a higher species number and abundance typically found in the first year of the farming cycle in the nursery fishponds. The results increase knowledge of fishpond macrophyte assemblages and may be of interest for conservation of aquatic habitats.

1. Introduction

Worldwide, wetlands, including shallow lakes and ponds, are under severe threat related to management, land use, and climate change (Klotz and Linn, 2001; Houlahan et al., 2006; Ramsar Convention on Wetlands, 2018). Profound changes have been documented in shallow lakes, among them eutrophication, high turbidity, and reduced diversity of aquatic biota, including macrophyte species (Kosten et al., 2009; Phillips et al., 2016). In recent years, macrophytes have been attracting attention and are listed as biological quality elements in the Water Framework Directive 2000/60/EC (WFD, 2000). Macrophyte species have considerable impact on ecosystem functioning, influencing light, temperature, and water flow; stabilizing sediments; and reducing erosion and turbidity (Carpenter and Lodge, 1986; Madsen et al., 2001). They affect biogeochemical processes in water and/or sediment and can improve water quality (Dhote and Dixit, 2009; Rejmánková, 2011). Macrophytes provide structure and, as primary producers, are a base of the food chain for heterotrophic organisms, including fish (Carpenter and Lodge, 1986; Bakker et al., 2016). This is of particular importance in fishponds (Francová et al., 2019).

Shallow man-made fishponds have been an integral part of the European agricultural landscape for centuries. Although originally designed specifically for fish rearing, fishponds represent important biotopes, harbouring a substantial fraction of the local and regional wetland biodiversity along with their primary fish production function (Wezel et al., 2014).

Macrophyte assemblages differ widely among fishponds, however, environmental factors driving their composition and abundance *in situ*

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are poorly understood. Fish farm management may interfere with rearing of various age- and weight-classes of fish, use of supplementary feeding, liming, manuring, and winter and/or summer drainage (Francová et al., 2019). Fish stock, for example, may suppress macrophyte growth by increasing turbidity, uprooting while foraging, or by feeding on them directly (Ten Winkel and Meulemans, 1984; Bakker et al., 2016). Water physico-chemical parameters may be affected by the fishpond management, but also by the run-off from the surrounding landscape (Wezel et al., 2013). Nowadays, many fishponds in Central Europe are eutrophic to hypertrophic with low transparency which can negatively influence the occurrence of macrophyte species (Hejný et al., 2002; Pechar et al., 2002). Comparable to shallow lakes, macrophytes in fishponds may also be altered by seasonal and annual weather-related water level fluctuations (Blindow, 1992).

To increase our understanding of interactions between planned fish farm management and seasonal and inter-annual macrophyte dynamics, we surveyed macrophyte assemblages in the two most common fishpond management types: 'nursery' fishponds, used for the rearing of fish from sac-fry to two years, and 'main' fishponds, for production of three- to four-year-old marketable fish. We attempted to determine (1) how fishpond management type and environmental and/or land-use factors contribute to variation in macrophyte assemblages; (2) whether nursery and main fishponds differ in macrophyte species number, composition, and abundance; and (3) how these parameters differ relative to season and year of the farming production cycle.

2. Material and methods

2.1. Site description

The study area was located in the Vltava river catchment in South Bohemia (Fig. 1). The region has altitude ranging from 370 to 440 m asl, a temperate climate with a long-term mean annual air temperature of 8.9 °C, and mean annual precipitation of 634 mm (České Budějovice station 1981–2010; Czech Hydrometeorological Institute). Geologically, non-calcareous sediments prevail in the area (Czech Geological Survey, 2019).

Following a preliminary study of four fishponds in 2016, ten nursery fishponds of 4–13 ha and ten main fishponds of 9–30 ha with similar farm management within each category (nursery and main fishponds), were selected and surveyed in 2017. Fishpond mean depth ranged from 0.6 to 1.6 m (see Table 1 for fishpond characteristics and codes used throughout text). The fishponds are fed and inter-connected by small streams and/or man-made channels and can be drained and refilled. Many selected fishponds had shallow littoral zones supporting reeds and/or tall sedge beds. In most cases, the fishponds were surrounded by a mosaic of arable fields, woodlands, and/or grasslands, with a few contained within a single land-use type.

2.2. Macrophyte assessment

Macrophyte species occurring in permanent belt transects were surveyed during the growing season, once in spring (May–June) and once in summer (July–August). Belt transects running from shore-to-shore, perpendicular to the line of central flow, were spaced at regular intervals from the inlet to the dam in order to cover all areas of the fishpond (Fig. 2) with each divided into survey units of 2 × 5 m. In each case, the number of transects was adjusted to fishpond size: three transects for fishponds < 10 ha, four for 10–20 ha, and five for 20–30 ha (Table 1). Each transect was numbered in ascending order from inlet to outlet, and survey units were oriented from the right to left shore when facing the direction of flow (Fig. 2). The position of each was ascertained with a Garmin 64 st GPS unit using the WGS84 coordinate system and marked with sticks.

Presence of macrophytes along the near-shore zone was recorded by eye while wading and by eye and/or with a Humminbird 570 sonar

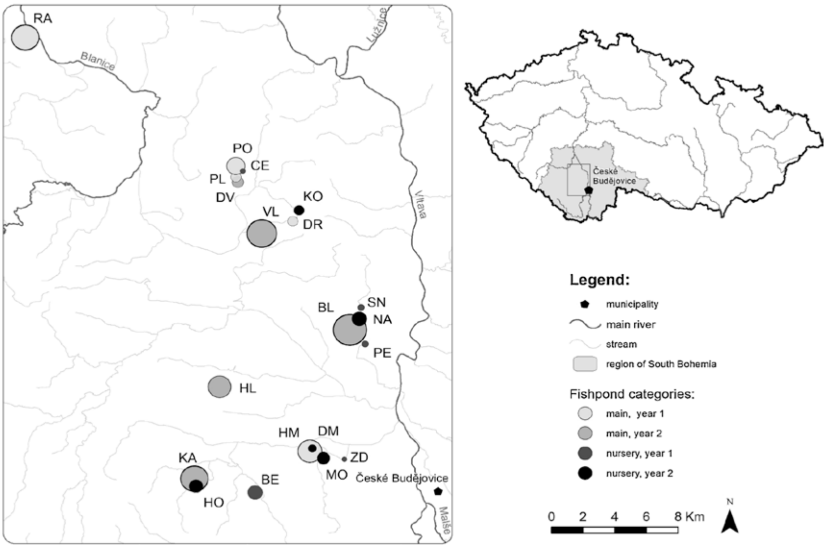

Fig. 1. Location of the fishponds under study (see Table 1 for identification codes and size, fishpond categories apply to 2017). Circle size corresponds to relative fishpond area.

Table 1
Characteristics of surveyed fishponds. Code: N = nursery, M = main fishpond, and the first two letters of the fishpond name; YPC = year 1 and/or 2 of production cycle (N-MO, N-NA, N-BL = year 1 in 2016 and year 2 in 2017, RA exception = year 1 in both years); * = fishponds with nature reserve status; Transects = number of transects surveyed; Sediment thickness categories: 1 = 0–30 cm, 2 = 30–50 cm, 3 = >50 cm; Drainage: partial summer drainage = psd, winter drainage = wd; Feed = supplementary feeding with cereals; Lime = application of ground limestone; Manure = use of organic manure; na = none applied.

Fishpond	Code/YPC	Size (ha)	Mean depth (m)	Transects	Sediment	Drainage	Feed	Lime	Manure
Motovidlo*	N-MO-1 and 2	11.6	0.6	4	2	psd-16	+	+	na
Návesný	N-NA-1 and 2	12.7	1.1	4	3	psd-16	+	+	na
Beranov	N-BE-1	13.0	1.4	4	1	wd/psd-17	+	+	na
Čekal	N-CE-1	5.0	0.8	3	2	wd/psd-17	+	+	na
Dolní Machovec	N-DM-2	7.4	0.9	3	2	na	+	+	na
Holašovický	N-HO-2	12.1	1.3	4	3	na	+	+	na
Kočínský	N-KO-2	9.2	1.0	3	3	psd-17	+	+	+
Pěnský	N-PE-1	6.0	0.9	3	2	wd/psd-17	+	+	na
Šnekl	N-SN-1	6.0	1.0	3	2	wd/psd-17	+	+	na
Zdráhanka	N-ZD-1	4.3	1.1	3	2	wd/psd-17	+	na	na
Blanský	M-BL-1 and 2	29.2	1.6	5	2	psd-17	+	+	+
Ražický*	M-RA-1	23.8	1.1	5	3	na	+	na	+
Dříteňský	M-DR-1	9.0	0.9	3	2	na	+	+	na
Dvořák	M-DV-1	10.0	1.1	4	2	psd-17	+	+	+
Hlásný	M-HL-2	20.0	1.1	5	2	na	+	+	+
Horní Machovec	M-HM-1	20.9	1.1	5	2	na	+	+	+
Kamenný	M-KA-2	24.0	1.2	5	2	na	+	+	+
Plaček	M-PL-1	9.0	1.0	3	3	na	+	+	na
Podhorský	M-PO-1	16.0	1.1	4	2	psd-17	+	+	+
Velký Luský	M-VL-2	26.0	1.5	5	2	na	+	+	+

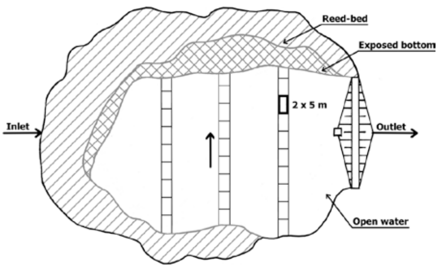

Fig. 2. Typical position of transects and survey units (2 × 5 m) in a fishpond. A reed-bed zone was not included in the survey, and the transects were set inward from the waterline or at the shoreline when a reed-bed zone was not present. In fishponds in which water levels were increased, the previously exposed bottom zone was included in the survey. The arrow indicates the direction of macrophyte assessment for all transects in all fishponds, from the right to the left bank with respect to the direction of flow.

from a boat in areas of deeper water. A rake was used for plant sampling. Abundance of macrophytes was assessed using the five-level Kohler scale (Kohler and Janauer, 1995) (Table 2). The Kohler values were transformed into plant mass estimates (PME): 'plant abundance', for each species per survey unit, using the function $y = x^3$, where y is plant abundance and x is the Kohler value (Janauer and Heindl, 1998) (Table 2). The method applied follows the European Standard (CEN EN 14184, 2014) and is recommended for monitoring performed under the WFD (2000).

Where possible, all macrophytes were determined to species level (Table A.1). Those not determined to species level, usually immature specimens, were assigned to the genus, with one or more probable species provided (Table A.1). Determination to the genus level was only included in species counts and in indicator species analysis (ISA) (Dufrêne and Legendre, 1997) (Section 2.5.) when no precisely determined species of the same genus occurred in the relevant dataset.

Five functional macrophyte groups were defined according to Denny (1987) and accepted with minor modifications by Cook (1990) and Pokorný and Květ (2004): submerged (Sub), free floating (Fre-flo), rooted with floating leaves (Flo-lea), amphiphytes (Amp), and helophytes (Hel). Two additional groups were defined: wetland annuals (Wet-ann), moisture-demanding annual species typically occurring on exposed fishpond bottoms and surviving unsuitable conditions as seeds in the soil seed bank; and terrestrial plants (Ter), all species not complying with the definitions of six previous species groups, typically growing in terrestrial environments and only incidentally occurring in wetlands where they are unable to survive long-term. These functional groups have higher explanatory values than single species when assessing the possible influence of transparency, water level fluctuation, and/or disturbance intensity (Table A.1). The red-listed species of vascular plants were classified according to the most recent national Red List (Grulich, 2012).

2.3. Environmental parameters

Water samples and physico-chemical parameters were obtained from the same point at each fishpond in mid-June and mid-August. Water transparency (Z_{SD}) was estimated with a 30 cm Secchi disk, and

Table 2
Kohler scaling (from Janauer and Heindl, 1998). PME or 'plant abundance' (= 3[rd] power of Kohler value); SU = survey unit (see Fig. 2).

