Aquatic Botany 159 (2019) 103131

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Macrophyte assemblages in fishponds under different fish farming management

Kateřina Francová[a,*], Kateřina Šumberová[b], Andrea Kučerová[c,d], Martina Čtvrtlíková[d], Michal Šorf[e,f], Jakub Borovec[g], Bořek Drozd[a], Georg A. Janauer[h], Jaroslav Vrba[d,e]

[a] University of South Bohemia in Ceske Budejovice, Faculty of Fisheries and Protection of Waters, CENAKVA, Institute of Aquaculture and Protection of Waters, Na Sádkách 1780, 370 05, České Budějovice, Czech Republic
[b] Institute of Botany of the Czech Academy of Sciences, Department of Vegetation Ecology, Lidická 25/27, 602 00, Brno, Czech Republic
[c] Institute of Botany of the Czech Academy of Sciences, Department of Functional Ecology, Dukelská 135, 379 82, Třeboň, Czech Republic
[d] Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, Na Sádkách 702/7, 370 05, České Budějovice, Czech Republic
[e] University of South Bohemia in Ceske Budejovice, Faculty of Science, Branišovská 1760, 370 05, České Budějovice, Czech Republic
[f] Mendel University, Faculty of AgriSciences, Zemědělská 1665/1, 613 00, Brno, Czech Republic
[g] Biology Centre of the Czech Academy of Sciences, SoWa Research Infrastructure, Na Sádkách 7, 370 05, České Budějovice, Czech Republic
[h] University of Vienna, Department of Limnology and Bio-Oceanography, Althanstraße 14, 1090, Vienna, Austria

ARTICLE INFO

Keywords:
Aquatic plants
Biodiversity
Central Europe
Fish
Ponds

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*

---

* Corresponding author.
E-mail addresses: kfrancova@frov.jcu.cz (K. Francová), katerina.sumberova@ibot.cas.cz (K. Šumberová), andrea.kucerova@ibot.cas.cz (A. Kučerová), martina.ctvrtlikova@hbu.cas.cz (M. Čtvrtlíková), michal.sorf@centrum.cz (M. Šorf), Jakub.Borovec@bc.cas.cz (J. Borovec), drozd@frov.jcu.cz (B. Drozd), georg.janauer@univie.ac.at (G.A. Janauer), jaroslav.vrba@prf.jcu.cz (J. Vrba).

https://doi.org/10.1016/j.aquabot.2019.103131
Received 7 March 2019; Received in revised form 21 June 2019; Accepted 5 July 2019

