

FEATURE ARTICLE



Diffusive methane emissions from temperate semi-intensive carp ponds

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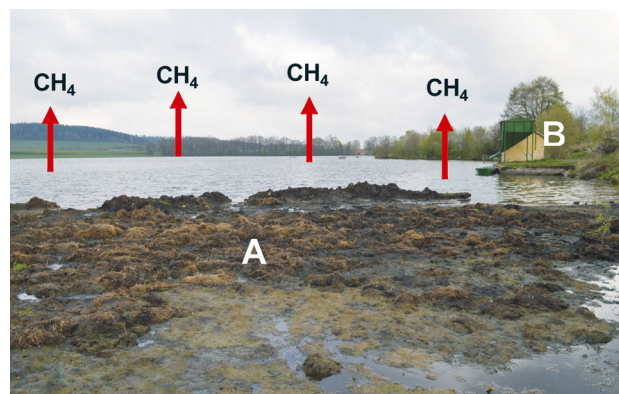
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ABSTRACT: Manuring and supplementary feeding are common practices used to sustain high fish production in temperate semi-intensive carp ponds. However, the low use efficiency of added nutrients and organic matter may cause carp ponds to be 'hot spots' of methane (CH₄) production and emission. Surface CH₄ concentrations were measured and diffusive CH₄ flux was estimated using a wind-based transboundary layer model in 3 nursery and 3 main carp ponds with different feeding rates and organic loading during 1 growing season. Mean (±SD) concentrations of CH₄ were 1.3 ± 0.9 μM and 0.8 ± 0.8 μM in nursery and main ponds, respectively. All ponds were sources of CH₄, with diffusive CH₄ fluxes of 9.1 ± 6.8 mg C m⁻² d⁻¹ in nursery ponds and 6.4 ± 6.9 mg C m⁻² d⁻¹ in main ponds. Lower CH₄ concentration and diffusive flux in the main ponds were probably due to bioturbation caused by the larger carp and consequent oxidation of the sediment. Seasonal dynamics of CH₄ were mainly related to temperature. Methane concentration and diffusive flux levels recorded in this study were within the range of those reported in natural water bodies worldwide. Our results provide information on the role of carp aquaculture in greenhouse gas emission in temperate regions.

KEY WORDS: Methane · Greenhouse gas emission · Aquaculture pond · Freshwater · Seasonality · Temperature

1. INTRODUCTION

Globally averaged atmospheric methane (CH₄) concentration has increased from approximately 650 to



Emission of diffusive methane from a temperate fishpond and inputs inducing CH₄ production in carp ponds: (A) manuring and (B) feeding.

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(Faculty of Fisheries, University of South Bohemia)

1810 ppb since the pre-industrial era (Saunois et al. 2016). Freshwater environments play an important role in the global carbon cycle (Cole et al. 2007, Battin et al. 2008), and recent CH₄ global emissions surveys from freshwater ecosystems have shown that natural lakes, man-made reservoirs, and river systems, especially in tropical areas, are significant sources of CH₄ emissions to the atmosphere (Bastviken et al. 2011, Borges et al. 2015b). Data from smaller artificial water bodies used for aquaculture are scarce, yet small natural lakes, reservoirs, and fishponds play an important role in carbon cycling (Downing 2010, Abnizova et al. 2012).

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CH₄ is known to be produced in anoxic sediments (Bastviken et al. 2004), but recent evidence also infers its production in the aerobic water column (Grossart et al. 2011, Bogard et al. 2014). CH₄ is transferred from water to the atmosphere through diffusion or released by ebullition or through aerenchym tissue of littoral emergent aquatic plants (Bastviken et al. 2004). Nutrients, organic matter, temperature, and sediment are the main drivers of CH₄ production in aquatic ecosystems (Huttunen et al. 2003). Oxygen is an important factor in CH₄ production and consumption (Huttunen et al. 2006, Juutinen et al. 2009); lack of oxygen enhances CH₄ production in sediment, while its presence promotes its microbial oxidation (Bastviken et al. 2002, Attemeyer et al. 2016). The characteristics of catchment features, including vegetation and land use (Maberly et al. 2013, Borges et al. 2015a,b), temperature, rainfall, and wind speed influence CH₄ production, transport, and emission from aquatic ecosystems (Natchimuthu et al. 2014, Emilson et al. 2018).

