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Macrozoobenthos assemblage patterns in European carp (*Cyprinus carpio*) ponds – the importance of emersed macrophyte beds

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Abstract – Qualitative and quantitative differences in benthic macrozoobenthos distribution in carp pond littoral zones (macrophyte areas; LM) and pelagic zones (macrophyte-free areas; MF) were assessed in four commercial carp (*Cyprinus carpio*) grow-out ponds in the Czech Republic (semi-intensive management) and Austria (organic management) monthly over the growing season (June-September) of 2016 and 2017. While differences in environmental parameters and granulometric composition between LM and MF were statistically non-significant ($p > 0.05$), organic matter content was significantly higher ($p < 0.05$) in LM. Average macrozoobenthos density and biomass in LM (mean 431 ind.m^{-2} and 6.78 g.m^{-2}) was usually significantly higher ($p > 0.05$) than MF (371 ind.m^{-2} and 3.17 g.m^{-2}). A similar trend was observed for zoobenthos diversity, with LM having a higher diversity (76 taxa) than MF (47 taxa). At the start of the growing season, chironomid density was higher ($p < 0.05$) in muddy MF zones, regardless of management type, while oligochaete density was higher in muddy LM. The density of both groups later declined, such that density was significantly higher ($p > 0.05$) in sandy substrates, regardless of habitat or management type. Our data suggest a significant drop in macrozoobenthos density and biomass compared with historical data, mainly due to new management techniques (fertilisation, supplementary feeding) and intensification (higher stock densities), suggesting that pond management is crucial as regards benthic invertebrate development and diversity. Our results indicate that emersed LM beds positively influence macrozoobenthos performance in carp ponds, potentially making them biodiversity hotspots. Further, LM beds can be regarded as invertebrate harbours, and hence should be protected and encouraged.

Keywords: Macroinvertebrates / fishpond / emergent macrophytes

Résumé – Schémas d'assemblage du macrozoobenthos dans les étangs à carpes européennes (*Cyprinus carpio*) – l'importance des herbiers de macrophytes. Des différences qualitatives et quantitatives dans la distribution du macrozoobenthos benthique dans les zones littorales des étangs à carpes (zones à macrophytes; LM) et les zones pélagiques (zones sans macrophytes; MF) ont été évaluées dans quatre étangs de grossissement de carpes commerciales (*Cyprinus carpio*) en République tchèque (gestion semi-intensive) et en Autriche (gestion écologique) chaque mois pendant la saison de croissance (juin-septembre) de 2016 et 2017. Alors que les différences de paramètres environnementaux et de composition granulométrique entre LM et MF étaient statistiquement non significatives ($p > 0,05$), la teneur en matière organique était significativement plus élevée ($p < 0.05$) dans LM. La densité moyenne du macrozoobenthos et la biomasse dans LM (moyenne de 431 ind. m^{-2} et 6,78 g. m^{-2}) étaient généralement significativement plus élevées ($p > 0.05$) que dans MF (371 ind. m^{-2} et 3,17 g. m^{-2}). Une tendance similaire a été observée pour la diversité du zoobenthos, LM présentant une diversité plus élevée (76 taxons) que MF (47 taxons). Au début de la saison de croissance, la densité des chironomes était plus élevée ($p < 0.05$) dans les zones MF boueuses, quel que soit le type de gestion, tandis que la densité des oligochètes était plus élevée dans les zones LM boueuses. La densité des deux groupes a ensuite diminué, de sorte que la densité était nettement plus élevée ($p > 0.05$) dans les substrats sableux, quel que soit le type d'habitat ou de gestion. Nos données

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suggèrent une baisse significative de la densité et de la biomasse du macrozoobenthos par rapport aux données historiques, principalement en raison de nouvelles techniques de gestion (fertilisation, alimentation complémentaire) et de l'intensification (densités de stock plus élevées), ce qui suggère que la gestion des étangs est cruciale en ce qui concerne le développement et la diversité des invertébrés benthiques. Nos résultats indiquent que les herbiers de LM émergéss influencent positivement la performance du macrozoobenthos dans les étangs à carpes, ce qui en fait potentiellement des points chauds de la biodiversité. En outre, les herbiers de LM peuvent être considérés comme des abris pour les invertébrés et doivent donc être protégés et encouragés.

Mots clés : Macroinvertébrés / étang de pisciculture / macrophytes émergents

1 Introduction

Ponds built for common carp production probably constitute the largest area of artificial wetland in Europe (Setlikova *et al.*, 2016). Many of these carp ponds were built on the former sites of marshes, swamps and floodplains, which, to a certain extent, predetermines their plant assemblage structure, which is often characterised by a eulittoral zone overgrown with 'hard' emergent vegetation consisting mostly of *Phragmites australis* and *Typha* sp. beds (Francova *et al.*, 2019). These shallow littoral areas, overgrown by emergent plant communities, accumulate higher amounts of sedimentary organic matter than deeper, open water areas (Dykyjova and Ulehlova, 1978). In the 1970s, a comprehensive evaluation of littoral zones was performed under the framework of the IBP (International Biological Programme) Wetland Project (Dykyjova and Kvet, 1978), which emphasised their essential role as regards the functioning of carp pond ecosystems and the provision of complex ecosystem services.

As a wetland habitat, littoral macrophyte beds provide many important ecosystem services, particularly as regards biodiversity, nature protection, water retention and mitigation of bank erosion (Cizkova *et al.*, 2019). Further, the aquatic macroinvertebrate community represents an important link in the productivity of lentic systems (James *et al.*, 1998), being an essential link in the food chain of pond ecosystems and one of the most important natural food components in common carp (*Cyprinus carpio*) nutrition (Weber and Brown, 2009; Rahman *et al.*, 2010). Monitoring of pond environments, therefore, need to focus not only on abiotic factors but also on planktonic and benthic invertebrates, whose abundance and diversity reflect the quality of the pond ecosystem (Dvorak and Imhof, 1998). The qualitative and quantitative composition of the invertebrate component in pond littoral zones can be negatively affected by hydromorphological degradation of the shoreline, which leads to loss of habitat and physical complexity (Strayer and Findlay, 2010; Brauns *et al.*, 2011). As such, littoral invertebrates are considered as bioindicators for assessing the hydromorphological state of ponds and lakes (Moss *et al.*, 2003; Miler *et al.*, 2013), while macroinvertebrates in deeper waters clear of macrophytes are used to assess the pond's trophic status (Saether, 1979).