Kohler value	Descriptive scale	PME
1	**very rare** (not more than five individuals of a species per SU)	1
2	**rare** (more than five individuals, but still few; patchy distribution within the SU)	8
3	**frequent** (larger patches and more frequent than 'rare')	27
4	**abundant** (small and large, and often higher, plant stands distributed over most of the SU)	64
5	**very abundant** (plant stands massively distributed over the SU, up to total cover)	125

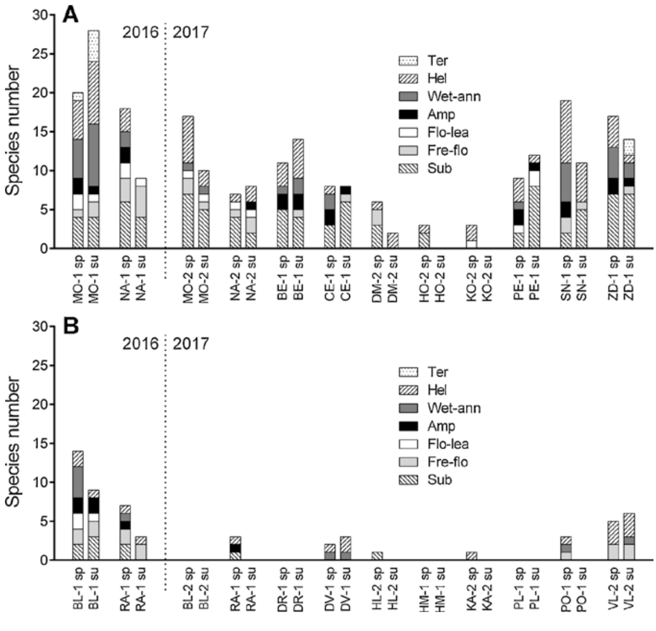

Fig. 3. Macrophyte number of species in (A) nursery and (B) main fishponds (see Table 1 for codes) in spring (sp) and summer (su), divided into functional groups. Sub = submerged, Fre-flo = free floating, Flo-lea = rooted with floating leaves, Amp = amphiphytes, Wet-ann = wetland annuals, Hel = helophytes and Ter = terrestrial. Note that only four fishponds were surveyed in 2016.

water temperature (T), dissolved oxygen concentration (DO), pH, and conductivity (Cond) were measured in the water column with a YSI Professional Plus multi-parameter probe. Samples for analysis of total phosphorus (TP), soluble reactive phosphorus (SRP), N-NO_3, N-NH_4, chlorophyll *a* (Chl-*a*), Ca, and acid neutralisation capacity (ANC 4.5 and 8.3) were transported to the accredited laboratories of the Povodí Vltavy State Enterprise on the day of sampling. Prior to transportation, samples for SRP, NO_3-N, and NH_4-N were filtered *in situ* using 0.45 µm nylon syringe filters. All samples were stored under refrigeration and analysed the following day.

Concentrations of TP, SRP, and Ca were assessed using inductively-coupled plasma spectrometry (Agilent 8800 ICP-QQQ; EN ISO 17294-2, 2004EN ISO 17294-2, 2004). Spectrophotometry and ion liquid chromatography were used for N-NO_3 and N-NH_4 analysis (Shimadzu UV-1650PC; ISO 7150-1, 1994; Dionex ICS-1000; EN ISO 10304-1, 2009). Concentrations of Chl-*a* were determined spectrophotometrically after extraction in hot ethanol (Shimadzu UV-1650PC; ISO 10260, 1992), and alkalinity was determined by titration (ANC 4.5 and 8.3; ISO 9963-1, 1994).

Land-use within a 500 m radius surrounding each fishpond was classified according to the Corine database using the categories artificial surface, water bodies, agriculture, and forest/semi-natural area (CORINE, 2016). The ratio of the two prevailing categories, agriculture and forest/semi-natural, was used in order to minimise the number of explanatory variables. Fishpond borders were determined from the Dibavod database (DIBAVOD, 2017) with water surface area adjusted accordingly. All data were processed in ArcGIS 10.6 (ESRI, 2017).

The thickness of the muddy fine (< 2 mm particles) sediment was measured in each survey unit and grouped into three categories: 1 = 0–30 cm, 2 = 30–50 cm, and 3 = > 50 cm. The category represented in > 50% of survey units was used in the distance-based redundancy analysis (db-RDA) (Legendre and Anderson, 1999) (Section 2.5).

2.4. Fish farm management practices

Standard fish farming practices were applied in the selected fishponds, with management targeted at maximizing production while maintaining fish health (Francová et al., 2019).

Fish stock was 95% common carp *Cyprinus carpio*, with fish grown to 150–300 g in the nursery fishponds and 2–3 kg in the main fishponds. The remaining fish stock consisted of grass carp *Ctenopharyngodon idella*, silver carp *Hypophthalmichthys molitrix*, tench *Tinca tinca*, pike *Esox lucius*, zander *Stizostedion lucioperca* and European catfish *Silurus glanis*. Additionally, coarse fish such as bream *Abramis brama*, gibel carp *Carassius gibelio* and topmouth gudgeon *Pseudorasbora parva*, occurred in the fishponds. The surveyed fishponds were in the first and/or second year of a typical biennial production cycle (year 1 and/or year 2), with the exception of M-RA-1, which was stocked annually with two-year-old fish for production of three-year-old marketable fish. Mean biennial fish production 2016–2018 was 800 kg ha^{-1} in the nursery fishponds and 1300 kg ha^{-1} in the main fishponds. Two fishponds are protected as nature reserves, N-MO-1 and 2 due to the presence of a critically endangered plant species, *Nymphoides peltata*, and M-RA-1, which harbours populations of bird species requiring reed beds. The stocking density in these protected fishponds is kept at approximately the half of the typical fishpond density. In addition to natural zooplankton and zoobenthos, fish received supplemental feed in the form of cereal, pulverised for juvenile fish, at a mean rate of 1200 kg ha^{-1} yr^{-1}. Fish were fed 3–5 times per week, depending on water physico-chemical parameters, from May through September. Supplemental feeding was delayed in year 1 in the nursery fishponds, as the youngest fish fed on natural sources. Ground limestone (mean 400 kg ha^{-1}) was

Table 3
Species number, abundance (sum of abundances of all species in all survey units per fishpond), and transparency values (Secchi depth in cm) in each of the studied fishponds (see Table 1 for codes) during spring (sp) and summer (su) surveys. * = fishponds with nature reserve status.

	Species number				Abundance				Transparency			
	2016		2017		2016		2017		2016		2017	
Fishpond	sp	su	sp	su	sp	su	sp	su	sp	su	sp	su
N-MO-1 and 2*	20	28	17	10	8353	8921	3466	5064	45	60	35	80
N-NA-1 and 2	19	11	7	8	3391	1863	4574	98	35	25	20	11
N-BE-1			11	14			491	33			40	42
N-CE-1			9	8			558	488			22	10
N-DM-2			6	2			1494	2			25	20
N-HO-2			3	0			131	0			23	13
N-KO-2			3	0			10	0			25	12
N-PE-1			11	12			762	717			85	42
N-SN-1			20	11			449	494			25	15
N-ZD-1			17	14			1003	708			45	24
M-BL-1 and 2	14	9	0	0	635	49	0	0	35	30	28	30
M-RA-1*	7	3	3	0	627	205	3	0	25	15	12	12
M-DR-1			0	0			0	0			35	25
M-DV-1			2	3			3	4			30	21
M-HL-2			1	0			4	0			18	11
M-HM-1			0	0			0	0			20	22
M-KA-2			1	0			1	0			25	35
M-PL-1			0	0			0	0			9	10
M-PO-1			3	0			10	0			70	32
M-VL-2			5	6			29	11			40	30

spread on the fishpond bottom immediately after harvest draining or just prior to refilling for the next production cycle. Occasionally, manure was applied at an average rate of 1400 kg ha^{-1}. Some nursery fishponds were winter-drained, and all were partially summer-drained prior to stocking, i.e. in year 1 (Table 1). The N-KO-2 fishpond was unintentionally partially dry due to drought in summer 2017, as were M-BL-2, M-DV-1, and M-PO-1 (Table 1).

Management data were provided by the companies Rybářství Hluboká CZ s.r.o. and Blatenská ryba s.r.o. While detailed numerical data on fish stock, feeding, liming, and manuring were used for analysis, they are not provided in detail here, as they represent internal company data.

2.5. Data analysis

To visualize species richness and the representation of seven defined functional groups of plant species in the fishponds, we displayed each fishpond in each survey period, spring and summer of 2017, and, when applicaple, of 2016 (Fig. 3). For the remaining analyses, only data from 2017 were used. To assess how fishpond management type and environmental and adjoining land-use factors contributed to occurrence and abundance of observed macrophyte species, db-RDA with Bray-–Curtis disimilarity measure was applied. As some functional groups included a low number of species, seven original groups were merged for the purpose of db-RDA into two groups: aquatic and amphiphyte species, comprising the original groups Sub, Fre-flo, Flo-lea, and Amp; and all other species, including the groups Wet-ann, Hel, and Ter. Spearman rank order correlation was applied to assess relationships between pre-selected explanatory variables (Tables A.2 and A.3). The sum of macrophyte species abundances in each fishpond and eight environmental variables including fishpond management type, specifically reflecting age and size of fish stock and partially other factors listed in Table 1, as well as Z_{SD}, T, Cond, SRP, NH_4-N, prevailing sediment thickness category, and ratio of agricultural:forest/semi-natural area, were selected for db-RDA. Environmental variables were log (x +1) transformed, and the forward selection procedure was applied to identify explanatory variables significantly affecting macrophyte abundance. The simple effects of each environmental variable (and their respective levels) were evaluated to give the general overview of the significance and explained variability of all pre-selected variables. A Monte Carlo permutation test with 9999 permutations was run in a split-plot design, with split plots representing each fishpond in spring and summer and a whole plot of each fishpond encompassing both surveys. The statistical package R 3.5.1 (R Core Team, 2018) was used for Spearman rank order correlation, while db-RDA was performed in CANOCO 5.11 (Ter Braak and Šmilauer, 2012).

The multiple response permutation procedure (MRPP) (McCune et al., 2002) based on macrophyte species numbers and abundances in each fishpond was applied to describe differences between (i) nursery and main fishponds, (ii) spring and summer surveys, and (iii) production years 1 and 2. The MRPP used a Bray-Curtis distance measure in a hierarchical (split-plot) design similar to that described in the db-RDA. Results of spring and summer surveys of each fishpond were depicted in split-plots without permutations, while whole plots representing each fishpond were allowed to permute freely. Due to the model design, the number of permutations was restricted to 199. The agreement statistic 'A' indicates whether within-group homogeneity is higher than randomly expected; A = 1 indicates that samples are identical within groups, while A = 0 when within-group heterogeneity equals that expected by chance. The MRPP analysis was conducted using the *vegan* 2.5-2 package of R 3.5.1 (Oksanen et al., 2018; R Core Team, 2018).

Macrophyte species abundances in each fishpond were used in the ISA to assess prevalence of species in nursery and main fishponds. A Monte Carlo permutation test with 999 randomised runs was carried out using the hierarchical (split-plot) design described above to determine the significance of the indicator value (IndVal) ($P \leq 0.05$), with IndVal ranging from zero (no indication) to 100 (total indication). The ISA was performed using the labdsv 1.8-0 package of R 3.5.1 (Roberts, 2016; R Core Team, 2018).

3. Results

3.1. Macrophyte assessment

Sixty-five species, including 14 red-listed, were observed in the fishponds in 2016 and 2017. Sixty-three species including 13 red-listed, among them *Bolboschoenus yagara*, *Elatine hydropiper*, *Limosella aquatica*, *Nymphoides peltata*, and *Potamogeton trichoides*, were recorded in the nursery fishponds, while 27 species, including red-listed *Elatine hexandra* and *E. triandra*, were recorded in the main fishponds (Table A.1). Higher species and functional diversity, expressed as number of species and functional groups, respectively, was detected in all survey periods in the majority of the nursery fishponds compared to the main fishponds (Fig. 3). Comparisons of macrophyte species and functional diversity and abundance between spring and summer surveys, and between production years 1 and 2, showed high inter-pond variation (Table 3, Fig. 3), with both species number and abundance usually decreasing in summer. Species and functional diversity and abundance in the fishponds surveyed in both years 2016 and 2017 (N-MO-1 and 2, N-NA-1 and 2, M-BL-1 and 2, M-RA-1) decreased dramatically in 2017. The two main fishponds surveyed in 2016 exhibited species and functional diversity and abundance comparable to the diversity and abundance of many of the nursery fishponds in 2017 (Table 3; Fig. 3). Similar patterns were not detected in 2017 for any main fishpond in production year 1 compared to nursery fishponds.

Although our survey units were placed in the flooded sections of the fishponds, a substantial proportion of the overall species pool comprised non-aquatic species, primarily wetland annuals, helophytes, and terrestrial species (Table A.1, Fig. 3). Nevertheless, their abundances were low to negligible compared to that of aquatic and amphibious plants (Table A.4).

Fishpond management type was the key factor influencing macrophyte species number and abundance, explaining up to 24.5% of the variation, while transparency explained up to 6.7%, when using the model with the aquatic + amphiphyte functional group (db-RDA; Fig. 4; Table 4). When fish biomass was used as a proxy for fish stock, it explained up to 13.9% of variation (Table 4). Other selected variables (T, Cond, SRP, NH_4-N, prevailing sediment thickness category, agricultural:forest/semi-natural) had no significant association with macrophyte occurrence in the fishponds (Table A.5).