In some countries, fishponds are an important component of lentic ecosystems (Pechar 2000). Fishponds occupy a surface area of 1200 km² in France, 410 km² in the Czech Republic, 420 km² in Germany, 25 669 km² in China, and 87 500 km² worldwide (Pokorný & Hauser 2002, Four et al. 2017, Xiong et al. 2017). In addition to rearing fish, fishponds provide ecosystem functions such as flood regulation along with retention of water, sediments, organic matter, nutrients, and micropollutants and may be important in maintaining biodiversity (Oertli et al. 2005, Boyd et al. 2010, Gaillard et al. 2016).

Semi-intensive carp polyculture is the main aquaculture production system in the Czech Republic and Central Europe as a whole (Gál et al. 2016). In this system, common carp *Cyprinus carpio* L. represents approx. 90% of the total fish production, with the remainder comprising predatory fishes such as northern pike *Esox lucius* L., perch *Perca fluviatilis* L., eel *Anguilla anguilla* L., wels catfish *Silurus glanis* L., grass carp *Ctenopharyngodon idella* Valenciennes 1844, silver carp *Hypophthalmichthys molitrix* Valenciennes 1844, bighead carp *H. nobilis* Richardson 1845, whitefish of the genus *Coregonus*, and tench *Tinca tinca* L. (Potužák et al. 2007). A key component of this production system is its reliance on a combination of natural and artificial feed (Adámek 2014). In practice, young-of-the-year fish are kept in nursery ponds and, from the second year, are held in main ponds until harvesting (Pokorný & Pechar 2000). This system is intended to reduce competition for food and maximise the use of natural pond re-

sources in the production of fish biomass (Pokorný & Pechar 2000, Rahman et al. 2006).

Practices employed for high fish production often lead to eutrophication and deterioration of pond ecosystems (Pechar 2000), raising environmental concerns including those associated with the release of greenhouse gases (Williams & Crutzen 2010). The production of easily degradable organic matter coupled with the development of anoxic conditions on the bottom of eutrophic water bodies enhances the production of CH₄ and its subsequent evasion to the atmosphere (Gelesh et al. 2016). Indeed, Juutinen et al. (2009) found that CH₄ concentrations were higher in lakes with an anoxic hypolimnion and higher concentrations of total phosphorus than in lakes with an oxic hypolimnion and low concentrations of total phosphorus.

Aquaculture ponds are highly supplemented with organic matter and nutrients through feed, manuring, and, often, high concentrations of nutrients in their supply water and runoff from the catchment area (Pokorný & Pechar 2000, Adámek 2014). Low efficiency in use of the added material is common and causes accumulation of organic matter (Potužák et al. 2007). Some authors have considered ponds as hotspots of CH₄ production (Yang et al. 2015, 2018a,b). Liu et al. (2016) reported that the conversion of rice paddies into crab ponds combined with fishponds reduced CH₄ emissions by 50%. Based on sedimentation rates, Boyd et al. (2010) showed that aquaculture ponds sequester 0.21% of global carbon emissions annually, with high rates of carbon containment in tilapia and carp ponds. They further recommended that fishpond managers might receive incentives to mitigate emissions of greenhouse gases from fishponds into the atmosphere. However, they also stated that sufficient data are not available on CH₄ and CO₂ *in situ* emissions from fishponds to confirm a positive net carbon sequestration. Studies of CH₄ emissions in various pond types from different geographic and climatic regions are needed to resolve these contrasting views.