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

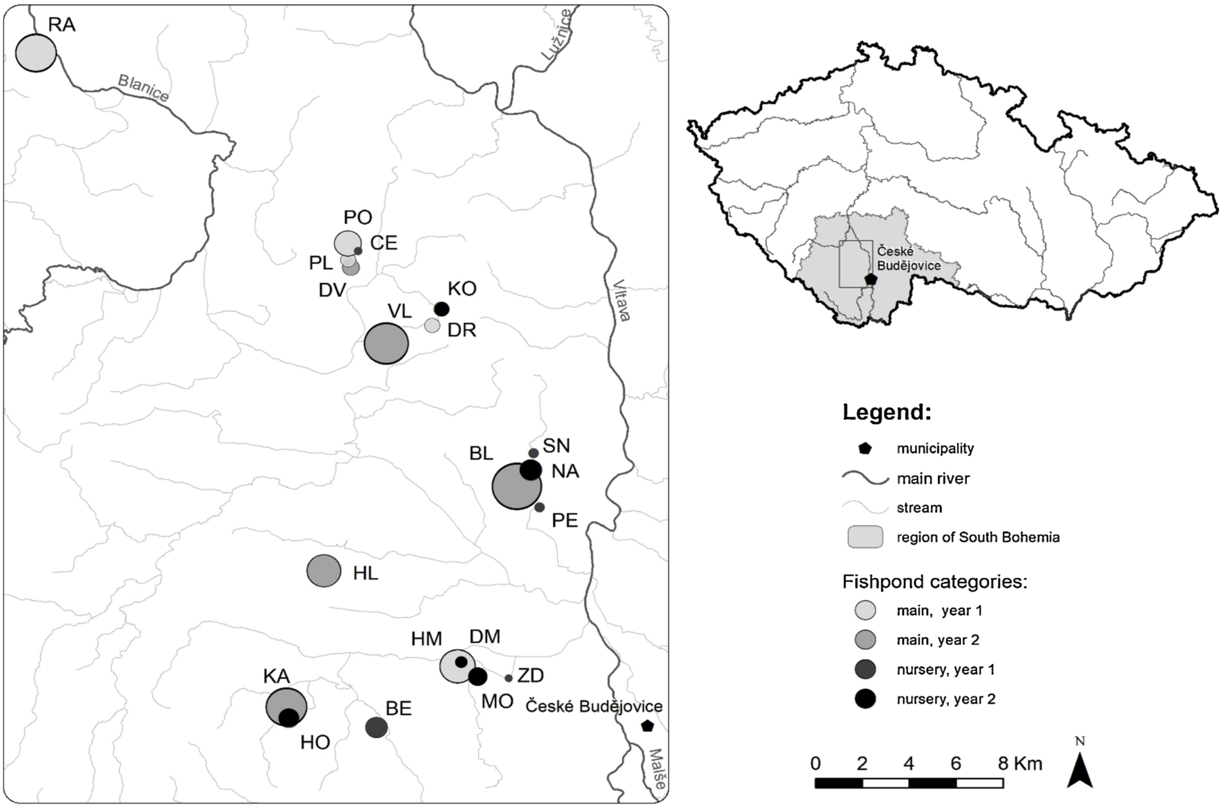

Fig. 1. Location of the fishponds under study (see Table 1 for identification codes and size, fishpond categories apply to 2017). Circle size corresponds to relative fishpond area.

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	+	+	+

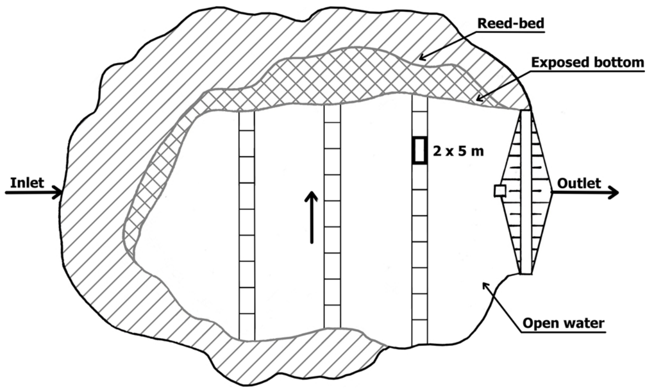

Fig. 2. Typical position of transects and survey units (2 × 5 m) in a fishpond. A reed-bed zone was not included in the survey, and the transects were set inward from the waterline or at the shoreline when a reed-bed zone was not present. In fishponds in which water levels were increased, the previously 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' (=3rd 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