The number of macrophyte species differed significantly in nursery and main fishponds (MRPP: A = 0.1129, P = 0.005) but not between spring and summer surveys (A = 0.0216, P = 1) or production years 1 and 2 (A = 0.1129, P = 0.4; only data from 2017 were considered). Similarly, macrophyte abundance differed significantly between nursery and main fishponds (MRPP: A = 0.0995, P = 0.01), but no significant difference was detected between spring and summer surveys (A = 0.0177, P = 1) or between years 1 and 2 (A = 0.0010, P = 0.565). The highest abundance had *Nymphoides peltata* (abundance score: 6190), which was found at N-MO-1 and 2 and N-PE-1, then *Stuckenia pectinata* (5310), and *Potamogeton crispus* (2109), both regularly occurring in the nursery fishponds. *Typha latifolia* (8) and *Glyceria maxima* (6) had the highest abundance in the main fishponds. These species partly overlapped with the indicator species (Tables A.1, A.4).

The nursery fishpond indicator species were mainly submerged macrophytes and included *Stuckenia pectinata*, *Potamogeton crispus*, *Myriophyllum spicatum*, and the amphiphyte *Callitriche palustris*. Though not significant, the helophytes *Glyceria maxima*, *Carex vesicaria*, and *Typha latifolia* were indicator species for the main fishponds (Table A.4).

3.2. Environmental parameters

The fishponds exhibited wide variation in water physico-chemical parameters and showed high nutrient concentrations (Table 5). Excessive TP concentration (median of 170 μg L^{-1} in nursery and 165 μg L^{-1} in main fishponds) resulted in high phytoplankton biomass (median Chl-*a* concentration 125 and 120 μg L^{-1} in nursery and main fishponds, respectively) leading to low transparency in most fishponds (median: 25 cm) (Tables 5, A.5), usually decreasing in summer (Table A.6).

A single fishpond (N-BE-1) was classed as sediment thickness category 1, with the majority being sediment category 2 or, in some cases, category 3 (Table 1).

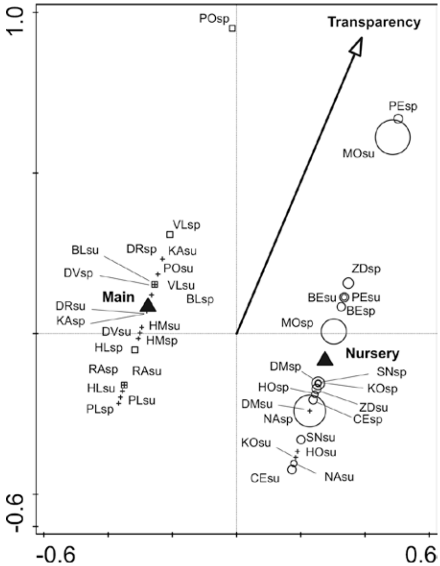

Fig. 4. Results of distance-based redundancy analysis (db-RDA) for submerged, free floating, rooted species with floating leaves and amphiphytes (aquatic + amphiphyte group in Table 4) in nursery and main fishponds (see Table 1 for codes) during spring (sp) and summer (su) surveys in 2017. The size of squares (main fishponds) or circles (nursery fishponds) corresponds to the sum of abundances of all species in all survey units per fishpond; + indicates fishponds with a sum < 2.

4. Discussion

4.1. Fishpond species, functional diversity and threatened species

Our study contributes to the knowledge of the role of man-made waterbodies in the maintenance of wetland biodiversity (Sayer et al., 2008; Juříček, 2012; Wezel et al., 2014), as wetlands and their macrophytes exhibit a rapid decline worldwide (Kingsford et al., 2016).

High variation in macrophyte assemblages was demonstrated among fishponds. In addition to aquatic and amphiphyte species, the species pool comprised a range of wetland annuals, helophytes, and terrestrial species, similarly to Juříček (2012). These semi-aquatic plants were able to germinate in low water levels at the beginning of the growing season and to survive in shallow water for long periods after flooding. However, these species are more typical of reed-bed and exposed bottom habitats (Francová et al., 2019), and the present study was conducted exclusively in the flooded areas of the fishponds; thus, the overall plant species diversity in the fishponds was likely higher than demonstrated.

Altogether 14 red-listed macrophytes were recorded in the studied fishponds, with 13 of them found in nursery fishponds. Lower nutrient status and less intensive disturbance probably allowed some nursery fishponds to act as refugia for less competitive species, e.g. low-growing annual wetland species. Currently, these species are almost exclusively found in fishponds with regular water level drawdown, typically

Table 4

Results of distance-based redundancy analysis (db-RDA) with forward selection procedure. Groups: All = all macrophyte species; Aqu + amp (aquatic + amphiphyte) = submerged, free floating, rooted with floating leaves, and amphiphytes (Fig. 4); Others = wetland annuals, helophytes, and terrestrial species; Expl. var. – total explained variation adjusted to the degrees of freedom and number of cases. Management type expressed as a category (Nursery × Main) and fish stock as biomass (kg ha^{-1}).

Groups	Expl. Var.	Management type	Transparency
All	18.5%	17.3% (pseudo-F = 7.9, P = 0.002)	5.4% (pseudo-F = 2.6, P = 0.04)
Aqu + amp	27.5%	24.5% (pseudo-F = 12.3, P = 0.001)	6.7% (pseudo-F = 3.6, P = 0.02)
Others	13.4%	11.3% (pseudo-F = 4.8, P = 0.01)	6.6% (pseudo-F = 3.0, P = 0.02)
Groups	**Expl. Var.**	**Fish stock**	**Transparency**
All	8.0%	10.4% (pseudo-F = 4.4, P = 0.003)	4.4% (pseudo-F = 2.0, P = 0.04)
Aqu + amp	11.6%	13.9% (pseudo-F = 6.1, P = 0.002)	
Others	6.7%	9.1% (pseudo-F = 3.8, P = 0.009)	

Table 5

Physico-chemical water parameters of fishponds surveyed in 2017. Z_{SD} = transparency, T = temperature, DO = dissolved oxygen, Cond = conductivity, TP = total phosphorus, SRP = soluble reactive phosphorus, Chl-*a* = chlorophyll *a* and ANC = acid neutralisation capacity.

Parameters	Nursery Median (range)	Main Median (range)
Z_{SD} (cm)	25 (10–85)	25 (9–70)
T (°C)	22.4 (20.2–26.9)	22.0 (20.3–26.3)
DO (%)	61 (17–158)	63 (12–113)
pH	8.0 (7.3–9.3)	7.6 (7.3–8.8)
Cond (mS m^{-1})	688 (407–974)	668 (485–969)
TP (μg L^{-1})	170 (21–860)	165 (29–400)
SRP (μg L^{-1})	10 (0–360)	7 (0–67)
NO_3-N (μg L^{-1})	20 (0–70)	30 (0–540)
NH_4-N (μg L^{-1})	20 (10–390)	20 (10–320)
Chl-*a* (μg L^{-1})	125 (10–490)	120 (30–440)
Ca (mg L^{-1})	27.5 (21–42)	29.0 (23–35)
ANC-4.5 (mmol L^{-1})	2.0 (1.2–3.0)	2.1 (1.6–2.8)

nursery fishponds but also main fishponds in production year 1. These fishponds probably harbour the most numerous populations of wetland annuals such as *Spergularia echinosperma*, but also a helophyte *Bolboschoenus yagara*, floating-leaved *Nymphoides peltata* and many other wetland plant species compared to any of wetland habitats in Central Europe (Kaplan et al., 2015, 2016).

4.2. Interactions within fishponds

Plant species in the fishponds exist within a structure of interactions among the abiotic environment, biota, and aquaculture practices, and these relationships are dynamic at different time scales (Francová et al., 2019). Fishpond management type, including fish stock, was the variable exhibiting the greatest influence on macrophytes. Farming practices such as supplementary feeding, liming, manuring, and winter and summer drainage have an important impact on macrophyte species composition, as they affect overall light availability, nutrient cycling, water pH, bottom sediment, the soil seed bank, and establishment of species requiring exposed substrates for germination (Hejný et al., 2002). Our data show that macrophyte assemblages differing in species and functional diversity may develop in fishponds under similar farming practices. This can be explained by different species pools in each studied fishpond, which are possibly related to the factors not covered by our data, e.g. different past development or a level of connectivity between fishponds (see Hassall et al., 2012 for lakes).

Regularly drained fishponds are potentially more suitable for helophytes, wetland annuals, and even for some submerged macrophytes such as *Zannichellia palustris*, as their soil seed banks and/or aboveground populations are able to recover at regular intervals on exposed wet substrates or in shallow water (Hejný, 1960). However, frequent and prolonged summer droughts may have a negative impact on aquatic (e.g. *Chara braunii*), amphiphyte (e.g. *Elatine triandra*), and moisture demanding wetland annual species (e.g. *Eleocharis ovata*) and helophytes (e.g. *Sagittaria sagittifolia*) (Hejný, 1960; Francová et al., 2019).

Although water physico-chemical conditions varied among fishponds, only transparency showed an impact on macrophyte species. Differences in other parameters were probably too small, and most of the macrophyte species in our dataset show a wide range of nutrient and water pH tolerance (Lacoul and Freedman, 2006; Chytrý, 2011). Some sensitive macrophyte species with potentially high indicator value (e.g. *Littorella uniflora*) have declined due to land use changes and fish farming intensification in the past decades (Francová et al., 2019).

We found no direct link of macrophyte species with sediment thickness, presumably because the overall number of macrophyte species was limited, and those with broad ecological range were dominant. Moreover, even though sediment thickness differed among fishponds, most of them had the prevailing sediment thickness category 2 (30–50 cm). Based on our own experience, the fishpond sediments are composed of erosion particles originating from watershed, organic particles from seston, macrophytes and fish farm management (e.g. fish feed, manure). The part of sediment does not stay in fishponds for a long time as it is washed out during the fishpond harvesting. Both deposition and washing out of the sediments may have an impact on vegetation dynamics, but reliable evidence is missing yet.

4.3. Nursery fishponds

Macrophytes thrived in nursery fishponds with lower fish stock pressure and higher water transparency, especially in spring of year 1 with lowest fish stock pressure. The impact of juvenile fish, primarily common carp but including other species and coarse fish, on the fishpond ecosystem increased throughout the growing season. This cascading top-down pressure resulted in a dramatic increase in Chl-*a* and a parallel decrease in water transparency, as also reported by Sommer et al. (2012). During the growing season, older and larger carp change feeding from plankton to zoobenthos, which increases turbidity and causes macrophyte uprooting (see also Ten Winkel and Meulemans, 1984).

Differences in macrophyte species composition and abundance in the spring and summer surveys of the same production year in nursery fishponds could be caused by various factors. Even a short-term clear water state after partial summer drainage at N-ZD-1 in spring 2017 enabled the development of a higher abundance of macrophytes, but they declined in the returning turbid state few weeks later. Lower farming intensity in N-MO-1 and 2 under nature reserve protection was linked with higher transparency (Table 3). Phenology of species and interspecific competition also played a role, with the thermophilous *Nymphoides peltata* tending to increase cover later in the growing season (Van der Velde, 1980). This was strongly reflected in an increase in overall macrophyte abundance in N-MO-1 and 2 from spring to summer in both 2016 and 2017 (Table 3). In N-MO-1 and 2, *N. peltata* outcompeted relatively less sensitive and more common species including *Stuckenia pectinata* (data not shown). On the other hand, *Potamogeton crispus* displayed a typical autumnal-vernal phenology (Rogers and Breen, 1980), dying off in high summer, reflecting an overall decrease in macrophyte abundance observed in N-DM-2 and N-HO-2 (data not shown).

4.4. Main fishponds

Low macrophyte species numbers (N = 27) and abundances were recorded in the main fishponds, primarily due to extreme conditions caused by high stocks of market-sized carp, which prevented the survival of most aquatic plant species. Main fishponds do not even provide very suitable habitat for common free-floating macrophytes such as *Lemna minor* and *Spirodela polyrhiza* due to water movement caused by wind and/or fish (Chytrý, 2011). Further, these macrophytes can also be consumed by grass carp *Ctenopharyngodon idella* and birds. Common carp, the dominant fish stocked, was unlikely to be the only factor influencing vegetation dynamics in the fishponds studied. Nevertheless, we observed pronounced seasonal and inter-annual vegetation dynamics in some main fishponds, primarily related to water level fluctuation. In M-BL-1 (2016), for example, 14 species were recorded in spring due to a low water level, with helophytes and wetland annual species occurring in shallow areas that the mature fish could not access. While this species number was comparable to that commonly found in nursery fishponds, the species number decreased, with no macrophytes recorded in M-BL-2 (2017), when water levels were higher.