Submergent and emergent littoral zone vegetation is an integral part of the aquatic environment (Bazzanti *et al.*, 2010). In carp ponds, littoral macrophyte habitats are valuable ecosystem components with high relevance for their appropriate functioning (Francova *et al.*, 2019). The ecotones formed by pond littoral zone vegetation increase local biodiversity compared to open, macrophyte-free areas (Dvorak and Imhof, 1998; Petr, 2000; Wetzel, 2001). Several studies on carp pondshave examined phytophilous invertebrates colonising the stems and leaves of littoral macrophytes (Sychra and Adamek, 2010; Sychra *et al.*, 2010; Setlikova *et al.*, 2016); however, data on macroinvertebrates living in littoral macrophyte substrate and root systems is largely missing. Owing to the high heterogeneity of bottom substrates, obtaining zoobenthos samples in littoral beds can be difficult, not least due to the presence of plant roots and dead parts in various stages of decomposition. As such, sampling of carp pond macrozoobenthos has been almost exclusively carried out in macrophyte-free areas (Lellak, 1969; Matena, 1989), which are more homogeneous than pond littoral zones. Further, qualitative and quantitative macrozoobenthos composition will differ in sediments overgrown by 'hard' emersed plants and macrophyte-free bottoms. While previous studies have provided data on environmental factors influencing the performance of benthic invertebrates in aquatic macrophyte root systems (Sagova *et al.*, 1993; Sagova-Mareckova, 2002a, b; Sagova-Mareckova and Kvet, 2002), these studies were performed in fishless water bodies; hence, while relevant, their conclusions may not compare well with conditions in carp aquaculture ponds. To increase our knowledge of macroinvertebrate community functioning in carp ponds, therefore, we monitored the macrozoobenthos of both macrophyte-free areas (herein MF) and the substrate and root systems of littoral macrophyte areas (herein LM) in a series of carp ponds under either semi-intensive or organic management.

2 Material and methods

2.1 Study sites

In total, eight on-growing carp ponds were selected for the purposes of this study (Tab. 1), four in the Blatná and Hluboká regions of South Bohemia (Czech Republic; 410–460 m a.s.l.) and four in the Waldviertel region of Niederösterreich (Austria; 639–661 m a.s.l.). All of the ponds are located in three watersheds (Lomnice, Lužnice and Otava) of the River Vltava drainage area (Fig. 1). The four Austrian fishponds employ organic (ORG) management methods (for details see Adamek *et al.*, 2019; Anton-Pardo *et al.*, 2020), while the Czech fishponds employ conventional (CONV) semi-intensive methods (Tab. 1). Four of the ponds (two Austrian and two Czech) have a muddy (MU) bottom (Neuteich (NEU), Langerteich (LAN), Podsilniční (POD), Šnekl (SNE)), while the other four (Haslauerteich (HAS), Gebhartsteich (GEB),

Table 1. Stocking rates at the study ponds.

Pond	Fish species	Category	ind.ha^{-1}	kg.ha^{-1}
NEU/ORG	CC	yearling	1255	85.4
	CL	yearling	141	3.7
LAN/ORG	CC	yearling	1264	148.7
	SL	yearling	97	1.9
	TT	spawner	23	10.6
HAS/ORG	CC	two- to three-year-old	245	166.9
	TT	three-year-old	57	13.1
	CL	yearling	19	0.5
	EL	yearling	15	5.3
	SL	one- to three-year-old	16	4.8
GEB/ORG	CC	two- to three- year-old	208	219.8
	TT	three-year-old	61	18.2
SNE/CONV	CC	sac fry	175 000	
POD/CONV	CC	two-year-old	979	244.8
	EL	sac fry	2577	
PAN/CONV	CC	three-year-old	492	369.2
SKA/CONV	CC	three-year-old	704	478.5
	EL	yearling	12	2.3

Fish abbreviations: CC = common carp *Cyprinus carpio*; CL = common whitefish *Coregonus lavaretus*; TT = tench *Tincatinca*; EL = Northern pike *Esox lucius*; SL = pikeperch *Sander lucioperca*. For pond abbreviations see Table 2. Other abbreviations: ORG = organic management, CONV = conventional management.

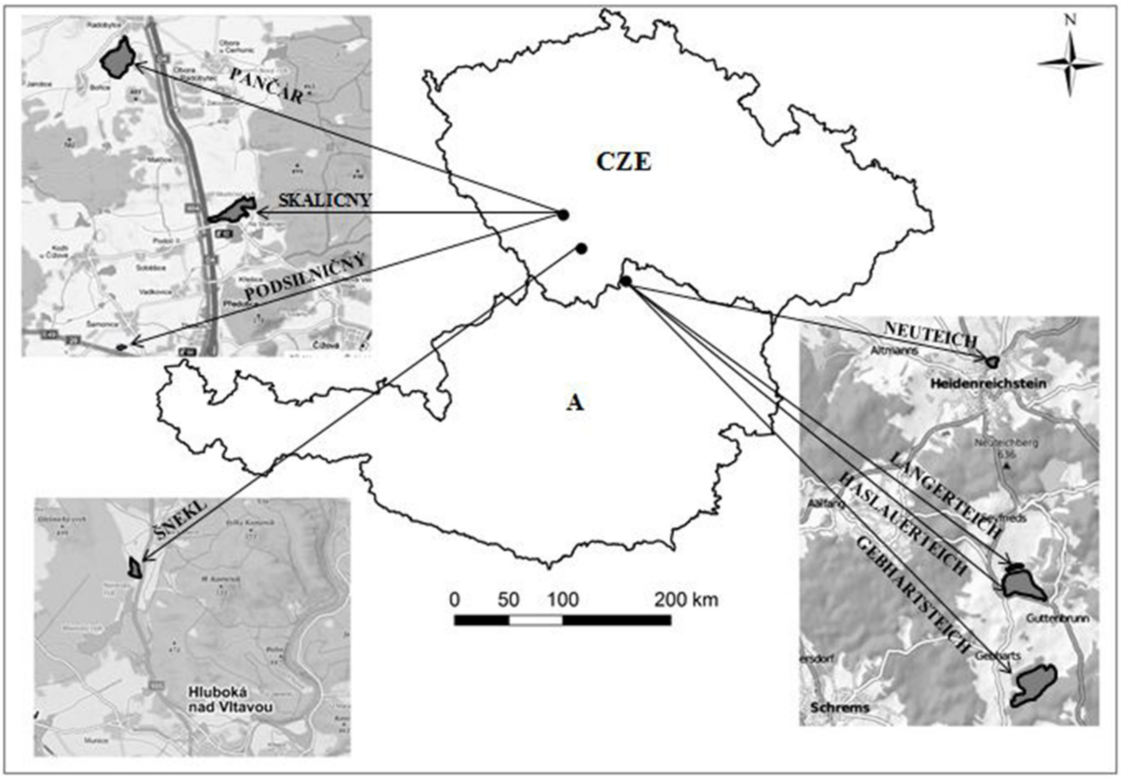

Fig. 1. Location of the ponds used in this study.