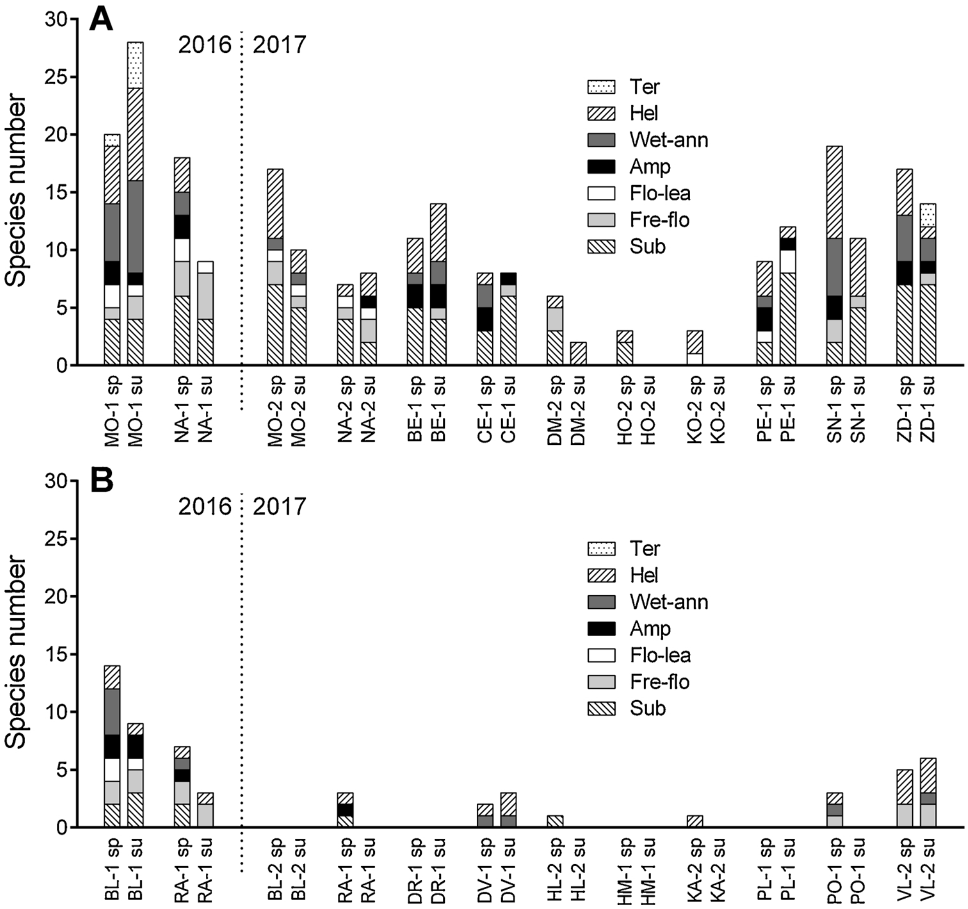

Fig. 3. Macrophyte number of species in (A) nursery and (B) main fishponds (see Table 1 for codes) in spring (sp) and summer (su), divided into functional groups. Sub = submerged, Fre-flo = free floating, Flo-lea = rooted with floating leaves, Amp = amphiphytes, Wet-ann = wetland annuals, Hel = helophytes 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 $\mu g\ L^{-1}$ in nursery and 165 $\mu g\ L^{-1}$ in main fishponds) resulted in high phytoplankton biomass (median Chl-*a* concentration 125 and 120 $\mu g\ L^{-1}$ 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).