4.5. Significance of this research and future perspectives

While maintenance of traditional fish farming is desirable (Falkowski and Nowicka-Falkowska, 2004), it is essential that farming practices would be adjusted in light of environmental changes. Climate change could enhance the spread of aggressive thermophilous macrophytes such as *Najas minor*, a species newly introduced to South-Bohemia and recorded in two of our fishponds. Thermophilous species, such as *Trapa natans* and *Nymphoides peltata*, had almost disappeared from our study area, but have recently started to thrive in some localities, particularly during extremely warm growing seasons. Although these species are listed in the national Red List (Grulich, 2012), they could easily turn to aggressive weeds, as shown by the excessive growth of *T. natans* in N-NA-1 in 2016 (data not shown) or by Chorak et al. (2019).

Our results show that nursery fishponds can still harbour rather high macrophyte diversity. Further studies of the diversity of macrophytes and other groups of organisms and their relation to fish farming management could be of interest for conservation of fishpond habitats.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.aquabot.2019.103131.

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CHAPTER 3

DRIVERS OF PLANT SPECIES COMPOSITION OF ECOTONAL PLANT COMMUNITIES IN TWO FISHPOND TYPES

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Drivers of plant species composition of ecotonal plant communities in two fishpond types

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ABSTRACT

Plant species of reed bed and exposed bottom zones were surveyed in fishponds used for rearing common carp *Cyprinus carpio* L. fry (nursery) and those used for rearing to market size (main). The results showed significant differences in plant species diversity and abundance, but no significant difference was found in functional diversity between the nursery and main ponds, if all the data involving two specific vegetation zones were analysed together. On the level of particular vegetation zones the results were as follows: while plant species and functional diversity, and abundance were similar in reed beds of both fishpond types, these characteristics significantly differed in the exposed bottom zones of nursery and main ponds. Zone width and shore slope showed high effects on development of reed beds, whereas fishpond management type and land use were the most important factors impacting plant species communities of exposed bottoms. Partial summer drainage was shown to enhance plant species and functional diversity as well as abundance of typical species of reed beds and exposed bottoms in both fishpond types. Our results are applicable not only to conservation of fishpond biodiversity but also to the management and preservation of other artificial water bodies as well as shallow lakes.

***Key words:** Central Europe, fish, land use, ponds, reed beds, wetland plants*

1. Introduction

Artificial fishponds have been an integral part of the European landscape for centuries, with most dating from the 14^{th} through 16^{th} centuries (Hoffmann, 1996; Francová et al., 2019a). In recent years, interest in fishponds is increasing as, in addition to commercial fish production, they provide a range of economic and ecosystem advantages such as water retention, flood protection, and support of biodiversity. Although wetland plants represent an essential segment of pond biota as they provide habitats and/or food sources for many organisms and affect physical conditions and biogeochemical cycles (Carpenter and Lodge, 1986; Rejmánková, 2011), little is known of key factors determining structure and species composition of fishpond plant assemblages relative to the multiple factors potentially acting within these highly dynamic systems (Šumberová et al., 2005; Potužák et al., 2016; Francová et al., 2019a).

As in other temperate lentic systems, e.g. shallow lakes, alluvial pools, and farm ponds, macrophyte diversity in fishponds is primarily driven by the environment, management, and land use in the surrounding landscape (Akasaka et al., 2010; Broyer and Curtet, 2012; Waldon, 2012; Hrivnák et al., 2013). Influence of many elements is scale-dependent. While geographic factors such as altitude, climate, and geology show the greatest effect over large and geomorphologically variable regions (Mikulyuk et al., 2011; Lukács et al., 2015; Sun et al., 2018; Angiolini et al., 2019), the impact of local factors usually increases over small areas and regions with uniform geomorphology. In addition to management practices and land use, local factors include the age, history, and trophic status of the water body; water chemistry, water depth, and water level fluctuations; frequency, intensity and direction of wind and associated wave action; bank and shore morphology; sediment quality and thickness; connectivity of water bodies; fish, waterfowl, and mammal activity; and inter-specific competition within plant assemblages (Keddy and Fraser, 2000; Wantzen et al., 2008; Zelnik et al., 2012; Mętrak et al., 2014; Svitok et al., 2016; Rolls et al., 2018). Fishpond research is challenging due to complex interactions of many factors, and systematic studies of plant assemblages and drivers of their diversity are scarce. The potential of fishponds as habitat for rare and threatened plant species (see examples of such species in, e.g., Kaplan et al., 2015; Kaplan et al., 2016; Richert et al., 2016) suggests an urgent need to better explore underlying factors and processes responsible for fishpond macrophyte diversity and distribution patterns. Thorough understanding of fishpond ecosystem functioning is crucial to development of measures to mitigate serious threats to fishpond biota, particularly with respect to progressive climate change.

Our recent study of plant assemblages in the open-water zones of fishponds identified management type, based largely on fish age and stocking density, and water transparency as critical factors shaping structure and species composition of aquatic plant assemblages (Francová et al., 2019b). Similar results have been demonstrated in fishponds in France (Broyer and Curtet, 2012) and Belgium (Lemmens et al., 2013). Water level fluctuation is likely another important factor shaping fishpond vegetation (Hejný, 1971, 1978; Francová et al., 2019b). Central European fishponds have been traditionally kept drained in winter and/or summer after harvest and before restocking. However, in recent years, drainage has occurred spontaneously as a consequence of drought. Drainage generally encourages germination and recruitment of wetland plants, particularly those of reed beds and exposed bottoms (mudflats), some amphiphytes, and even some aquatic plants. Additionaly, these plants benefit from the absence of fish stock pressure in shallow water and on wet substrates during their further development. Conversely, drainage is detrimental to species sensitive to low water levels associated with frost in winter and intense substrate desiccation in summer (Hejný, 1960; Hejný et al., 2002).

We hypothesize that fishpond plant communities that are less dependent on water, typically species occupying reed beds and exposed bottoms, are affected, not only by fishpond rearing-stage type, but also by land use, area of relevant vegetation zones, and the shore slope, as these factors have been identified as important regulators of wetland vegetation structure and species composition in natural lakes (Alahuhta et al., 2012; Palmik et al., 2013; van Leeuwen et al., 2014).

The primary objective in this study was to determine differences in plant species and functional diversity, and abundance of reed beds and exposed bottom vegetation in two types of fishponds stocked with fish of different age, biomass and associated management, and to determine the relationship of these differences to land-use, the extent of reed bed and exposed bottom zones, and shore slope. Reed beds and exposed bottoms were selected due to their close contact with the surrounding landscape.

2. Methods

2.1. Site description

Ten nursery (= used for inicial fish rearing) and ten main ponds (= used for rearing of fish to market size) were surveyed in South Bohemia, Czech Republic in 2017 (Fig. 1, Appendix 1). The fishponds were stocked chiefly with common carp *Cyprinus carpio* L. (95%). With the exception of the main pond Ražický, all fishponds were managed in a two-year production cycle. Since 2002, the fishponds were managed in the same way, i.e. the nursery and main ponds served for the same purpose continually. All nursery ponds were partially drained in summer prior to stocking in the first year of the production cycle, and the main ponds Dvořák, Podhorský and Blanský partially dried during summer due to drought. However, slightly lower water level and subsequently exposed bottoms also appeared at least at some pond parts and for some period in other main ponds, exceptions were the ponds Horní Machovec, Plaček and Ražický. The surveyed ponds are part of a connected pond systems.

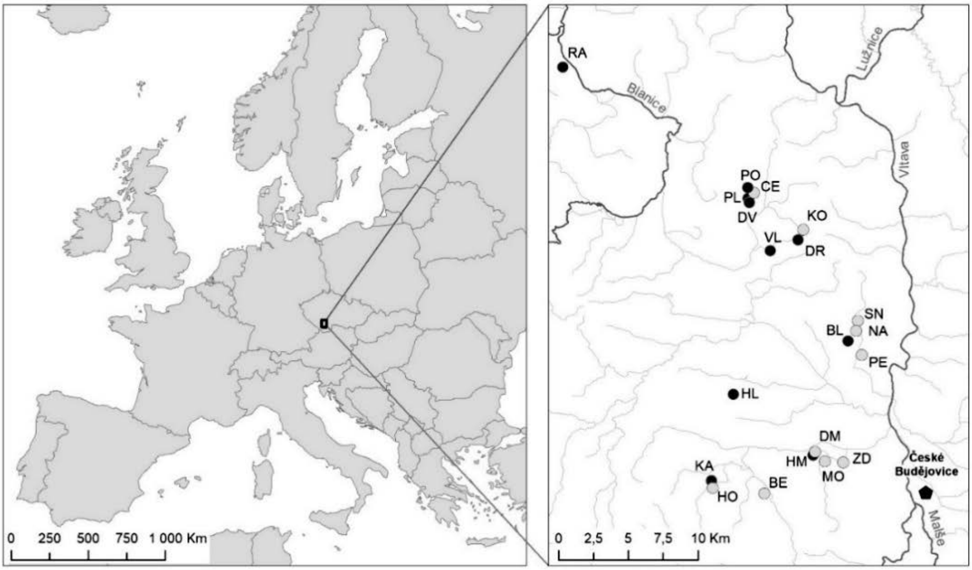

Figure 1. *Position of the studied fishponds in Europe and in the region of České Budějovice, South Bohemia (for fishpond codes and GPS coordinates see Appendix 1).*

All were eutrophic to hypertrophic, 4–29 ha in area, and 0.6–1.6 m deep (Table 1). Detailed information of the fishponds and their management is provided in Francová et al. (2019b). The landscape in the study area is formed by a mosaic of several land use types, with predominating arable land, and patches of grasslands and forests.

2.2. Plant species survey

We focused on plant species of areas in which reeds and/or tall sedges occurred at abundance >25%, i.e. reed and/or sedge beds (ReBe), and areas of exposed bottom with reed abundance <25% and water level below the sediment surface (ExBo). ExBo usually occurred in a zone between ReBe and the open water area of the fishpond, but, in the absence of ReBe, was in direct contact with terrestrial vegetation on the pond banks.

The plant species of ReBe and ExBo were recorded in 2 × 2 m plots, once in spring from May 22 to June 14 and once in summer from July 25 to August 11 in 2017. The abundance of each plant species was estimated using the new, nine-grade *Braun-Blanquet* scale (van der Maarel, 1979). The plots were located at perpendicular shore-to-shore transects that were located at regular intervals along shore (Fig. 2). When ReBe and ExBo zones were present, plots were located at the centre of the zone. The positions of transect lines were determined by Garmin GPSMAP 64st and marked with sticks. A 50 m tape was used to measure the width of ReBe and ExBo zones along a transect and to locate the plot central position. The number of transect lines depended on the fishpond size and the number of plots on the presence or absence of the relevant zones (three transect lines for <10 ha, up to twelve plots; four for 10–20 ha, up to sixteen plots; and five for 20–30 ha, up to twenty plots (Francová et al., 2019b).

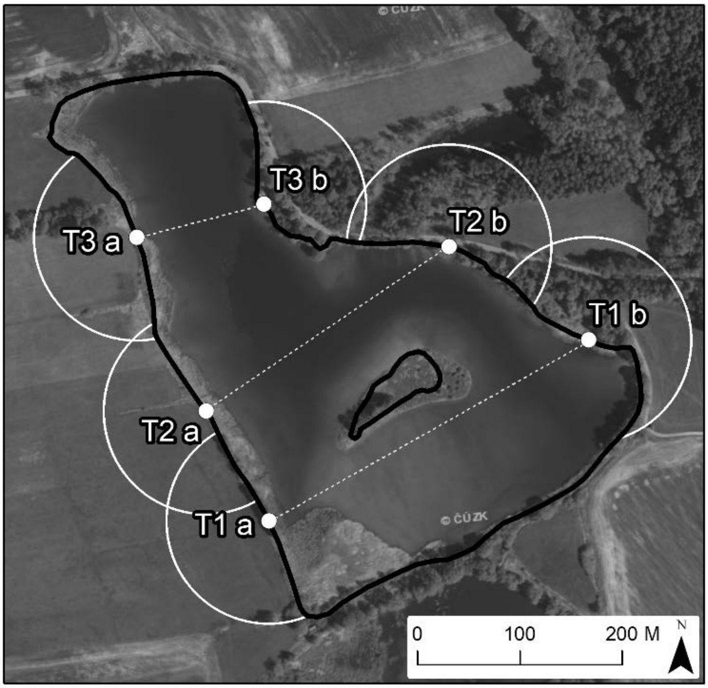

Figure 2. *The position of transects (T1-3) in one of the studied fishponds, Beranov. Letters "a" and "b" indicate respectively shorelines. Arcs represent 100 m land use buffer zone. Only a reed bed was present, as the fishpond was fully flooded.*

Threat categories of plants are based on the recent national Red List of vascular plants (Grulich, 2012) and identification of non-native species on Pyšek et al. (2012). Species identified only to genus were considered in overall plant species counts only when no other determined representative of that genus was included in a dataset. Functional groups of plants were as defined by Francová et al. (2019b) based on previous studies (Denny, 1987; Cook, 1990; Pokorný and Květ, 2004) and personal observation. Six groups of plants occurred in the studied plots: submerged, free floating, amphiphytes, helophytes, wetland annuals, and terrestrial plants, with an additional group, 'trees,' defined as the seedlings of wetland or terrestrial trees germinating in ExBo and/or in ReBe after water level drawdown (Appendix 2).