Skaličný (SKA) and Pančár (PAN)) are characterised by mostly sandy (SA) bottoms (Tab. 2). All of the ponds have a regularly developed 1–5 m wide littoral area with emersed vegetation creating an interface between the terrestrial and aquatic zones. The littoral macrophyte belts are mainly comprised of common reed (*Phragmites australis*), supplemented by patches of cattail (*Typha* sp.) and watergrass (*Glyceria* sp.), the whole corresponding to the foederatio-*Phragmition communis* classification provided by Hejny and Husak (1978).

Table 2. Main characteristics of the eight study ponds.

Pond name	Abbreviation	Country	No. of samples	Prevailing substrate	Pond area	Management	GPS position
Neuteich	NEU	AUT	40	muddy	4.10	organic	48.871N, 15.123E
Langerteich	LAN	AUT	40	muddy	2.69	organic	48.826N, 15.134E
Haslauerteich	HAS	AUT	40	sandy	48.45	organic	48.821N, 15.134E
Gebhartsteich	GEB	AUT	40	sandy	57.00	organic	48.799N, 15.138E
Šnekl	SNE	CZE	30	muddy	4.00	conventional	49.091N, 14.411E
Podsilniční	POD	CZE	40	muddy	1.94	conventional	49.354N, 14.029E
Pančár	PAN	CZE	40	sandy	34.33	conventional	49.407N, 14.028E
Skaličný	SKA	CZE	40	sandy	21.45	conventional	49.378N, 14.061E

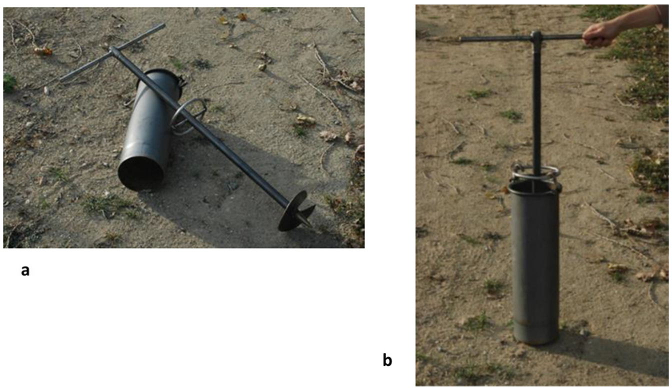

Fig. 2. Drilling core sampler: (a) disassembled before use, (b) assembled and ready to collect a sediment sample.

2.2 Sampling technique and sample processing

Physico-chemical environmental indicators were monitored before macrozoobenthos sampling commenced. In each fishpond, five replicates of each variable, that is, oxygen concentration and saturation, temperature (YSI ProODO, YSI Inc./Xylem Inc., USA), pH (YSI 63 meter, YSI Inc./Xylem Inc., USA) and conductivity (EC Testr 11+, Eutech Instruments Ltd., Singapore), were measured at a depth of 20 cm.

Sampling was performed at monthly intervals during the growing season (May – September) of 2016 and 2017. Five replicate substrate samples were obtained from the LM and MF areasof each pond using a drilling core sampler (Fig. 2; Adamek and Sychra, 2012). Where possible, samples were taken up to a depth of 10 cm (deeper penetration below this limit was impossible in sandy substrate), with a sample volume of between 1.5 and 2 L, depending on the substrate structure and root density.

Once collected, the samples were preserved in 4% buffered formaldehyde and, after three-months storage, macroinvertebrates were separated out and placed into three groups, namely Chironomidae, Oligochaeta and Varia (others), which included irregularly or sporadically occurring taxa such as Nematoda, Hirudinea, Mollusca, Isopoda, Acari, Hemiptera, Ephemeroptera, Megaloptera, Odonata, Trichoptera, Coleoptera, Ceratopogonidae, Limoniidae, Tabanidae, Ephydridae, Chaoboridae, Simuliidae and Cecidomyiidae. For each group, density (ind.m^{-2}) and biomass (g.m^{-2}) were determined. Invertebrates were determined to lowest possible taxonomical level (mostly species) using common and, when appropriate, updated keys. Samples of bottom substrate were also taken at each locality, again using the drilling core sampler, in order to determine particle size structure (granulometry) and content of organic substance, the latter assessed by loss on ignition.

2.3 Statistics

The density of zoobenthos (Oligochaeta and Chironomidae) was calculated for each interaction/factor separately as well as between factors, that is, habitat (LM × MF), management (ORG × CONV) and substrate (SA × MU). Varia were not assessed for density due to their sporadic and irregular occurrence; however, this group was determined to the lowest possible taxa, thus the number of taxa could be compared between habitats (LM and MF). Varia were included into total biomass (g.m^{-2}), thus biomass includes all benthic invertebrates. In order to compare bottom fauna density and biomass, we used factorial analysis of variance (Factorial ANOVA) in the software packages STATISTICA 12 (StatSoft, USA) and Statistix 8.1 (Analytical software, 2003), taking into account different factors such as substrate and/or management. Least significant difference (LSD) at the 5% level was used for multiple comparison tests between interactions. Differences in environmental variables were assessed using the non-parametric Mann–Whitney U test in STATISTICA 12 (StatSoft, USA). Environmental variables were only measured to assess their suitability for fish and bottom fauna, thus interactions between pond environments were omitted.

3 Results

3.1 Environmental variables

Briefly, environmental variables did not differ significantly between ponds. While smaller and larger differences were recorded between LM and MF areas, all differences were non-significant (Fig. 3). Differences in granulometric composition between the LM and MF area were statistically non-significant ($p > 0.05$). As expected, organic matter content was significantly higher ($p < 0.05$) in LM areas (Tab. 3).