Previous studies of the environmental impact of fishponds in temperate regions focussed on eutrophication and its impact on pond biodiversity and downstream water bodies (Pechar 2000, Banas et al. 2008, Všeticková et al. 2012, Všeticková & Adámek 2013, Hlaváč et al. 2014, Four et al. 2017). CH₄ emissions from temperate fishponds have to date not been addressed.

The aims of this study were to determine and compare levels of dissolved and diffusive CH₄ in nursery and main fishponds in the South Bohemia

region (Czech Republic) and to investigate the factors influencing this. Main ponds receive higher doses of manure and grains, thus providing substrate for methanogenesis, in addition to producing excessive phytoplankton biomass. We assumed that environmental factors and fishery management practices are synergistic in creating conditions favourable for CH₄ emission and expected to find higher concentrations and emissions in main ponds than in nursery ponds.

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted from April to October 2017 in 3 nursery ponds: Beranov, Roubíček, and Zběhov, and 3 main ponds: Kvítkovický, Posměch, and Dehtář, located in the upper catchment of the Vltava River near České Budějovice in South Bohemia, Czech Republic. These ponds were created during the 15th and 16th centuries and have been used for fish production since then. Sediments were removed from Beranov 12 yr ago and from Kvítkovický 15 yr ago whereas there have been no sediments removed from Roubíček, Zběhov, Posměch and Dehtář in the last 20 yr. Annually, nursery ponds receive up to 0.5 t of feed per hectare in the form of cereals and are not manured. Main ponds receive 1–2 t each of feed and manure per hectare. Descriptions of the ponds are given in Table 1.

2.2. Physico-chemical water characteristics

The physico-chemical characteristics of water were measured once a month at the deepest part of the ponds, near the outlet. Dissolved oxygen, temperature, and pH were recorded using a YSI Exo2 multi-

parameter probe. Water transparency was measured with a Secchi disk, and depth was measured using a graduated stick. Depth-integrated water samples from the whole water column were taken with a Van Dorn water sampler and transported to the hydrochemistry laboratory of the Institute of Hydrobiology (Biology Centre of the Czech Academy of Science, České Budějovice) for further analyses. The samples for analyses of dissolved organic carbon (DOC), dissolved nitrogen (DN), nitrate nitrogen (NO₃-N), soluble reactive phosphorus (SRP), and total suspended solids (TSS) were filtered through glass-fibre filters with nominal porosity of 0.4 µm (type GF5, Macherey-Nagel). Samples were analysed within 24 h or kept frozen at –20°C.

Levels of TSS were determined gravimetrically on GF5 filters dried to constant weight at 105°C. Total organic carbon (TOC), total nitrogen (TN), DOC, and DN were determined on a Shimadzu TOC-L_{CPH} analyser, working on the principle of high-temperature (750°C) catalytic oxidation of water samples and detection of the combustion products CO₂ and NO_x using non-dispersive infrared (NDIR) and chemiluminescence detectors, respectively. Samples were acidified with HCl and sparged with oxygen to remove inorganic carbon before analysis. Total inorganic carbon (TIC) was determined on a Shimadzu TOC-L_{CPH} analyser by sparging acidified samples with purified oxygen to convert the inorganic carbon compounds CO₂, bicarbonate, and carbonate to gaseous CO₂, which was detected by the NDIR detector. Particulate organic carbon (POC) was determined as the difference between the TOC in unfiltered samples and DOC in the samples filtered through GF5 filters. Total phosphorus (TP) was determined by the molybdate method after perchloric acid digestion according to Kopáček & Hejzlar (1993). SRP was analysed according to Murphy & Riley (1962). Ammonium nitrogen (NH₄-N) was determined by

the spectrophotometric method with bis-pyrazolon according to Kopáček & Procházková (1993). NO₃-N was quantified using direct spectrophotometry in the UV region at 220 and 270 nm with correction for organic substances (Carvalho et al. 1998, Kalinichenko & Demutskaya 2004). Chlorophyll *a* (chl *a*) was analysed spectrophotometrically after acetone extraction following Lorenzen (1967).