2.3. Parameters

The land-use within a 100 m radius surrounding each end of the transect, omitting the fishpond area, was classified according to the Corine database (Fig. 2) (CORINE, 2016): 1.1.2 discontinuous urban fabric; 2.2.1 non-irrigated arable land; 2.3.1 pastures, meadows, and other permanent grasslands under agricultural use; 2.4.3 land principally occupied by agriculture, with significant areas of natural vegetation; 3.1.1 broad-leaved forest; 3.1.2 coniferous forest; 3.1.3 mixed forest; and 5.1.2 water bodies. Fishpond borders were determined from the Dibavod database with water surface areas adjusted (DIBAVOD, 2017). Data were processed in ArcGIS 10.6 (ESRI, 2017). The shoreland slope gradient was subjectively noted *in situ* and categorized on a scale from 1 (gentle) to 3 (steep).

2.4. Data analyses

To calculate mean abundance of each plant species, the new Braun-Blanquet scale was transformed to % abundance: r = 0.02%, + = 0.1%, 1 = 2.5%, 2m = 5.0%, 2a = 8.75%, 2b = 18.75%, 3 = 37.5%, 4 = 62.5%, and 5 = 87.5% (van der Maarel, 1979). Plant abundance expressed on an ordinal scale from 1 to 9 replaced the original alpha-numeric values of the Braun-Blanquet nine-degree scale in statistical analyses.

Analyses of similarity (ANOSIM) based on the Bray-Curtis distance measure with 9999 permutations was employed to reveal possible differences in plant species and functional diversity, and abundances among the following groups: (i) spring vs. summer survey, (ii) nursery vs. main ponds, (iii) nursery ReBe vs. main ReBe, and (iv) nursery ExBo vs. main ExBo. The results of ANOSIM are defined by the R value ranging from 0 (equal distribution between tested groups) to 1 (high dissimilarity between tested groups). We found no significant difference between the spring and summer surveys; thus, their mean values of plant abundances were then used in all other analyses.

Non-metric multidimensional scaling (NMDS) with Bray-Curtis distance measure was used to see differences in plant species abundances between these groups: nursery ReBe vs. main ReBe and nursery ExBo vs. main ExBo. Additionally, NMDS analyses were overlaid with the following factors: (i) fishpond management type (nursery or main), (ii) land-use categories, (iii) the width of ReBe and ExBo zones, and (iv) shore slope.

ANOSIM was performed using the statistical package *vegan* 2.5–6 for R 3.6.1 (Oksanen et al., 2019; R Core Team, 2019), and CANOCO 5.12 was used for NMDS (Ter Braak and Šmilauer, 2012).

3. Results

Eighty-five plant species including four tree species at seedling stage were found in 206 plots (154 in ReBe and 52 in ExBo) in the selected fishponds during spring and summer surveys in 2017. This included 11 red-listed species, among them *Carex bohemica, Elatine triandra* and *Leersia oryzoides,* and 5 non-native species among which were *Bidens frondosus* and *Epilobium adenocaulon* (Appendix 2).

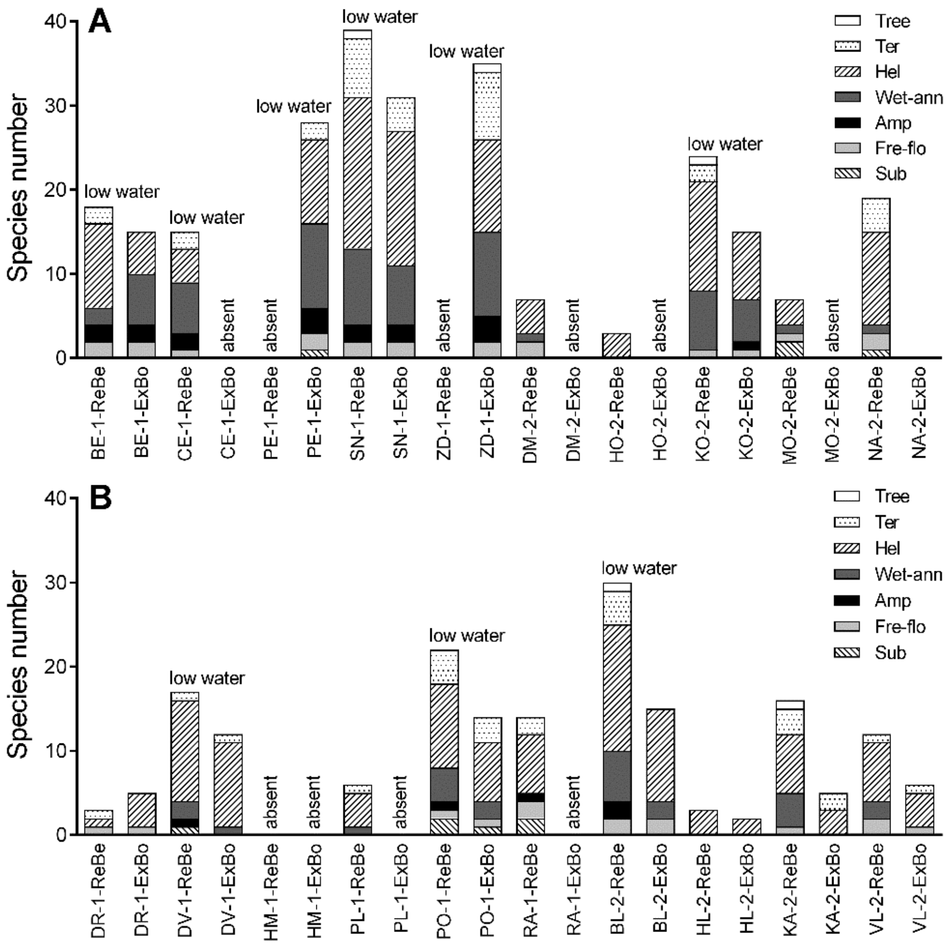

Figure 3. *Plant species number in nursery (A) and main (B) fishponds (see Appendix 1 for fishpond codes and Appendix 2 for particular species) and their reed bed (ReBe) and exposed bottom (ExBo) plots. The numerals 1 and 2 indicate first and second year of production cycle. Functional groups: Sub = submerged, Fre-flo = free floating, Amp = amphiphytes, Wet-ann = wetland annuals, Hel = helophytes, Ter = terrestrial, and Tree = tree seedlings. Low water = low water level at the beginning of growing season.*

The highest number of species fell into the functional groups helophytes (n = 34), wetland annuals (n = 17), and terrestrial species (n = 19). Species present in lower numbers included: amphiphytes (n = 5), trees (n = 4), submerged (n = 3), and free-floating macrophytes (n = 3) (Appendix 2).

Plant species numbers differed between fishpond management types and zones and among individual plots within a fishpond (Table 1). Higher plant species numbers and higher numbers of wetland annuals and amphiphytes were primarily found in the nursery ponds in the first year of the production cycle than in the nursery ponds in the second year of the production cycle or in the main ponds in any year of the production cycle (Fig. 3). Both nursery and main ReBe plots contained a mean of five species, while nursery ExBo plots had a mean of 10 species and main ExBo plots four (Table 1).

Table 1. *Characteristics of the nursery and main ponds and number of plots and species in plots. ReBe = reed bed and ExBo = exposed bottom zones.*

Fishpond type	**Nursery**		**Main**	
Area (ha)[a]	9 (4–13)		19 (9–29)	
Depth (m)[a]	1.0 (0.6–1.4)		1.2 (0.9–1.6)	
Number of plots	93		113	
Number of plant species	75		51	
Zone	**ReBe**	**ExBo**	**ReBe**	**ExBo**
Number of plots	69	24	85	28
Number of plant species	56	59	50	29
Number of plant species per plot[a]	5 (1–23)	10 (2–25)	5 (1–18)	4 (1–10)

[a] mean (range)

In ReBe, *Phragmites australis* was the most common species, occurring in 74% of plots, and showed highest abundance (mean of 30%). Other species with high frequency and abundance in ReBe were *Glyceria maxima* at 20% and 23%, respectively, and *Typha angustifolia* at 19% and 20%, respectively. The species showing highest mean frequency in ExBo plots was also *Phragmites australis* in 49% of plots with *Juncus effusus* (34%) and *Lythrum salicaria* (32%) being the second and the third. The highest abundance in ExBo plots had *Callitriche palustris* (9%) and *Elatine triandra* (6%) (Table 2).

ANOSIM based on plant species and functional diversity, and abundance confirmed no significant difference between spring and summer surveys (e.g. abundance $R = -0.0463$, $p = 0.95$). ANOSIM revealed significant difference in plant species diversity and abundance ($R = 0.1888$, $p = 0.0058$; $R = 0.1208$, $p = 0.0262$, respectively) but no significant difference was found in functional diversity ($R = 0.0447$, $p = 0.1514$) between nursery and main ponds, if all the data involving ReBe and ExBo were analysed together. On the level of particular vegetation zones, ReBe zones in nursery ponds did not significantly differ in plant species and functional diversity, and abundance from main pond ReBe zones ($R = -0.0119$, $p = 0.5159$; $R = 0.0365$, $p = 0.2683$; $R = -0.0293$, $p = 0.6527$, respectively), a significant difference was observed in plant species and functional diversity, and abundance between nursery ExBo and main ExBo zones ($R = 0.5300$, $p = 0.0053$; $R = 0.4341$, $p < 0.01$; $R = 0.3207$, $p = 0.0298$, respectively).

NMDS also showed higher species and functional diversity and greater numbers of wetland annual and amphiphyte species in nursery ponds compared to main ponds (Fig. 4A, C). In ReBe plots dominated by *Phragmites australis*, almost no other species were found, and shore slope and width of the zone were among the most important variables (Fig. 4A, B). Non-metric multidimensional scaling for ExBo plots revealed higher influence of all analysed variables, with non-irrigated arable land and land principally occupied by agriculture with significant areas of natural vegetation among the most important (Fig. 4D).

Table 2. *Plant species in 154 plots in reed beds and 52 plots in exposed bottoms. Species found at >5% and/or average abundance >1% are in bold.*

	Reed bed		Exposed bottom	
Species name	Abundance (%)	Frequency (%)	Abundance (%)	Frequency (%)
Terestrial				
Calamagrostis epigejos	4.50	**16**	2.24	**17**
Cirsium palustre	1.30	1	0.10	**2**
Poa trivialis	1.30	1	0.58	**9**
Urtica dioica	0.15	**14**	0.66	**15**
Cirsium arvense	0.06	1	0.02	**6**
Helophytes				
Phragmites australis	**30.11**	**74**	0.74	**49**
Glyceria maxima	**22.64**	**20**	0.40	**28**
Typha angustifolia	**19.55**	**19**	0.00	0
Juncus effusus	**17.35**	**20**	0.94	**34**
Typha latifolia	**16.16**	**15**	1.09	**13**
Carex acuta	**10.04**	**8**	0.61	**17**
Bolboschoenus yagara	**8.01**	**8**	1.97	**17**
Carex vesicaria	3.35	**13**	1.67	**25**
Phalaris arundinacea	2.11	**7**	0.36	**17**
Poa palustris	0.97	**5**	1.26	**4**
Lycopus europaeus	0.49	**11**	0.05	**9**
Lythrum salicaria	0.29	**21**	0.32	**32**
Oenanthe aquatica	0.15	**16**	0.86	**28**
Iris pseudacorus	0.10	1	2.50	**8**
Typha angustifolia/Typha latifolia	0.10	1	0.02	**8**
Leersia oryzoides	0.08	**3**	2.50	**2**
Sparganium erectum	0.07	**2**	0.02	**8**
Alisma plantago-aquatica	0.07	**3**	0.05	**6**
Juncus articulatus	0.07	**3**	1.30	**4**
Galium palustre	0.06	**8**	0.06	**11**
Solanum dulcamara	0.06	**6**	0.00	0
Bolboschoenus sp.	0.02	**2**	2.50	**8**
Myosoton aquaticum	0.00	0	1.30	**4**
Scutellaria galericulata	0.00	0	0.02	**8**
Wetland annuals				
Carex bohemica	1.30	**3**	0.42	**13**
Rumex maritimus	0.59	**6**	0.04	**15**
Persicaria hydropiper	0.57	**16**	1.85	**28**
Alopecurus aequalis	0.57	**6**	1.99	**17**