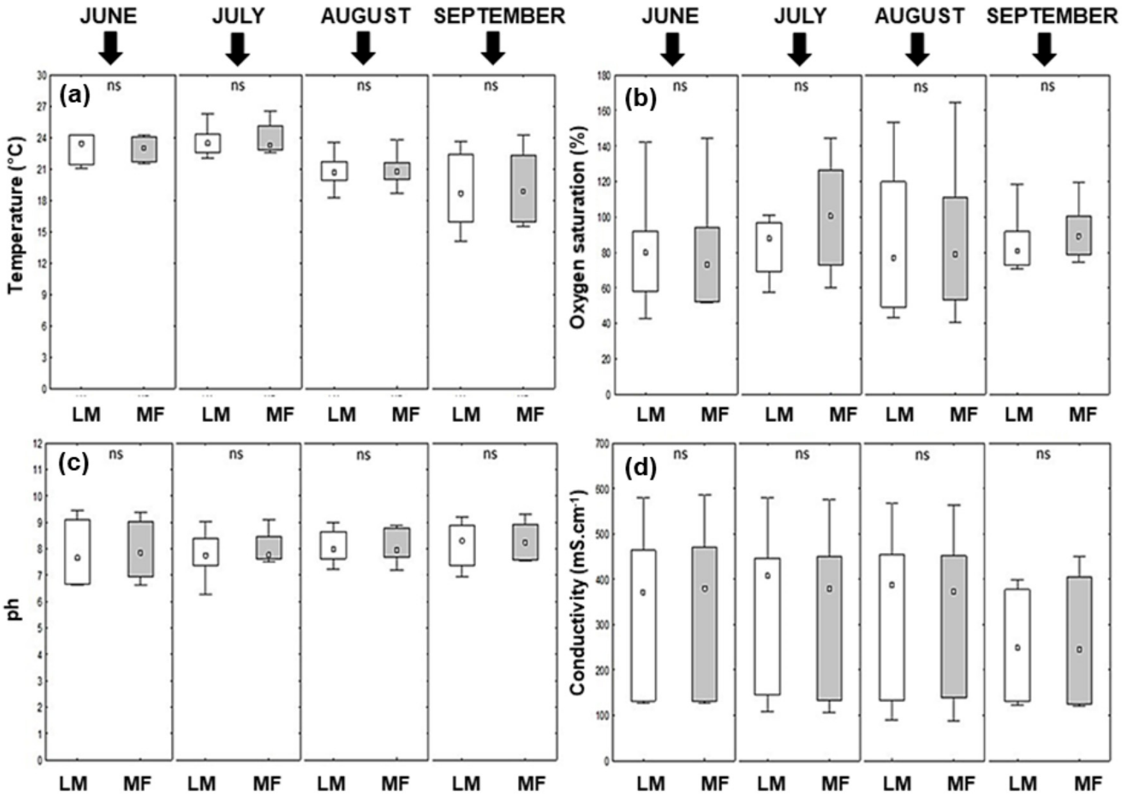

Fig. 3. Box plots for average monthly environmental variable values in the littoral macrophyte (LM) and macrophyte-free (MF) areas: (a) temperature, (b) oxygen saturation (%), (c) pH, (d) conductivity. Note: central square = median, box = interquartile range, whiskers = non-outlier range (1.5 × interquartile range), points = outliers, ns = non-significant (p > 0.05).

Table 3. Mean values ± SD for granulometric composition (%) and organic matter content (%) in the littoral macrophyte (LM) and macrophyte-free (MF) areas.

Size of grains (μm)	LM	MF	*p*
>3000	13.38 ± 7.79	9.38 ± 6.49	ns
710–3000	32.22 ± 16.04	32.73 ± 16.79	ns
500–709	13.65 ± 5.02	13.48 ± 3.37	ns
250–500	25.43 ± 12.82	28.28 ± 11.17	ns
106–250	12.64 ± 8.35	13.58 ± 6.37	ns
53–106	1.89 ± 2.07	1.70 ± 1.54	ns
<53	0.49 ± 0.52	0.42 ± 0.52	ns
Organic matter (%)	5.21 ± 3.55	2.14 ± 1.43	*

Note: ns = non-significant, *$p < 0.05$.

3.2 Macrozoobenthos assemblage

Chironomid density was significantly higher ($p < 0.05$) in the MF areas in June (LM = 421 ind.l^{-1}, MF = 596 ind.l^{-1}), regardless of pond management or substrate; in September, however, chironomid density was significantly higher ($p < 0.05$) in the LM areas (LM = 388 ind.l^{-1}, MF = 171 ind.l^{-1}; Fig. 4a). Oligochaete numbers did not differ significantly ($p > 0.05$) between the LM and MF areas throughout the growing season (Fig. 4b). While there was no significant difference ($p > 0.05$) in the total biomass of benthic invertebrates over the growing season, biomass was usually higher in the LM areas, reaching a maximum in September (11.41 g.m^{-2}) and minimum in August (3.84 g.m^{-2}; Fig. 4c). In comparison, highest total biomass in the MF areas was recorded in June (6.20 g.m^{-2}) and the lowest in August (1.41 g.m^{-2}; Fig. 4c). When comparing MU and SA substrates in the LM and MF areas, chironomid density was significantly higher in MU in June,whereas non-significantly ($p > 0.05$) in SA in July and significantly higher ($p < 0.05$) in August and September (Fig. 5a). Highest mean oligochaete density was recorded in MU substrate in June and July at LM (1077 and 1085 ind.l^{-1}, respectively), levels being significantly higher ($p < 0.05$) than MF in July. No significant differences ($p > 0.05$) were recorded in substrate between the MF and LM areas (Fig. 5c). Chironomid density was significantly higher ($p < 0.05$) in LM areas under CONV management in June and September (Fig. 5b), while oligochaete density was higher in both LM and MF areas in ORG ponds (Fig. 5d). Macrozoobenthos biomass was usually slightly higher in LM areas in both MU and SA substrates, except for non-significant ($p > 0.05$) differences in MU substrate in August and September (Fig. 5e). Higher, though non-significant ($p > 0.05$), biomass values were generally recorded in CONV ponds,except for August ($p > 0.05$) and September ($p < 0.05$), when biomass values were higher in ORG ponds at the start of the growing season, though less so over the rest of the season (Fig. 5f). Assessments of mean macrozoobenthos density (ind.m^{-2}) and biomass (g.m^{-2}), and their interactions with habitat, pond management and substrate,