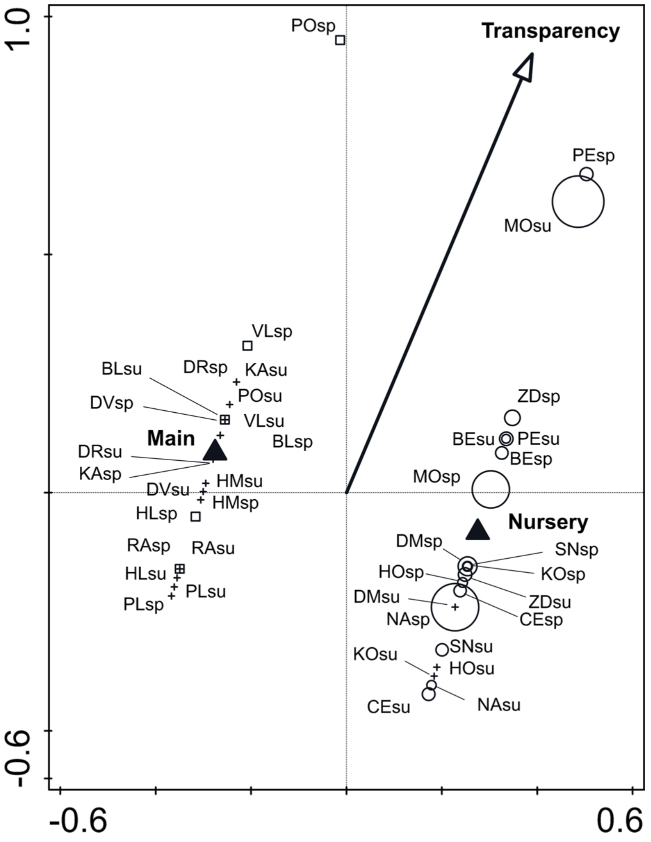

Fig. 4. Results of distance-based redundancy analysis (db-RDA) for submerged, free floating, rooted species with floating leaves and amphiphytes (aquatic + amphiphyte group in Table 4) in nursery and main fishponds (see Table 1 for codes) during spring (sp) and summer (su) surveys in 2017. The size of 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.

Acknowledgements

This study was partly supported by the Ministry of Education, Youth and Sports of the Czech Republic under the project CENAKVA (LM2018099), projects No. LM2015075 and No. EF16_013/0001782 – SoWa Ecosystems Research, by the Ministry of Agriculture project No. QK1810161. This paper was further supported by the Czech Science Foundation projects No. 14-36079G – Centre of Excellence PLADIAS and No. 17-09310S; and by the Czech Academy of Sciences (RVO 67985939). The authors thank U. Schmidt-Mumm and N. Exler for helpful suggestions regarding work planning, P. Dvořák for providing sonar, S. Grill for processing the GIS data, J. Potužák (Povodí Vltavy State Enterprise) for help with water analysis, and fish farmers of Rybářství Hluboká CZ s.r.o. and Blatenská ryba s.r.o. We thank Lucidus Consultancy for language editing service and anonymous reviewers for valuable comments.

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.

References

Bakker, E.S., Wood, K.A., Pagès, J.F., Veen, G.C., Christianen, M.J., Santamaría, L., Nolet, B.A., Hilt, S., 2016. Herbivory on freshwater and marine macrophytes: a review and perspective. Aquat. Bot. 135, 18–36.

Blindow, I., 1992. Long-and short-term dynamics of submerged macrophytes in two shallow eutrophic lakes. Freshw. Biol. 28, 15–27.

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370.

CEN EN 14184, 2014. Water Quality Guidance Standard for the Surveying of Aquatic Macrophytes in Running Waters.

CORINE, 2016. Corine Land Cover (CLC) 2012, Version 18.5.1. European Environment Agency, Copernicus Programme. https://land.copernicus.eu/paneuropean/corine-land-cover.

Cook, C.D.K., 1990. Aquatic Plant Book. SPB Acad. Publ., Hague.

Chorak, G.M., Dodd, L.L., Rybicki, N., Ingram, K., Buyukyoruk, M., Kadono, Y., Chen, Y.Y., Thum, R.A., 2019. Cryptic introduction of water chestnut (*Trapa*) in the northeastern United States. Aquat. Bot. 155, 32–37.

Chytrý, M., 2011. Vegetace České republiky 3. Vodní a mokřadní vegetace. Academia, Praha (in Czech).

Czech Geological Survey, 2019. http://www.geology.cz/extranet-eng. Accessed 16 April 2019.

Denny, P., 1987. Mineral cycling by wetland plants – a review. Arch. Hydrobiol. Beih. 27, 1–25.

Dhote, S., Dixit, S., 2009. Water quality improvement through macrophytes – a review. Environ. Monit. Assess. 152, 149–153.

DIBAVOD, 2017. In: Masaryk, T.G. (Ed.), Digital Base of Water Management Data (DIBAVOD). Water Research Institute. http://www.dibavod.cz/).

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

EN ISO 10304-1, 2009. Water Quality – Determination of Dissolved Anions by Liquid Chromatography of Ions – Part 1: Determination of Bromide, Chloride, Fluoride, Nitrate, Nitrite, Phosphate and Sulphate.

EN ISO 17294-2, 2004. Water Quality – Application of Inductively Coupled Plasma Mass Spectrometry (ICP-MS) – Part 2: Determination of 62 Elements.