	Reed bed		Exposed bottom	
Species name	Abundance (%)	Frequency (%)	Abundance (%)	Frequency (%)
Wetland annuals				
Persicaria lapathifolia	0.32	**6**	0.48	**26**
Eleocharis ovata	0.07	**2**	0.68	**8**
Ranunculus sceleratus	0.07	**2**	0.09	**11**
Rorippa palustris	0.02	**4**	0.56	**9**
Epilobium sp.	0.00	0	0.10	**9**
Peplis portula	0.00	0	2.50	**2**
Amphiphytes				
Callitriche palustris	0.80	**6**	**9.48**	**17**
Elatine triandra	0.68	**3**	**6.12**	**13**
Juncus bulbosus	0.06	1	0.07	**6**
Free floating				
Lemna gibba /Lemna minor	1.42	**18**	0.09	15
Lemna minor	0.56	**17**	0.63	**17**
Spirodela polyrhiza	0.43	**21**	0.09	**26**
Submerged				
Riccia fluitans	**6.08**	**4**	0.10	**2**
Utricularia australis	1.41	**6**	0.00	0
None				
Galium sp.	0.08	**5**	0.02	**6**
Eleocharis sp.	0.00	0	0.10	**6**

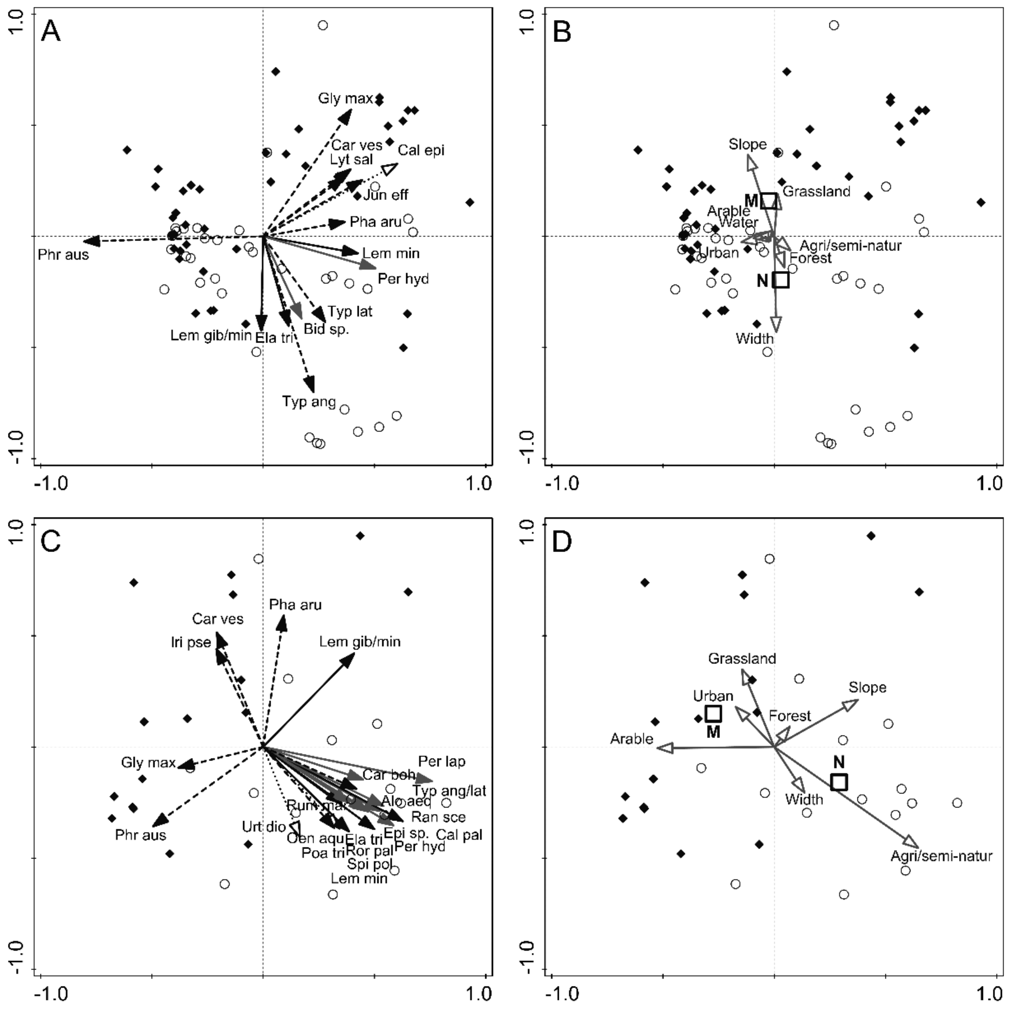

Figure 4. *Results of non-metric multidimensional scaling showing species correlated with ordination axes with at least 35% in ReBe (A) and ExBo (C), and their relationship with environmental variables in ReBe (B) and ExBo (D). Black diamonds = main and empty circles = nursery ponds. Plant functional groups (A, C): black = amphiphytes, grey = wetland annuals, dashed line = helophytes, dotted line = terrestrial. In B and D, fishpond management type: nursery (N) and main (M), land use categories: 1.1.2 discontinuous urban fabric, included as urban; 2.2.1 non-irrigated arable land as arable; 2.3.1 pastures, meadows, and other permanent grasslands under agricultural use as grasslands; 2.4.3 land principally occupied by agriculture, with significant areas of natural vegetation as agri/semi-natur; all forests were merged into a single category forest; and 5.1.2 water bodies as water.*

4. Discussion

4.1. Differences between fishpond types and zones

We detected higher plant species diversity and abundance in the littoral zones of nursery ponds compared to main ponds. Differences of functional diversity were only significant for the data from ExBo zone, with higher functional diversity found in nursery ponds. Our recent survey of plant diversity in the open-water zone showed similar results (Francová et al., 2019b), with fishpond management type, primarily reflecting fish age and stocking density, identified as the major factor influencing plant species diversity and abundance.

In the present study, we expected lower importance of factors associated with aquaculture husbandry compared to those related to adjoining land use, due to the position of ExBo and ReBe zones on the ecotone of freshwater and the surrounding land (Keddy and Fraser, 2000). However, an impact of land use type was demonstrated only in ExBo, while zone width and shore slope were the most important factors in ReBe. The results showed that a steep slope was associated with decreased width of the ReBe zone. The fishponds with a gentle slope developed wider areas covered by ReBe communities (Fig. 4B). Under these conditions, the co-existence of more plant species was likely if open-canopy communities such as *Typha angustifolia* stands are present (Fig. 4A).

The use of the surrounding landscape is likely to affect fishpond vegetation via modification of pond environmental conditions (shading of the banks, leaf litter accumulation, and nutrient runoff from arable fields) as well as by dispersal of seeds, spores, and vegetative propagules into the fishpond (Alahuhta et al., 2012; Mętrak et al., 2014; Grzywna et al., 2018). We presume that these factors apply at each fishpond, with plant species composition reflecting a unique combination of surrounding land-use categories and the overall landscape mosaic.

The low impact of land use on species composition of ReBe in this study might be surprising, as reed beds are usually in direct contact with the terrestrial environment, while exposed bottom extends on a moisture gradient toward the open water. Some assessed transects, however, had no reed beds, and the exposed bottom was directly connected with the surrounding forests, grasslands, or agricultural land, thus being expected as more exposed to seed dispersal and other impacts related to these land-use categories. The open sediments in the ExBo zones offered suitable microsites for germination of a range of species. Species with high demands for substrate moisture such as amphiphytes *Callitriche palustris* and *Elatine trindra* and wetland annuals *Eleocharis ovata* and *Ranunculus sceleratus* occurred mainly on muddy bottoms (see also Hejný 1960 for ecological requirements of particular species). Sandy margins of exposed pond bottoms are optimal for germination of wetland species with lower moisture demands (e.g. *Alopecurus aequalis* and *Persicaria lapathifolia*) (Hejný, 1960) and various species, mainly ruderals, arable weeds, and grassland species such as *Barbarea vulgaris* and *Taraxacum* sect. *Ruderalia* growing in the surrounding terrestrial habitats (MacDonald and Cavers, 1991; Milberg, 1993). However, in most of the ExBo plots only a few terrestrial species were represented, or they did not occur at all. It may have several explanations, particularly filtering of the seed rain from the surrounding landscape by the ReBe zone. Moreover, the sandy fishpond margins in many of the studied fishponds were occupied by reed beds and exposed muddy bottoms represent extreme conditions, not suitable for germination and recruitment of terrestrial species. Indeed, an extraordinary high number of terrestrial species was found in ExBo plots at the nursery pond Zdráhanka, the fishpond without ReBe zone and with areas of open sandy substrates in the littoral zone. On the other hand, in the ExBo of the nursery pond Pěnský only a single terrestrial species, *Urtica dioica*, was found, although ReBe zone was missing there as well. Such a low number of terrestrial species is probably related to prevailing muddy substrata and possibly also to surrounding forest, eliminating seed rain of many common terrestrial taxa including ruderal species.

Reed bed stands are generally less conducive to recruitment of other species due to strong competition for space, light, and nutrients (Hejný and Husák, 1978). In particular, communities dominated by *Phragmites australis* are characterised by high quantities of litter, which prevents germination of species requiring open mineral substrates (Holdredge and Bertness, 2011). According to our personal observations, only a limited number of wetland plants, including *Bidens frondosus* and *Lycopus europaeus* and ruderals such as *Galium aparine* and *Urtica dioica*, will germinate on a thick litter layer. Other species, for instance *Calamagrostis epigejos*, spread into reed beds from the banks. In any case, total number of species occurring in ReBe plots and potentially originating in terrestrial plant communities, was very low, similarly as in ExBo plots (see Fig. 3 and Appendix 2). It was not possible to compare our results with those of other studies of the influence of land use type, as this is the first analysis of which we are aware of reed bed and exposed bottom zones in this context. Research of this topic in other areas and types of water bodies considered the whole water body without distinguishing the vegetation zones or plant communities (Alahuhta et al., 2012; Grzywna et al., 2018), dealt exclusively with the aquatic zone (Akasaka et al., 2018), or identified several communities but without detailed analysis (Mętrak et al., 2014).

4.2. Fish farm management as one of the determinants of plant species diversity

A broad range of management measures are applied to both nursery and main ponds (Francová et al., 2019b). Some practices, including manuring and lack of summer drainage, often combined with nutrient runoff from the agriculture landscape, have led to the decline of sensitive plant species, typically poor competitors with low nutrient demands such as *Pseudognaphalium luteoalbum, Spergularia echinosperma,* and *Tillaea aquatica*. All these species used to grow in the study area in the past but currently they are extirpated from the fishponds in this region or occur there extremely rarely, and we did not found any of them in our study sites (Květ et al., 2002; Kaplan et al., 2016, 2018). On the other hand, mowing of vegetation leads to reduction in competitive species with high biomass production (Palmik et al., 2013) and thus to prevention of rapid terrestrialisation of the fishpond littoral zone. Small fishponds may become completely terrestrialised due to low water depth, and are particularly endangered by serious drought episodes associated with progressive climate change in Central Europe (Potop et al., 2010). However, in fishponds with sufficiently high water level the fish stock, particularly common carp >1 year, effectively supresses both aquatic and littoral vegetation under high stocking density (Francová et al., 2019b). High fish stock pressure was associated with low plant diversity even in ReBe zones (Fig. 3) with no plants recorded in the littoral of some main ponds.

Management practices supporting overall high plant species diversity include (i) lower fish stocking density, (ii) increased proportion of carnivorous fish at the expense of planktonophages and benthophages (Jůza et al., 2019), and (iii) biennial management cycles enabling regeneration of plant communities during the first production year with lower fish stock pressure, as with sac fry in nursery ponds (Francová et al., 2019b). The latter often includes maintenance of low water levels during the first year after fish harvesting (Francová et al., 2019a,b), supporting the development of an exposed bottom zone and survival of rare and threatened species including *Bolboschoenus yagara, Carex bohemica, Eleocharis ovata, Limosella aquatica, Elatine* spp. and *Scirpus radicans,* that in the central European agricultural landscape grow mainly in fishponds (Kaplan et al., 2015; Kaplan et al., 2017; Kaplan et al., 2018a).

Importance of specific management measures to conservation of plant and animal diversity in cultural landscape compared to absence of any management has been reported for various types of wetlands: fishponds (Broyer and Curtet, 2012; Lemmens et al., 2013; Wezel et al., 2014), fish storage ponds (Šumberová et al., 2006), farm ponds (Lewis-Phillips et al., 2019; Sayer et al., 2012), irrigation ponds in paddy fields (Yoon et al., 2019), and wet meadows

(Gaucherand et al., 2015). High conservation value of managed ponds compared to other types of water bodies, particularly at the regional level, was stressed also by Williams et al. (2004).