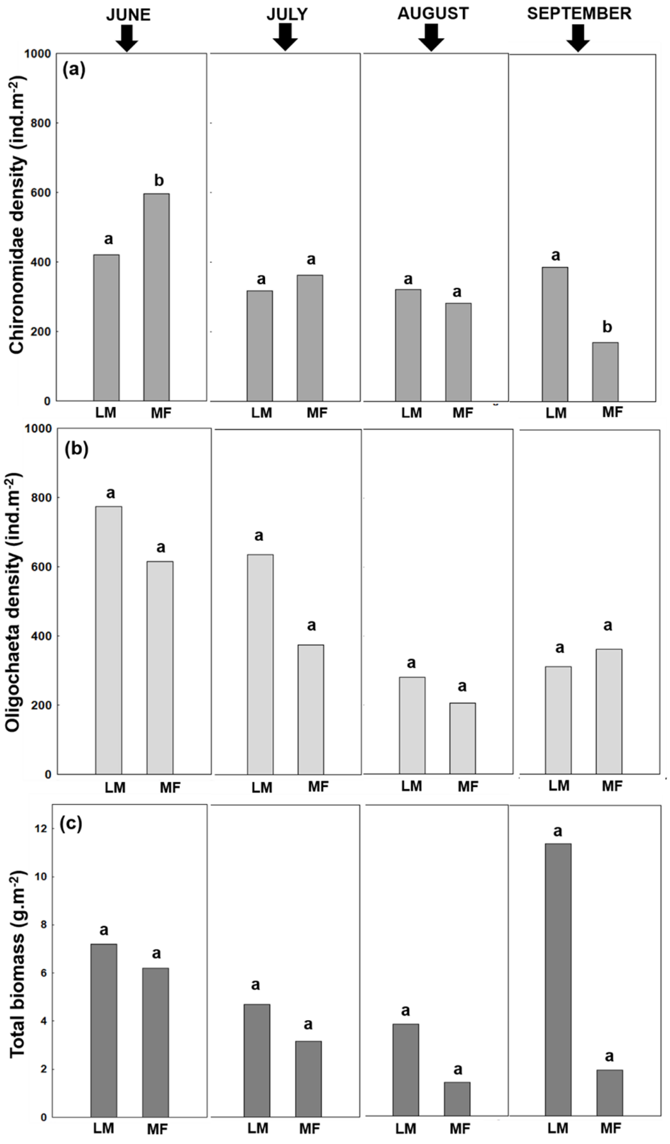

Fig. 4. Macrozoobenthos density (ind.m^{-2}) and biomass (g.m^{-2}) in the littoral macrophyte (LM) and macrophyte-free (MF) areas: (a) chironomid density in ind.m^{-2}, (b) oligochaete density in ind.m^{-2}, (c) total biomass in g.m^{-2}.

showed that chironomid density was mostly higher in MF areas when considering management and substrate, except for MF CONV SA (248 ind.m^{-2}), where values were significantly lower ($p < 0.05$) than at LM CONV SA (576 ind.m^{-2}; Tab. 4). Oligochaete density showed the opposite trend, with mean levels mostly higher (though not significantly so) in LM areas in relation to management and substrate, the one exception being in LM ORG SA, where mean values were lower than at MF ORG SA. Biomass was generally higher in LM areas (non-significant), except for LM CONV MU (4.14 g.m^{-2}), which was lower than MF CONV MU (6.24 g.m^{-2}), though again the difference was non-significant ($p > 0.05$).

Altogether, 76 and 47 benthic macroinvertebrate taxa were recorded in the LM and MF areas, respectively. On average, eight (range: 3–17) taxa were recorded in LM and six (3–12) in MF areas per sampling ($p > 0.05$; Appendix 1). The corresponding Shannon-Wiener index for the complete dataset showed a higher macrozoobenthos diversity in LM areas (2.958) compared with MF areas (2.461). Tubificids (mostly Tubificidae g. sp., *Limnodrilus hoffmeisteri* and *Tubifex tubifex*) and naidids (mainly *Bothrioneurumvejdovskyanum*, *Stylaria lacustris* and *Ophidonais serpentina*) were the dominant benthic invertebrates in both habitats, except for *Stylaria* which occurred exclusively at LM sites (Appendix 1). The blackworm (*Lumbriculus variegatus*) was also recorded in higher numbers in LM areas (40.2 ind. on average) than MF areas (4.6 ind.). Chironomids, mainly the subfamilies Chironominae (genera *Chironomus*, *Endochironomus*, *Glyptotendipes*, *Polypedilum* and others) and Tanypodinae (*Procladius* sp.), were frequent in both habitats, though there were marked differences in densities recorded. While *Glyptotendipes*, *Microtendipespedellus* gr., *Synendotendipes* and *Kiefferulustendipediformes* were more abundant in LM areas, *Chironomus*, *Endochironomus* and *Polypedilum* occurred more frequently, or exclusively (*Einfeldiadissidens*), in MF areas (Appendix 1). Representatives of leeches (Hirudinea: mainly *Helobdella stagnalis* and *Erpobdella octoculata*), snails (Gastropoda), the water louse (*Asellus aquaticus* and *Proasellus coxalis*), water bugs (Hemiptera: *Sigara* and others) and aquatic insect larvae (Ephemeroptera, Odonata and Trichoptera)and water beetles (Coleoptera) occurred almost exclusively in LM areas.

4 Discussion

4.1 Environmental variables

While no significant differences ($p > 0.05$) were recorded in environmental variables between LM and MF areas in the ponds, some of the differences were worth noting. Aside from June (mid-summer), water temperatures, for example, were usually lower in LM areasdue to shading from the emersed vegetation. Similarly, oxygen concentrations and saturation values were also lower over the same period (again, not in June) due to the decomposition of accumulated organic matter, which was significantly higher ($p < 0.05$) in LM areas (Tab. 3). A decrease in pH and oxygen saturation (Fig. 3) was previously documented by Sychra *et al.* (2010) in extensive reed beds just one metre from the open water zone, while Ulehlova and Pribil (1978) confirmed that decomposition processes in the pond littoral resulted in an increase in CO_2 production, causing a concomitant drop in pH in relation to the carbonate equilibrium.