ESRI, 2017. ArcGIS Desktop, Version 10.6. Environmental Systems Research Institute, Redlands, CA.

Falkowski, M., Nowicka-Falkowska, K., 2004. Dependence of biodiversity of fishpond vegetation upon the intensity of fish farming. Teka Commiss. Protect. Formation Nat. Environ. 1, 51–56.

Francová, K., Šumberová, K., Janauer, G., Adámek, Z., 2019. Effects of fish farming on macrophytes in temperate carp ponds. Aquac. Int. 27, 413–436.

Grulich, V., 2012. Red List of vascular plants of the Czech Republic: 3rd edition. Preslia 84, 631–645.

Hassall, C., Hollinshead, J., Hull, A., 2012. Temporal dynamics of aquatic communities and implications for pond conservation. Biodivers. Conserv. 21, 829–852.

Hejný, S., 1960. Ökologische Charakteristik der Wasser und Sumpfpflanzen in den Slowakischen Tiefebennen. Verlag der Slowakischen Akademie der Wissenschaften, Bratislava (in German).

Hejný, S., Hroudová, Z., Květ, J., 2002. Fishpond vegetation: an historical view. In: Květ, J., Jeník, J., Soukupová, L. (Eds.), Freshwater Wetlands and Their Sustainable Future: A Case Study of the Třeboň Basin Biosphere Reserve, Czech Republic. Parthenon Pub. Group, Unesco, Paris, pp. 63–96.

Houlahan, J.E., Keddy, P.A., Makkay, K., Findlay, C.S., 2006. The effects of adjacent land use on wetland species richness and community composition. Wetlands 26, 79–96.

ISO 7150-1, 1994. Water Quality – Determination of Ammonium. Part 1: Manual Spectrometric Method.

ISO 9963-1, 1994. Water Quality – Determination of Alkalinity. Part 1: Determination of Total and Composite Alkalinity.

ISO 10260, 1992. Water Quality, Measurement of Biochemical Parameters; Spectrometric Determination of chlorophyll-*a* Concentration.

Janauer, G.A., Heindl, E., 1998. Die Schätzskala nach Kohler: Zur Gültigkeit der Funktion $f(y) = ax^3$ als Maß für die Pflanzenmenge von Makrophyten. Verh. Zool.-Bot. Ges. Österreich 135, 117–128 (in German).

Juříček, M., 2012. Flora and vegetation of fishponds in the Bohemian-Moravian Highlands. Acta Rerum Nat. 13, 33–51.

Kaplan, Z., Danihelka, J., Štěpánková, J., Bureš, P., Zázvorka, J., Hroudová, Z., Ducháček, M., Grulich, V., Řepka, R., Dančák, M., Prančl, J., Šumberová, K., Wild, J., Trávníček, B., 2015. Distributions of vascular plants in the Czech Republic. Part 1. Preslia 87, 417–500.

Kaplan, Z., Danihelka, J., Štěpánková, J., Ekrt, L., Chrtek, J.Jr., Zázvorka, J., Grulich, V., Řepka, R., Prančl, J., Ducháček, M., Kúr, P., Šumberová, K., Brůna, J., 2016. Distributions of vascular plants in the Czech Republic. Part 2. Preslia 88, 229–322.

Kingsford, R.T., Basset, A., Jackson, L., 2016. Wetlands: conservation's poor cousins. Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 892–916.

Klotz, R.L., Linn, S.A., 2001. Influence of factors associated with water level drawdown on phosphorus release from sediments. Lake Reserv. Manag. 17, 48–54.

Kohler, A., Janauer, G.A., 1995. Zur Methodik der Untersuchung von aquatischen Makrophyten in Fließgewässern. In: Steinberg, C.H., Bernhardt, H., Klapper, H.

(Eds.), Handbuch Angewandte Limnologie Ecomed Verlag. Landsberg-Lech, pp. 1–22 (in German).