Table 1. Fishpond location and characteristics. C₀: common carp *Cyprinus carpio* fingerlings; C₂–C₄: 2–4 yr old common carp; P₀: northern pike *Esox lucius* fingerlings; P₁ = 1 yr old northern pike

Fishpond	Type	GPS coordinates		Area (ha)	Depth (m)		Fish
		°N	°E		Max	Mean	
Beranov	Nursery	48° 58' 46"	14° 19' 16"	13.3	2.5	1.0	C ₀ –C ₂
Zběhov	Nursery	48° 59' 32"	14° 18' 19"	2.0	1.5	0.4	P ₀ –P ₁
Roubíček	Nursery	48° 58' 52"	14° 15' 41"	4.4	1.4	0.5	C ₀ –C ₂
Kvítkovický	Main	48° 57' 48"	14° 15' 41"	24.0	3.0	1.1	C ₃ –C ₄
Posměch	Main	48° 59' 46"	14° 17' 42"	36.6	3.2	1.2	C ₂ –C ₄
Dehtář	Main	48° 0' 30"	14° 18' 21"	228	6.5	2.2	C ₂ –C ₄

2.3. Sediments

Sediments were collected in July and October 2017 with a core tube sampler at the deepest point near the pond outlet and in a littoral shallow part of the pond. Three samples were collected at each site in tubes with a diameter of 5 cm, and the top 5 cm of sediment were sliced and pooled into a single sample. Samples were freeze-dried and analysed for sediment TN, TP, and TOC in the same laboratory as water analyses. TP_{sed} was determined by the molybdate method after perchloric acid digestion according to Kopáček et al. (2001). TOC_{sed} and TN_{sed} were determined by elemental analysis on a varioMICRO Cube analyser (Elementar Analysensysteme). Samples were acidified with HCl before analysis, and inorganic carbon was removed as CO_2 (Kopáček et al. 2001).

2.4. Surface-water CH_4 concentration

Surface CH_4 concentrations were measured using the headspace technique as described by Bastviken et al. (2004). In the field, water samples were taken from 10 cm below the surface with a 50 ml syringe capped with a needle mounted on a 3-way valve. The first water sample was used to remove air, and a new water sample of 40 ml was drawn into the syringe and adjusted to 20 ml. A headspace was then created by adding 20 ml of ambient air and shaking for 1 min to equilibrate the CH_4 concentration in the water and air enclosed in the syringe. The headspace gas was then transferred into 12 ml pre-evacuated exetainer vials equipped with chlorobutyl septa (vial type 3, order code 839W/GL, LabCo). Ambient CH_4 concentrations were also determined from air samples collected on the same sampling day to correct for background concentrations of air in the headspace (Bastviken et al. 2010). Headspace CH_4 concentration was determined in the laboratory of the Department of Ecosystem Biology (Faculty of Science USB, České Budějovice) using an HP 6890 gas chromatograph (Agilent) equipped with a 0.53 mm \times 30 m GS-Alumina column and a flame ionization detector. Calibration was done with certified $CH_4:N_2$ mixtures (Linde) in concentrations of 1.7, 10, 100, 1000, and 10000 ppm of CH_4 . The detection limit for CH_4 analysis was 0.1 ppm, and the precision of measurements was $\pm 3\%$. The quantity of CH_4 that remained dissolved in the syringe water sample was calculated from headspace CH_4 concentrations using Henry's law adjusted for *in situ* temperature according to

Wiesenburg & Guinasso (1979). CH_4 concentration in the original water sample was then obtained by dividing total CH_4 quantity in the headspace and in the syringe water corrected for ambient air concentration by the volume of water sample (Bastviken et al. 2010). The results were considered representative for the month in which the samples were taken.