4.2 Macrozoobenthos assemblage

As the bottom substrate of carp pond macrophyte beds is heavily overgrown with rhizomes, tillers and roots (Fiala, 1978), the quantitative evaluation of macrozoobenthos is methodologically demanding and usually requires laborious manipulation of specialised sampling devices. As a result, most of the few studies that have been undertaken have focused primarily on phytophilic organisms (Korinkova, 1971; Dvorak, 1978; Sychra *et al.*, 2010), that is, those associated

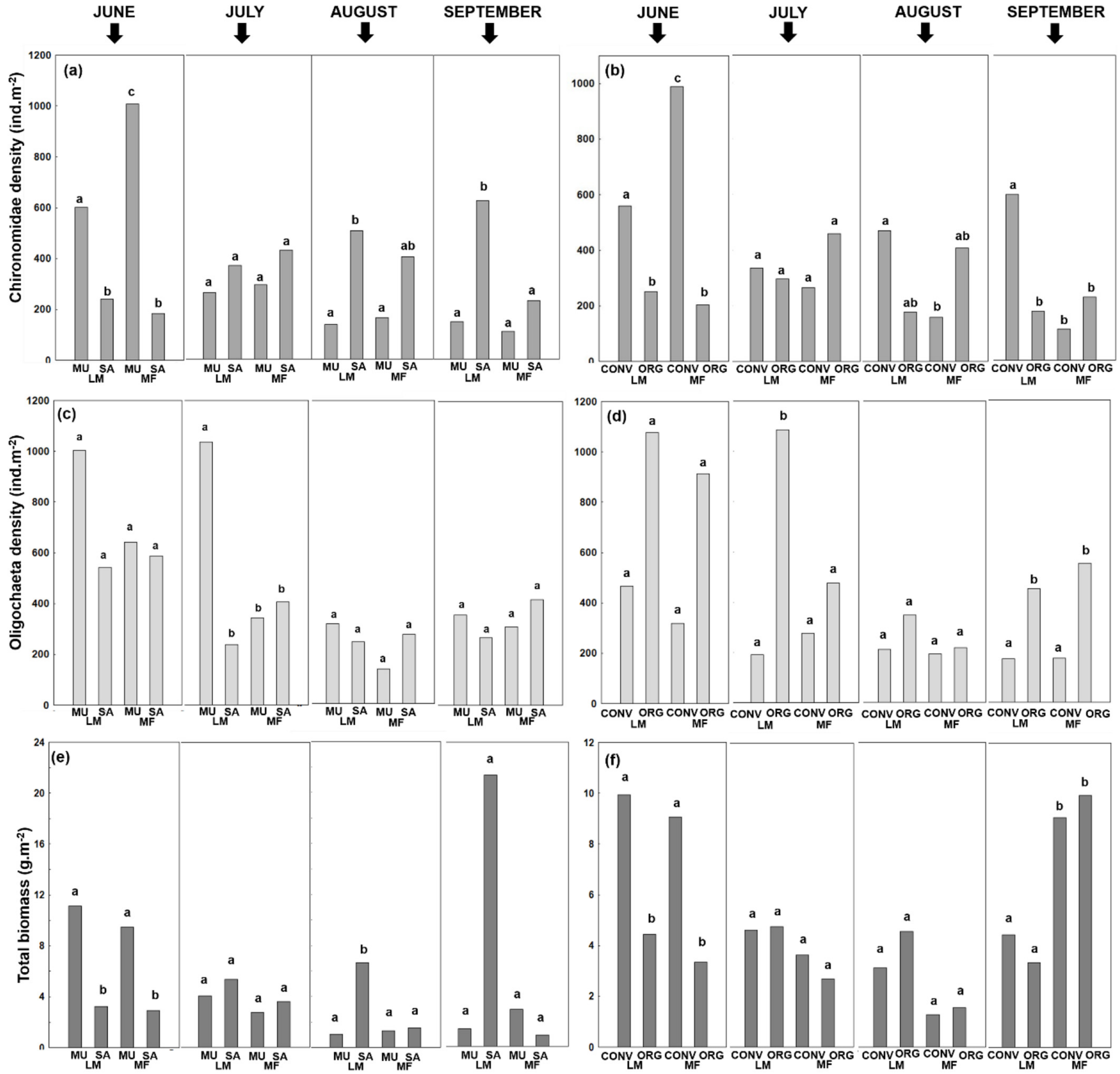

Fig. 5. Macrozoobenthos density (ind.m^{-2}) and biomass (g.m^{-2}) in the study ponds throughout the sampling period: (a) chironomid density (ind.m^{-2}) and (c) oligochaete density (ind.m^{-2}) in littoral macrophyte (LM) and macrophyte-free (MF) areas with different substrates (MU = muddy, SA = sandy), (b) chironomid density (ind.m^{-2}) and (d) oligochaete density (ind.m^{-2}) in LM and MF areas under different management (ORG = organic, CO = conventional), (e) macrozoobenthos biomass (g.m^{-2}) in LM and MF areas with different substrates (MU = muddy, SA = sandy), (d) macrozoobenthos biomass (g.m^{-2}) in LM and MF areas under different management (ORG = organic, CO = conventional). Note: All values expressed as means. Means with different superscripts show significant differences between interactions within a taxa group (Chironomidae or Oligochaeta) and month (LSD test, $p < 0.05$).

with submerged plant stems and leaves between the pond bottom and the water's surface, and have avoided the plant root systems. Sychra *et al.* (2010), for example, used a benthic sweep net to monitor the density and composition of phytophilic macroinvertebrates living in LM beds close to the bank and close to open water. They found that tubificids (Oligochaeta), leeches (Hirudinea), water mites (Hydrachnidia), corixids (Corixidae) and caddisfly (Trichoptera) larvae (free-swimming and free-moving invertebrates with tracheal gill breathing, ectoparasites, gatherers/collectors and taxa preferring pelal and inorganic substrates) were all more abundant nearer to open waters, while those habitats closer to the shore were characterised by naidids and enchytraeids (Oligochaeta), aquatic snails (Gastropoda), the water louse, aquatic beetles (Coleoptera) and dipteran (Diptera) larvae, representing grazers and scrapers, shredders and invertebrates

Table 4. Mean macrozoobenthos density (ind.m^{-2}) and biomass (g.m^{-2}) at the study ponds over the sampling period, with different interactions representing particular ponds.