Kosten, S., Kamarainen, A., Jeppesen, E., Van Nes, E.H., Peeters, E.T., Mazzeo, N., Sass, L., Hauxwell, J., Hansel-Welch, N., Lauridsen, T.L., 2009. Climate-related differences in the dominance of submerged macrophytes in shallow lakes. Glob. Change Biol. 15, 2503–2517.

Lacoul, P., Freedman, B., 2006. Environmental influences on aquatic plants in freshwater ecosystems. Environ. Rev. 14, 89–136.

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multi-species responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24.

Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444, 71–84.

McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of Ecological Communities. MjM software design Gleneden Beach, Oregon.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. Vegan: Community Ecology Package, R Package, Version 2.5-2. https://CRAN.R-project.org/package=vegan.

Pechar, L., Přikryl, I., Faina, R., 2002. Fishpond management: ecological consequences. In: Květ, J., Jeník, J., Soukupová, L. (Eds.), Fresh Water Wetlands and Their Sustainable Future: A Case Study of the Třeboň Basin Biosphere Reserve, Czech Republic. Parthenon Pub. Group, UNESCO, Paris, pp. 31–169.

Phillips, G., Willby, N., Moss, B., 2016. Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? Aquat. Bot. 135, 37–45.

Pokorný, J., Květ, J., 2004. Aquatic plants and lake ecosystems. In: O'Sullivan, P.E., Reynolds, C.S. (Eds.), The Lakes Handbook Vol. 1, Limnology and Limnetic Ecology. Blackwell Sci. and Blackwell Publ., Malden, Oxford, Carlton, pp. 309–340.

Ramsar Convention on Wetlands, 2018. Global Wetland Outlook: State of the World's Wetlands and their Services to People. Ramsar Convention Secretariat, Gland, Switzerland. https://www.ramsar.org/sites/default/files/flipbooks/ramsar_gwo_english_web.pdf).

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for statistical computing, Vienna, Austria. http://www.R-project.org/.

Rejmánková, E., 2011. The role of macrophytes in wetland ecosystems. J. Ecol. Environ. 34, 333–345.

Roberts, D.W., 2016. Labdsv: Ordination and Multivariate Analysis for Ecology. R Package, Version 1.8-0. https://CRAN.R-project.org/package=labdsv.

Rogers, K., Breen, C., 1980. Growth and reproduction of *Potamogeton crispus* in a South African lake. J. Ecol. 68, 561–571.

Sayer, C.D., Davidson, T.A., Kelly, A., 2008. Ornamental lakes–an overlooked conservation resource? Aquat. Conserv. Mar. Freshw. Ecosyst. 18, 1046–1051.

Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J.J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M., Molinero, J.C., Mooij, W.M., Van Donk, E., Winde, M., 2012. Beyond the plankton ecology group (PEG) model: mechanisms driving plankton succession. Annu. Rev. Ecol. Evol. Syst. 43, 429–448.

Ten Winkel, E.H., Meulemans, J.T., 1984. Effects of fish upon submerged vegetation. Aquat. Microb. Ecol. 18, 157–158.

Ter Braak, C.J., Šmilauer, P., 2012. Canoco Reference Manual and User's Guide: Software for Ordination, Version 5.0. Microcomputer power, Ithaca.

Van der Velde, G., 1980. Studies in Nymphaeid-dominated Systems. Katholieke Universiteit te Nijmegen.

WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for Community action in the field of water policy. Off. J. Eur. Commun. L 327, 72.

Wezel, A., Arthaud, F., Dufloux, C., Renoud, F., Vallod, D., Robin, J., Sarrazin, B., 2013. Varied impact of land use on water and sediment parameters in fish ponds of the Dombes agro-ecosystem, France. Hydrol. Sci. J. 58, 854–871.

Wezel, A., Oertli, B., Rosset, V., Arthaud, F., Leroy, B., Smith, R., Angelibert, S., Bornette, G., Vallod, D., Robin, J., 2014. Biodiversity patterns of nutrient-rich fish ponds and implications for conservation. Limnology 15, 213–223.