2.5. Surface-water CH_4 emissions

Gas exchange between air and water (F) was calculated indirectly using the 2-layer model with the equation $F = k(C_{sur} - C_{eq})$, where C_{sur} is the gas concentration in surface water in $\mu\text{mol l}^{-1}$, C_{eq} is the gas concentration in surface water in equilibrium with the atmosphere in $\mu\text{mol l}^{-1}$, and k is the gas exchange constant (cm h^{-1}). The value of k was calculated from the local wind speed according to Crusius & Wanninkhof (2003): $k = k_{600} (Sc/600)^n$, where k_{600} is the gas transfer velocity for a Schmidt number of 600; Sc is the Schmidt number of CH_4 ; and n takes the value of -0.67 or -0.5 if the wind speed at 1 m height is lower or higher than 3 m s^{-1} , respectively (Crusius & Wanninkhof 2003). The value of k_{600} (cm h^{-1}) was calculated according to Crusius & Wanninkhof (2003) as $k_{600} = 1.68 + (0.228 \times \mu_{10}^{2.2})$, where μ_{10} is the local wind speed in m s^{-1} at a height of 10 m. The wind speed measured at 2 m was converted to a height of 10 m according to Crusius & Wanninkhof (2003): $\mu_{10} = 1.22 \mu_2$, where μ_2 is the wind speed at 2 m. Sc for CH_4 was calculated according to Wanninkhof (1992) with the following formula: $Sc_{CH_4} = 1897.8 - 114.28t + 3.2902t^2 - 0.039061t^3$, where t ($^{\circ}\text{C}$) is the water temperature at the time of CH_4 extraction. C_{eq} was determined from equation: $C_{eq} = \beta pCH_4$, where β is the solubility of CH_4 computed according to Wiesenburg & Guinasso (1979), and pCH_4 is the partial pressure of CH_4 in the atmosphere. The measured surface water CH_4 concentrations were compared to their respective concentrations in equilibrium with the atmosphere to obtain the level of CH_4 saturation.

2.6. Statistical analysis

Generalized linear mixed models (GLMMs) were used to assess significant differences in water quality parameters between pond types (Zeger & Liang 1992, Breslow & Clayton 1993). Non-parametric analysis of longitudinal data (nparLD) was used to test the effect of pond type on organic carbon, nitrogen, and phosphorus content in pond sediment (Noguchi

et al. 2012). A Wilcoxon signed rank test was used to evaluate differences in nutrient and organic matter content in sediment between the 2 sampling times. GLMM was also used to test the effect of pond type, sampling time, and their interaction on dissolved CH₄ in pond surface water, CH₄ saturation levels, and diffusive CH₄ flux. This analysis was followed by Tukey's post hoc tests to determine differences in CH₄ concentration, saturation, and flux within a pond type over time and differences between pond types at each sampling time. Partial least squares regression (PLSR) analysis was used to identify drivers of variation in CH₄ concentration and flux between pond types. Explanatory variables were log(x+1) transformed prior to regression analyses. Pond type, temperature, DO, DOC, POC, chl *a*, TP, TN in water, and TP_{sed} and TN_{sed} were selected as variables for regression analyses. The variable 'pond type' was considered as a nominal variable of 2 levels, i.e. nursery and main. The most important drivers of CH₄ concentration and flux were identified based on the weight of each predictor variable and total explanatory capacity (R² of Y and R² of X_i) of extracted components. GLMMs, nparLD, and the Wilcoxon test were performed in R version 3.4.4 (R Core Team 2018), and PLSR was conducted using Statistica 13 (STATISTICA advanced, module STATISTICA Multivariate Exploratory Technique; Statsoft).

3. RESULTS

3.1. Physico-chemical characteristics

The main ponds reflected the impact of nutrient and organic matter input through manuring and supplementary feeding, with significantly higher concentrations of TP, SRP, chl *a*, and TSS and significantly lower water transparency than in nursery ponds (Table 2, Fig. 1). TP concentrations gradually increased during the growing period, with the exception of a peak recorded in June in the main ponds (Fig. 1k). SRP showed the same temporal trend as TP both in nursery and in main ponds (Fig. 1j). Chl *a* increased (Fig. 1f) in both pond types, while TSS fluctuated throughout the summer with no discernible pattern (Fig. 1d). Surface water temperature increased during warmer months, ranging from 14 to 25°C (Fig. 1a), while DO decreased over time (Fig. 1c). Neither parameter differed significantly between pond types (Table 2). DOC (Fig. 1g), TOC (Fig. 1h), and TIC (Fig. 1i) concentrations increased over the monitored period, with only TOC concen-