4.3. Disturbance intensity in fishponds

The Intermediate Disturbance Hypothesis (Bornette and Amoros, 1996) suggests a framework for sustainable wetland management, applicable to fishponds, with the main ponds representing habitats with high disturbance pressure and low biodiversity, while the nursery ponds provide habitats with intermediate disturbance pressure and higher biodiversity. Non-managed ponds, with low disturbance pressure and low biodiversity, are rare in the study area and not included in our analysis. However, according to our observations, these ponds have extremely low plant species and functional diversity, being usually covered by dense stands of reeds, particularly *Phragmites australis* or *Phalaris arundinacea,* with an admixture of competitive nitrophilous herbs, mainly *Urtica dioica,* and/or wetland trees (*Alnus glutinosa* and *Salix* spp.). Aquatic vegetation is usually lacking due to extremely shallow or no water, or it is represented by simple assemblages formed by *Lemna* spp. and/ or *Spirodela polyrhiza.*

Reed beds, defined in the present study as having >25% abundance of the dominant reed species, may also be considered zones with low disturbance pressure and low biodiversity. Although reed beds in fishponds may be managed by mowing, this is currently rarely applied, as fish effectively control littoral vegetation. When fish disturbances are extreme, reed beds are often supplanted by open water or exposed bottom (Svidenský et al., 2014).

Exposed pond bottoms, with predominance of species showing ruderal strategy (Grime, 1977), e.g. *Bidens* spp., *Persicaria* spp., and *Eleocharis ovata,* should represent habitats subjected to high disturbance pressure. However, we found ExBo plots to be species-rich, not expected in highly disturbed habitats. We attributed the high species richness to variation of conditions within the ExBo. If we considered the duration of flooding as a measure of disturbance intensity, the areas of the ExBo zone with fine muddy sediment, near open water, and submerged for one year or more after each drainage period would constitute a highly disturbed habitat. The opposite case would be sandy fishpond shores that are usually under water for a substantially shorter period than are bottoms and thus exhibit higher species and functional diversity, similar to that of fish storage ponds (Šumberová et al., 2006). Small-scale variation was observed in our raw data but not displayed in results, as, due to their low number, we combined all data of ExBo plots for analysis.

The duration of flooding is probably one of the most important factors involved in similarities of ReBe and differences of ExBo between nursery and main ponds. The duration of flooding and impact of fish stock in ReBe of both fishpond types were similar due to its position in the upper part of the littoral. Any potential differences in species composition of the plots predominated by *Phragmites australis* are counteracted by the influence of this strong competitor. The differences in ExBo of nursery ponds regularly drained in summer from the irregularly summer-drained main ponds were readily observable. In fishponds subjected to consistent summer draining, species forming abundant and long-term soil seed banks, such as *Carex bohemica, Eleocharis ovata, Limosella aquatica,* and *Peplis portula,* dominate stands (Poschlod, 1996; Šumberová et al., 2012a; Šumberová et al., 2012b). In randomly drained fishponds, there was usually a high proportion of species that were dispersed by wind and/ or water from the surroundings, including the ReBe zone, such as *Juncus effusus, Lythrum salicaria,* and *Persicaria lapathifolia*.

Strong impact of water level fluctuation on vegetation structure and species composition, including intensity, timing, and duration of bottom submersion/exposure phases, has also been described in natural lakes and artificial reservoirs in regions across Europe (Carmignani and Roy, 2017; Fernández-Aláez et al., 1999; Krolová et al., 2013; Luken and Thieret, 2001).

5. Conclusions

Plant species diversity and abundance in littoral zones in the nursery and main ponds was apparently determined by disturbance pressure. Application of a biennial production cycle could enable regeneration of ReBe and ExBo macrophyte populations during the first year of the production cycle. During the second year of the cycle, higher disturbance pressure would prevent extensive ReBe propagation, while ExBo species and communities would be stored in the seed bank in the flooded bottom sediment. If fish production cycles are consistently applied long-term, a dynamic equilibrium enables coexistence of a range of plant species and communities with different ecological requirements. An open water zone colonized by aquatic plants may, when subsequently drained, provide habitat for exposed bottom species. This ideal situation with variation in plant species and communities occurs in nursery ponds, while main ponds usually lack aquatic vegetation due to high fish pressure. Therefore, reduced fish stock and more regular partial summer drainage in main ponds could enhance plant species diversity and abundance.

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CHAPTER 4

GENERAL DISCUSSION
ENGLISH SUMMARY
CZECH SUMMARY
ACKNOWLEDGEMENTS
LIST OF PUBLICATIONS
TRAINING AND SUPERVISION PLAN DURING THE STUDY
CURRICULUM VITAE

General discussion

Anthropogenic pressure on fishpond ecosystems increased during the past century with input measures including summer and/or winter drainage, fertilization, liming, supplementary feeding, duck rearing, and vegetation control. Furthermore, fish farming practices and, consequently, pond ecosystems and macrophytes, have always been affected by political and socio-economic situations, and the impact of climate change has also recently become an increasingly important factor. All these alternations have led to intensive eutrophication and higher fish stock pressure, but despite this, many fishponds still serve as habitats for numerous macrophyte species (Juříček, 2012; Wezel et al., 2014; Francová et al., 2019a). Furthermore, the pond systems consist of several to dozens of ponds that are managed in different ways and intensities. The management along with different environmental conditions (e.g. surrounding landscape, position on a stream, wave action) contribute to forming of a set of fishpond habitats (e.g. open water, reed bed, exposed pond bottom), supporting the uniqueness of each fishpond and creating habitats with various diversity in the landscape (Francová et al., 2019b, Francová et al., in preparation). The interactions among influences on fishponds are complex, and more study is needed to better understand ecosystem functioning in order to develop measures to mitigate negative pressure and propose best practices (Francová et al., 2019a). The following research contribute to better awareness and knowledge of macrophyte assemblages in fishponds.

The results of the open water zone study revealed that the fishpond management type, primarily reflecting fish age and stocking density, was the major factor limiting presence of macrophytes (Francová et al., 2019b), and showed significantly higher macrophyte species numbers and abundance in the nursery compared to main ponds. Similar results were obtained in fishpond surveys in France (Broyer and Curtet, 2012) and Belgium (Lemmens et al., 2013).

Higher plant species numbers and greatest abundance were observed in the nursery ponds in the first year of the production cycle, when common carp pressure was at its lowest. The impact of young fish on the pond ecosystem increased during summer of the first growing season. Over the course of several months, common carp grew from microscopic sac fry to fish of 10–30 g. Predation pressure of fish on zooplankton communities usually increases with fish growth, at least when no serious losses of fish occur (Vrba et al., 2018). This was reflected in an increase of chlorophyll *a*, lower water transparency, and decrease of macrophyte abundance. The reduced plant abundance in summer compared to the spring survey in the first year of the production cycle was usually not as pronounced as differences between the spring and summer of the second year. During the second year, one-year-old common carp grew to 150–300 g. High turbidity in fishponds was observed not only as a consequence of decreased zooplankton, a main food source for younger and smaller fish, but also due to disturbance of bottom sediment by carp foraging for the zoobenthos that is preferred by older and larger fish (Anton-Pardo and Adámek, 2015), a behaviour that also contributes to macrophyte uprooting and eradication (Roberts et al., 1995). Although common carp was the primary fish stocked in the surveyed ponds, macrophytes may also be affected by fish such as grass carp *Ctenopharyngodon Idella* and other animals, particularly birds (Kiorboe, 1980; Pípalová, 2006) and molluscs (Bakker et al., 2016).

All surveyed fishponds were characterised by high quantities of nutrients. Even when not recently manured, supplemental fish feeding and nutrient run-off from surrounding agricultural land, settlements, and other fishponds, as well as leaching from pond sediment, precludes a shift to a nutrient-poor state (Baxa et al., 2019; Francová et al., 2019b).

Although water chemistry, sediment thickness, and land use differed to some extent among the studied fishponds, only water transparency significantly affected macrophyte species.

Higher transparency was observed in a few nursery ponds in spring, allowing the increase of macrophyte abundance, but these systems usually deteriorated in summer, resulting in decreased abundance. Although various functional groups of macrophytes were present in the open water zone, submerged macrophytes were dominant in most of the nursery ponds in spring. These showed the largest decrease with deterioration in water transparency. On the other hand, macrophytes with leaves floating on the water surface such as *Nymphoides peltata* and *Trapa natans*, present in a limited number of fishponds, were probably adversely impacted by low water transparency only at early development stages when growing from the pond bottom to water surface. Increased fish activity leads to their uprooting and damage throughout the life cycle. It is likely that the uprooting is correlated with the decrease in transparency and, consequently, exacerbates the decrease in floating leaves and submerged species. The observed differences in other assessed parameters were probably too small to be reflected in macrophyte species composition, as most macrophytes in the dataset occupy a broad ecological range (Francová et al., 2019b).

The effect of fish farming practices, adjoining land use, zone width, and shore slope on plant species of reed bed and exposed bottom zones also demonstrated significant difference in plant species diversity and abundance between the nursery and main ponds, with the highest species diversity and abundance found in the nursery ponds, as in the open water zone study (Francová et al., 2019b; Francová et al., in preparation).

Plant species diversity and abundance did not significantly differ between the reed beds of nursery and main ponds, probably due to the reed bed position in the upper part of the littoral, outside the major area of fish activity. Dominance of *Phragmites australis*, a strong competitor for space, light, and nutrients (Hejný and Husák, 1978; Holdredge and Bertness, 2011), was associated with a high level of vegetation homogenisation in many of the fishponds. Homogenisation of plant communities is an important reflection of biodiversity loss in wetlands. It is enhanced by eutrophication and detrimental farming techniques related to rapid succession of competitive plants, including invasive species (Price et al., 2018).

The width of reed beds was correlated with slope: a gentle slope supported, and a steep slope restricted, reed bed development. Most fishponds studied had a gentle slope, allowing presence of extensive reed bed zones. In these stands, the presence of other species was possible in the open canopy of *Typha* spp. (Francová et al., in preparation).

Plant species diversity and abundance differed significantly between the nursery and main pond exposed bottoms and was impacted by fish farming practices and land use. Reed beds were lacking in some fishponds or segments of ponds, allowing propagules of terrestrial species from the surrounding landscape to be readily dispersed onto the exposed bottoms. Sandy fishpond margins in the upper segment of the pond littoral zone without reed beds are particularly vulnerable to germination and recruitment of a range of ruderal species, arable weeds, and grassland and forest species (Šumberová and Ducháček, 2017). Streams and channels supplying fishponds with water are probably also important dispersal vectors, introducing propagules of plants growing in the surrounding habitat (Šumberová et al., 2012a, b). However, in nursery ponds and other fishponds subjected to regular summer draining, one of the most important sources of vegetation on exposed bottoms is the persistent soil seed bank established by seeds accumulated in pond sediment (Bernhardt et al., 2008). Interactions of biological traits of species present in soil seed banks and/or seed rain with the morphology of exposed littoral zones, including slope and sediment characteristics, and with duration and periodicity of summer drainage are reflected in species composition and distribution patterns of plant assemblages of exposed pond bottoms (Šumberová et al., 2005, 2006).

Water level fluctuation was likely a critical factor shaping the species composition in reed beds. Its presence or absence may enhance or eliminate an influence of other aspects of the fishpond ecosystem on reed beds. For example, no reed beds were present in some main ponds with consistently high water levels that allowed fish access to the entire littoral zone (Francová et al., in preparation). The strong negative impact of high populations of benthivorous fish on reed beds was confirmed by field experiments in selected South-Bohemian fishponds (Zákravský and Hroudová, 2007). The influence of water level fluctuation on vegetation has been observed in other types of water bodies such as reservoirs and lakes (Krolová et al., 2013; Carmignani and Roy, 2017). On top of that, macrophyte assemblages in fishponds could be affected by multiple factors in addition to those addressed in this study such as plant interspecific competition and pond-specific historical development.