Ponds	Interaction	Density (ind.m^{-2})		Biomass (g.m^{-2})
		Chironomidae	Oligochaeta	
POD, SNE	LM*CO*MU	333^{ab}	92^{a}	4.14^{a}
	MF*CO*MU	527^{ca}	85^{a}	6.24^{ab}
NEU, LANG	LM*ORG*MU	212^{b}	1276^{b}	3.85^{a}
	MF*ORG*MU	256^{b}	683^{c}	1.84^{a}
GEB, HAS	LM*ORG*SA	255^{b}	212^{a}	14.59^{b}
	MF*ORG*SA	378^{abc}	445^{ac}	2.68^{a}
PAN, SKA	LM*CO*SA	576^{c}	466^{ac}	4.40^{a}
	MF*CO*SA	248^{b}	406^{ac}	1.78^{a}

Means values with different superscripts indicate significant differences (LSD test, $p < 0.05$) between interactions within a taxa group (Chironomidae and Oligochaeta).
Ponds: POD = Podsilniční, SNE = Šnekl, NEU = Neuteich, LANG = Langerteich, GEB = Gebhartsteich, HAS = Haslauerteich, PAN – Pančár, SKA – Skaličný; Habitat: LM = littoral macrophyte area, MF = macrophyte-free area. Management: CO = conventional, ORG = organic; Substrate: MU = muddy, SA = sandy.

preferring phytal and particulate organic matter microhabitats. Despite only sampling with a benthic sweep net, therefore, Sychra *et al.* (2010) were able to show that LM areas provide valuable habitat for a wide range of aquatic invertebrate taxa suited to more open-water areas and shallower bankside zones. Nevertheless, this form of sampling ignores another important macroinvertebrate habitat, the roots themselves and the bottom substrate; hence, important data is missed that would affect biomass, diversity and community scores. To address this, we employed a littoral drilling corer that is capable of penetrating the plant root systems and collecting all organisms in the upper 10 cm layer of muddy substrates. By using this novel approach, we were able to provide the first quantitative data on benthic animals in the substrate of pond macrophyte beds, previous (sporadic) data having been limited mainly to qualitative data.

In two of the few studies to have examined invertebrates in the substrate of pond macrophyte beds, Sagova *et al.*, (1993) and Sagova-Mareckova (2002a,b) examined the presence of colonising macroinvertebrates in pond LM areas, based on the premise that the roots of aquatic macrophytes provide oxygen that is subsequently released into the sediment (Sagova-Mareckova and Kvet, 2002). However, they found that this hypothesis was only strictly true in fishless water bodies. In comparison, the environmental conditions in carp pond littoral zones (both ours and other studies, *e.g.* Sychra *et al.*, 2010) differed considerably from those of fishless lentic habitats, being typified by lower oxygen concentration and saturation.

In our study, highest oligochaete and chironomid densities were recorded at all sites, regardless of substrate or pond management type, at the beginning of the growing season, that is, June. While biomass values in LM areas increased toward the end of growing season, mainly connected with the growth of aquatic insect larvae, overall macrozoobenthos abundance decreasedslightly, probably connected with increased grazing pressure by carp (see Anton-Pardo *et al.*, 2014) along with the emergence of adult aquatic insect stages (mostly chironomids; Matena, 1989). In a previous study, Dvorak (1978) provided early quantitative figures for pond LM macroinvertebrates, finding a mean density of 20 346 ind.m^{-2} and a biomass of 66.04 g.m^{-2}, figures many times higher than those in this study. Unfortunately, Dvorak (1978) does not mention the methods used for macroinvertebrate sampling; however, from the species list (dominance of chironomids, absence of oligochaetes) and sampling area description ("inner littoral in contact with fishpond pelagial 1-m distance from open water"), it is highly likely that the data are describing phytophilic invertebrates. Nevertheless, these data emphasise the importance of littoral zones for the production potential and capacity of carp pond ecosystems, as supported by our own data indicating a generally higher macrozoobenthos abundance in pond LM zones (Figs. 4a–c; Tab. 4), most likely associated with poorer fish access and increased cover reducing predation pressure (Sychra *et al.*, 2010) which, in turn, allows them to increase in size over the growing season.

As with the whole agricultural sector, fish farming has undergone significant intensification and diversification of production over the last century. In particular, new technological measureswere brought into carp pond management to enhance fish growth performance, including increased stocking densities, fertilisation, supplementary feeding and liming. These intensification practices, together with the influence of municipal and agricultural runoff and nutrient deposition, has led to a situation where most Czech carp ponds are considered eutrophic, or even hypertrophic (Pechar, 2000). These factors, alongside others, have resulted in lowered macrozoobenthos abundance and diversity, with values now much lower than those recorded in studies from the 1950s to 1970s. Lellak (1957), for example, recorded benthic invertebrate abundances ranging from 5955 to 12 400 ind.m^{-2}, while Korinkova (1971) calculated an average annual phytophilic organism density of 6240 ind.m^{-2}, significantly more than found in our study in LM areas. Further examination of our data suggests that fish stock and management type are important drivers affecting zoobenthos density and biomass. As shown in Figures 4 and 5, the patterns of carp pond macrozoobenthos density were somewhat ambivalent. In terms of pond management (ORG x CONV), similarly ambiguous results were obtained by Anton-Pardo *et al.* (2020), who evaluated zooplankton levels alongside macrozoobenthos density and biomass in carp ponds under conventional and organic management. Volatility in the density and biomass of macrozoobenthos could be caused by supplementary feeding practices, including where exactly it is provided. Adamek *et al.* (2016), for example, showed that macrozoobenthos density and biomass were significantly lower at those sites in a pond where feed cereals were dropped. Further, adult carp are commonly benthic feeders, showing a particular preference for chironomid larvae and pupae (Spataru *et al.*, 1980). This leads to a steeper decline in zoobenthos density in MF areas through the growing season as the prey are more easily available to carp grazing than in LM areas (Figs. 4a and 4b).

4.3 Importance of aquatic macrophyte beds for macrozoobenthos

With respect to carp food resources, the macrophyte mesohabitat plays two essential roles in the pond ecosystem, that is, it lowers carp predation pressure (Diehl and Kornijow, 1998) and increases the area colonised by aquatic invertebrates, including their developmental stages and air-breathing adults (Della Bella *et al.*, 2005; Sychra *et al.*, 2010), which provide a rich source of food as they become available at the macrophyte/open water interface (Newman, 1991). In our study, the occurrence of numerous benthic macroinvertebrate taxa was associated exclusively (or almost exclusively) with LM areas. This phenomenon is well known and has been described in various studies dealing with the phytophilic macroinvertebrates colonising macrophytes in pond littoral habitats (*e.g.* Dvorak and Imhof, 1998; Sychra and Adamek, 2010; Sychra *et al.*, 2010). The plant beds covering the littoral zone of ponds create ecotones, which frequently prove to have biodiversity higher than adjacent terrestrial and aquatic habitats (Pieczynska, 1972; Petr, 2000; Zbikowski and Kobak, 2007), the aquatic macrophytes being colonised by invertebrates as a life substrate, for direct feeding, for periphyton grazing (Soszka, 1975) or as a protection against foraging by fish (Petr, 2000). We also recorded a higher biodiversity of macroinvertebrates colonising the bottom substrate of LM areas compared to the MF pond bottom. It should be noted, however, that these higher diversity figures are not only associated with their direct occurrence on the pond bottom but probably also due to the inclusion of invertebrates from macrophytes during insertion of the sampling apparatus. This latter is probably the cause of the inclusion of such taxa as water bugs (*Sigara* and *Notonecta*), water beetles (*Donacia*, *Noterus* and others) and possibly some others (*e.g.* gastropods, mayfly *Cloeondipterum*, damselflies *Coenagrion* and *Ischnura*) in our samples, although their occasional occurrence directly on the bottom cannot be excluded.

5 Conclusion

This study provides the first truly quantitative data on the density and biomass of aquatic macroinvertebrates colonising the substrate and root systems in emersed macrophyte beds of the carp pond littoral. Macroinvertebrate density and biomass were generally higher in LM areas than that recorded in MF areas, with biodiversity in particular being significantly higher in the pond LM zone. Substrate and pond management type (CONV vs. ORG) were important driving factors shaping the macrozoobenthos communities observed in this study. We observed a dramatic drop in macrozoobenthos density and biomass compared with data from the 1950s to 1970s, primarily due to current management practices linked with production intensification. Our results suggest that emersed LM beds positively influence macrozoobenthosdensity and biomass when they form an integral part of carp pond ecosystems, potentially making them important biodiversity hotspots. Further, LM beds can be regarded as invertebrate harbours, and hence should be protected and encouraged.

Conflict of interest

The authors declare that they have no conflict of interest.

Supplementary Material

Supplementary Table S1. Original data zoobenthos.

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2021008/olm.

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Appendix 1: Macroinvertebrate taxa and their mean density (ind.m^{-2}) in the study ponds in 2016 and 2017.

Macroinvertebrate taxa	LM	MF
Nematoda sp.	0.8	
Dero digitata	2.4	6.9
Nais elinguis	0.5	0.4
Ophidonais serpentina	9.5	4.9
Slavina appendiculata		0.5
Stylaria	14.7	
Bothrioneurum vejdovskyanum	4.8	16.3
Psammoryctides barbatus	0.5	17.2
Limnodrilus hoffmeisteri	43.1	47.0
Tubifex tubifex	50.3	37.8
Tubificidae g.sp.	201.4	188.2
Branchiura sowerbyi	0.9	3.4
Lumbriculus variegatus	40.2	4.6
Eiseniella tetraedra	0.5	0.5
Erpobdella octoculata	19.1	3.5
Helobdella stagnalis	27.8	0.8
Alboglossiphonia heteroclita	2.9	0.8
Hemiclepsis marginata	3.8	
Lymnaea stagnalis	1.4	
Radix auricularia	0.5	
Physella acuta	0.4	
Gyraulus albus	0.4	
Planorbarius corneus	0.5	
Musculinum lacustre	0.9	0.4
Cristatella mucedo	+	
Asellus aquaticus	9.2	0.4
Proasellus coxalis	9.6	0.8
Eylais sp.	0.5	
Ranatra linearis		0.4
Ilyocoris cimicoides	1.3	0.4
Sigara falleni	4.3	0.4
Sigara sp. juv.	3.4	
Notonecta sp. juv.	0.5	
Corixa sp. juv.	1.0	0.5
Cloeon dipterum	5.1	1.2
Caenis lactea	0.4	
Caenis horaria	1.9	
Caenis robusta	0.5	
Sialis lutaria	0.4	0.5
Orthetrum cancellatum	1.4	1.0
Coenagrion sp.	0.4	
Ischnura elegans	0.5	
Aeschna sp. juv.	0.5	
Sialis lutaria	0.5	
Anabolia furcata	0.4	
Limnephilus fuscicornis	1.5	0.4
Limnephilus sp. juv.	0.9	0.4
Haliplus sp. larva	0.5	
Donacia sp. larva	1.9	
Hyphydrus ovatus	0.5	
Noterus crassicornis	0.5	
Noterus sp. larva	1.4	
Clinotanypus nervosus	0.4	0.4
Chironomus plumosus	63.8	105.4
Chironomus sp. juv.		3.9
Endochironomus albipennis	2.4	
Endochironomus sp.	9.6	16.0
Cryptochironomus cf. *obreptans*	2.4	
Cryptochironomus sp.		0.5
Parachironomus varus	0.5	0.9
Glyptotendipes barbipes	7.2	1.1
Glyptotendipes sp.	51.2	29.7
Microtendipes pedellus gr.	15.3	5.7
Synendotendipes sp.	6.8	2.3
Paratendipes albimannus gr.	1.0	
Polypedilum nubeculosum	18.4	31.0
Polypedilum sp.		1.1
Procladius sp.	27.9	23.3
Psectrocladius psilopterus gr.	2.9	
Cricotopus sp.	4.3	1.6
Acricotopus lucens		0.5
Ablabesmyia sp.	0.5	
Kiefferulus tendipediformis	8.7	
Phaenopsectra sp.		2.9
Einfeldia dissidens		18.3
Einfeldia sp.	0.5	
Ceratopogonidae g.sp.	0.5	4.6
Gonomyia sp.	3.9	
Tabanidae g.sp.juv.	0.5	
Hydrellia sp.	0.5	
Chaoborus crystallinus	9.6	2.0
Chaoborus flavicans	5.8	3.7
Simulium noelleri	0.5	
Ephydridae g.sp.	4.3	
Cecidomyiidae g.sp.	1.9	
Total (mean ± SD)	727 ± 921^{a}	594 ± 616^{a}
min–max	263–1126	63–897
n taxa (total)	76	47
n taxa (mean)	8^{a}	6^{b}
Min–max	3–17	3–12

Note: LM = littoral macrophyte beds, MF = macrophyte free areas. Mean values in the same row with different superscripts differ significantly ($p < 0.05$).