Based on the results of my research, field experience, and extensive literature search, we conclude that fishponds should be actively managed. First, with no fish-mediated disturbance and/or elimination of excessive stands of fast-growing dominant species (e.g. *Ceratophyllum demersum, Lemna gibba, Phragmites australis*) microsites for competitively weak plant species would be lost. Secondly, excessive growth of macrophytes in eutrophic waters leads to broad fluctuations in oxygen, pH, and nutrient concentration, developing extreme environmental conditions unsuitable for a range of organisms (Carpenter and Lodge, 1986). Thirdly, if the described conditions continue over the course of several years, excessive growth and die-off of macrophytes can lead to accumulation of high quantities of organic sediments and terrestrialization of the water body. Although regular intervention such as mowing of vegetation is feasible, this maintaining of thousands of eutrophic or hypertrophic fishponds in a state suitable for diverse biota would be costly. Hence, appropriate farming techniques seem to be the most expedient way to maintain fishpond habitats and their biodiversity. Modification of the pond culture toward lower intensity, particularly reducing nutrient input from manuring and supplemental fish feeding, would improve, not only ecological status of fishponds, but health of stocked fish and natural pond productivity. All salient factors should be identified and considered before changes in fish farming practices are instituted, irrespective of their purpose. Practices implemented without thorough knowledge of pond characteristics may result in unexpected harm to pond ecosystem equilibrium and impact conservation, biodiversity, and other ecosystem services as well as fish production. Therefore, a plan should be developed for each pond individually, considering nutrient level, proposed pond use, and current biota. Novel problems related to climate change and spread of invasive species are likely to arise, potentially necessitating management modifications (Jůza et al., 2019). For instance, different weather conditions and water deficiency may require adaptations to timing of fish stocking and to water level manipulations. It is evident from our studies that exposed pond bottoms have started to occur more often unintentionally. It might be seen as positive as this habitat is the important refuge of many threatened plant species, which are very scarce or even absent in other wetland habitats in central Europe (Kaplan et al., 2015, 2016; Richert et al., 2016). On the other hand, if the frequency and intensity of water level drawdown would further increase, it can lead to overgrowing in number of ponds, to spreading of a few highly competitive and species-poor littoral plant assemblages, and to a decline in less-competitive species, as well as the species with specific moisture and/or substrate demands. These processes may even cause loss of some fishponds with insufficient water supply.

Conclusions

1. Fishpond systems comprising ponds that vary in management with respect to rearing-stage use and farming practices represent a valuable tool for preserving wetland biodiversity.
2. Plant species development in the open water zone of fishponds reflects intensity of fish stock pressure and water transparency and can vary with year of production cycle.
3. Reed bed species populations are affected by shore slope and zone width, while the vegetation of exposed bottoms is more impacted by fishpond management type and adjoining land use.
4. Low plant diversity and other indicators of low ecosystem quality in a single year do not necessarily indicate that a fishpond is not valuable for nature conservation.
5. Consideration of macrophyte assemblages in fishponds needs to be incorporated into fish farm management plans in order to achieve a balance between fish production and biodiversity protection.

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English summary

Macrophyte assemblages in fishponds under different fish farming management

Kateřina Francová

Artificial fishponds have been an integral part of the European landscape for centuries. In addition to fish production, they provide important ecosystem services and habitats for biota, including macrophytes. The processes influencing macrophyte assemblages in fishponds are poorly understood and thus they were in the focus of this research.

The opening study introduces thesis with a review of available information of historical development of fishponds and relation between fish farm management practices and fishpond macrophyte assemblages. Relevant socio-economic factors and possible effects of climate change are also explored. Comparison with similar wetland habitats shows that fishponds represent valuable systems harbouring many macrophyte species and a range of their rare and threatened taxa.

The following study focuses on seasonal and inter-annual differences in vegetation in open water zones of nursery and main ponds. The results show significant effect of the fishpond management type on macrophyte assemblages with strong decrease in macrophyte species numbers and abundance with increasing fish stock pressure. Stands of aquatic macrophytes commonly more developed in the nursery ponds in the spring of the first year of the production cycle, but variability could be found between ponds for example due to lower water level. While the results showed distinctions in water chemistry, sediment thickness, and adjoining land use, only transparency exerted a significant effect on macrophyte assemblages. Differences in other measured parameters were probably too small to be reflected in macrophyte species composition. Additionally, most macrophytes in our dataset show a broad ecological range.

The last part of thesis reports analyses of plant species of reed bed and exposed bottom zones in the same selection of fishponds. As observed in the study of the open water zone, the highest species numbers and abundance were observed in the nursery ponds. The plants of reed beds were mostly affected by the width of the zone and shore slope. Lower slope in most fishponds often allowed development of the dense stands of *Phragmites australis*, which are highly competitive. They affect light and nutrient availability, produce a high amount of litter and so limit occurrence of other species. This as well as a position in the upper part of littoral, where they might not be affected by fish or water level disturbances so often, led to similarities in reed bed zones between fishpond types. In contrast more open reed bed stands with species such as *Typha angustifolia* and exposed bottoms allowed development of more species. The plants of exposed bottoms were affected by fishpond management type and adjoining land use type. The reason is lower fish stock pressure and more regular summer and/or winter drainage. Some fishponds or their parts did not have reed beds and exposed bottoms were then directly connected and influenced by surrounding landscape, e.g. ruderal and grassland species such as *Barbarea vulgaris* and *Taraxacum* sect. *Ruderalia* regularly occurred there.

Application of fish farming practices is important not only as it is a part of the national heritage, but also to avoid pond terrestrialization. However, modification of farming techniques to best suit individual pond conditions and to adapt to climate change is recommended. Reducing fish stock density when relevant and limiting nutrient input from manuring and supplemental fish feeding may aid recovery of fishpond ecosystems including macrophyte species assemblages.

Czech summary

Makrofyta v rybnících s různým typem rybářského hospodaření

Kateřina Francová

Rybníky jsou po staletí součástí evropské krajiny. Kromě rybářské produkce mohou poskytovat řadu ekosystémových služeb a prostředí pro biotu, včetně makrofyt. Procesy, které ovlivňují výskyt makrofyt v rybnících, nejsou ještě dostatečně známy, a proto na ně byl zaměřen tento výzkum.

Úvodní studie shrnuje dostupné informace o historickém vývoji rybníků a vzájemném vztahu mezi rybářským hospodařením a společenstvy makrofyt. Analyzuje se také působení socio-ekonomických faktorů a možný efekt klimatických změn. Porovnání s podobnými mokřadními ekosystémy ukázalo, že rybníky ještě stále představují cenné lokality pro makrofyta a řadu jejich vzácných a ohrožených druhů.

Další studie se zabývá sezónní a meziroční dynamikou vegetace vodní zóny ve výtažnících a hlavních rybnících. Výsledky ukazují signifikantní efekt typu rybníka, kdy se vzrůstajícím tlakem rybí obsádky klesal počet a abundance makrofyt. Vodní makrofyta se hojněji vyskytovala ve výtažnících na jaře prvního horka, ale mezi rybníky byly nalezeny diference například v důsledku nižší vodní hladiny. Přesto, že se rybníky lišily ve fyzikálně-chemických parametrech vody, tloušťce sedimentu a zastoupení jednotlivých typů přilehlé krajiny, pouze průhlednost měla signifikantní vliv na společenstva makrofyt. Rozdíly v ostatních parametrech byly pravděpodobně velmi malé, aby se odrazily ve druhovém složení. Navíc se většina makrofyt v našem datovém souboru vyznačuje širokou ekologickou valencí.

Poslední část dizertační práce se koncentruje na vegetaci zóny rákosin a obnaženého dna ve stejných rybnících. Podobně jako u vodní zóny byl největší počet rostlinných druhů a jejich abundancí nalezen ve výtažnících. Rostliny rákosin byly nejvíce ovlivněny šířkou zóny a sklonem břehu. Mírný sklon u většiny rybníků mnohdy dovolil rozvoj hustého porostu *Phragmites australis*, který je velice konkurenčně schopný, omezuje přístup světla a živin, ovlivňuje prostředí množstvím opadu, a tím brání výskytu dalších druhů. Tyto faktory zapříčinily podobnost zón rákosin mezi jednotlivými typy rybníků. Stejně tak jako postavení rákosin v horní části litorálu, kde nemusí být často vystaveny disturbancím ze strany rybí obsádky a kolísání vodní hladiny. Naproti tomu otevřenější rákosiny, kde byly zastoupeny druhy jako *Typha angustifolia*, a obnažená dna dovolila rozvoj většího počtu druhů. Na rostliny obnaženého dna měl vliv typ rybníka a typ přilehlé krajiny. Příčinou je nižší tlak ryb a pravidelnější letnění, popřípadě zimování výtažníků. Některé rybníky nebo alespoň jejich část neměla rákosiny a okolní krajina tak byla přímo spojena a ovlivnila obnažená dna, na kterých se potom mimo jiné vyskytovaly ruderální a polní druhy, jako např. *Barbarea vulgaris* a *Taraxacum* sect. *Ruderalia*.

Zachování rybářského hospodaření je důležité, nejen protože je součástí tradic, ale také proto, že zabraňuje zazemňování a postupnému zarůstání rybníků. Nicméně by mělo být přizpůsobeno odlišným podmínkám, které panují v jednotlivých rybnících, a klimatické změně. Snížení rybí obsádky, pokud je relevantní, a limitace vstupu živin ve formě hnojení a krmení by mohlo napomoci ke zlepšení stavu rybníků a stejně tak k obnovení společenstev makrofyt.

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List of publications

Peer-reviewed journals with IF

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Francová, K., Šumberová, K., Kučerová, A., Čtvrtlíková, M., Šorf, M., Borovec, J., Drozd, B., Janauer, G., Vrba, J., 2019. Macrophyte assemblages in fishponds under different fish farming management. Aquatic Botany 159, 103131. (IF 2018 = 2.143)

Francová, K., Šumberová, K., Kučerová, A., Šorf, M., Grill, S., Exler, N., Vrba, J. Littoral zones of temperate artificial fishponds support high plant species diversity. Manuscript.

Abstracts and conference proceedings

Francová, K., Šumberová, K., Čtvrtlíková, M., Kučerová, A., Borovec, J., Exler, N., Schmidt-Mumm, U., Janauer, G.A., 2017. Interconnection between fishpond management and aquatic macrophytes. In: EFFS (Eds.), 10th Symposium for European Freshwater Sciences, Abstract book, 2–7 July 2017, Olomouc, Czech Republic, p. 231.

Training and supervision plan during study

Name	Kateřina Francová	
Research department	2015–2020 – Laboratory of Applied Hydrobiology of FFPW	
Supervisor	Prof. Jaroslav Vrba	
Period	1st October 2015 until 22nd June 2020	

Ph.D. courses	**Year**
English language	2015
Pond aquaculture	2015
Applied hydrobiology	2016
Biostatistics	2016
Biology of aquatic macrophytes	2017
Scientific seminars	**Year**
Seminar days of RIFCH and FFPW	2016 2017 2018 2019
XVII. seminar of wetland ecology and hydrobotany, 20–21 February 2019, Třeboň, Czech Republic	2019
International conferences	**Year**
Francová, K., Šumberová, K., Čtvrtlíková, M., Kučerová, A., Borovec, J., Exler, N., Schmidt-Mumm, U., Janauer, G.A., 2017. Interconnection between fishpond management and aquatic macrophytes. In: 10th Symposium for European Freshwater Sciences (SEFS 10), 2–7 July 2017, Olomouc, Czech Republic, p. 231.	2017
Foreign stays during Ph.D. study at FFPW	**Year**
Prof. Thomas Hein and Prof. Georg A. Janauer, University of Natural Resources and Life Science, Vienna, Austria (3 months, learning about different methods used in macrophyte survey).	2016
Norber Exler, Ph.D. and Prof. Georg A. Janauer, Danube University, Krems, Austria (2 months, processing and analysing my own data).	2017
Pedagogical activities	**Year**
• Lecturing of bachelor and master students, discipline Fishery at FFPW in range of 27 teaching hours.	2016
• Lecturing of hosting students about fishponds, their biota and fish farming management during excursions and open days in range of 63 teaching hours.	2016–2018
• Consultancy of two B.Sc. and one M.Sc. theses.	2016–2019

Curriculum vitae

PERSONAL INFORMATION

Name: Kateřina
Surname: Francová
Born: 2nd March 1984, Písek, Czech Republic
Nationality: Czech
Languages: Czech (mother tongue)
English (C1 level – CAE certificate)
Contact: kfrancova@frov.jcu.cz

RESEARCH INTEREST

My research interest is in the field of ecology and management of freshwater ecosystems, especially fishponds and their macrophytes.

EDUCATION

2015–present Ph.D., specialisation Fishery, Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, Czech Republic

2008–2010 Dipl.-Ing., specialisation Agroecology, Faculty of Agriculture, University of South Bohemia in České Budějovice, Czech Republic
Thesis: Effect of inter-annual differences of selected meteorological parameters on species composition of the wet meadows near Třeboň

2005–2008 B.Sc., specialisation Agroecology, Faculty of Agriculture, University of South Bohemia in České Budějovice, Czech Republic
Thesis: Effect of moving on species composition and above-ground biomass of a eutrophic wet meadow

COMPLATED Ph.D. COURSES

Applied hydrobiology, Biology of aquatic macrophytes, Biostatistics, Pond aquaculture

RESEARCH STAY AND COLLABORATIONS

2016–2017 Prof. Thomas Hein and Prof. Georg A. Janauer, University of Natural Resources and Life Science, Vienna, Austria (3 months)

2017–2017 Norbert Exler, Ph.D. and Prof. Georg A. Janauer, Danube University, Krems, Austria (2 months)