tration differing significantly between pond types (Table 2). Despite the increase in TIC concentrations, water pH remained slightly alkaline, ranging from 7.2 to 8.9 (Fig. 1b) throughout the growing season and did not differ significantly between pond types (Table 2). NH₄-N (Fig. 1l), NO₃-N (Fig. 1m), DN (Fig. 1n), and TN (Fig. 1o) showed a slight decreasing trend during the study period. Only NH₄-N differed significantly between pond types (Table 2). TN_{sed}, TP_{sed}, and TOC_{sed} (Fig. 2) varied slightly with time, but the observed values did not differ significantly with sampling time according to a Wilcoxon test ($p > 0.05$). Sediment chemical characteristics did not differ significantly between pond types (Table 2). The quantity of visible low to moderately degraded leaves and woody detritus in the sediment samples was high in shallow littoral sediments collected near the inflows in both pond types. Sediments in the deepest part of the ponds were composed of fine

Table 2. Physico-chemical characteristics of pond water, organic matter, and nutrient sediment content. TSS: total suspended solids; DO: dissolved oxygen; DOC (POC), dissolved (particulate) organic carbon; TIC (TOC), total inorganic (organic) carbon; NH₄-N: ammonium nitrogen; NO₃-N: nitrate nitrogen; DN: dissolved nitrogen; TN: total nitrogen; SRP: soluble reactive phosphorus; TP: total phosphorus; TOC_{sed}: sediment TOC; TN_{sed}: sediment TN; TP_{sed}: sediment TP. Values are means ± SD of the growing season. Asterisks indicate significant differences between main and nursery ponds (generalized linear mixed model for water parameters and non-parametric analysis of longitudinal data for sediment parameters; $p < 0.05$)

Parameter	Main ponds	Nursery ponds
Wind (m s ⁻¹)	1.5 ± 0.8	1.3 ± 0.7
Water temp (°C)	20.9 ± 4.4	20.4 ± 4.1
pH	7.9 ± 0.3	7.7 ± 0.3
Secchi depth (m)*	0.5 ± 0.2	0.8 ± 0.5
TSS (mg l ⁻¹)*	35.2 ± 7.5	9.7 ± 3.8
DO (mg l ⁻¹)*	12.7 ± 4.3	18.7 ± 7.0
Chl <i>a</i> (µg l ⁻¹)*	82 ± 57	38 ± 24
DOC (mg l ⁻¹)	13.6 ± 1.4	4.1 ± 1.9
POC (mg l ⁻¹)	7.2 ± 1.7	4.2 ± 1.9
TOC (mg l ⁻¹)*	20.8 ± 2.6	18.9 ± 3.9
TIC (mg l ⁻¹)	23.7 ± 3.7	23.7 ± 5.2
NH ₄ -N (mg l ⁻¹)*	0.2 ± 1.2	0.13 ± 0.2
NO ₃ -N (mg l ⁻¹)	0.6 ± 0.3	1.0 ± 0.7
DN (mg l ⁻¹)	1.7 ± 0.2	2.0 ± 0.7
TN (mg l ⁻¹)	2.7 ± 0.3	2.6 ± 0.5
SRP (µg l ⁻¹)*	123 ± 189	20 ± 11
TP (mg l ⁻¹)*	0.4 ± 0.2	0.2 ± 0.01
TOC _{sed} (mg g ⁻¹)	56 ± 45	51 ± 31
TN _{sed} (mg g ⁻¹)*	6.5 ± 6.3	5.2 ± 3.3
TP _{sed} (mg g ⁻¹)	1.2 ± 0.8	0.7 ± 0.3

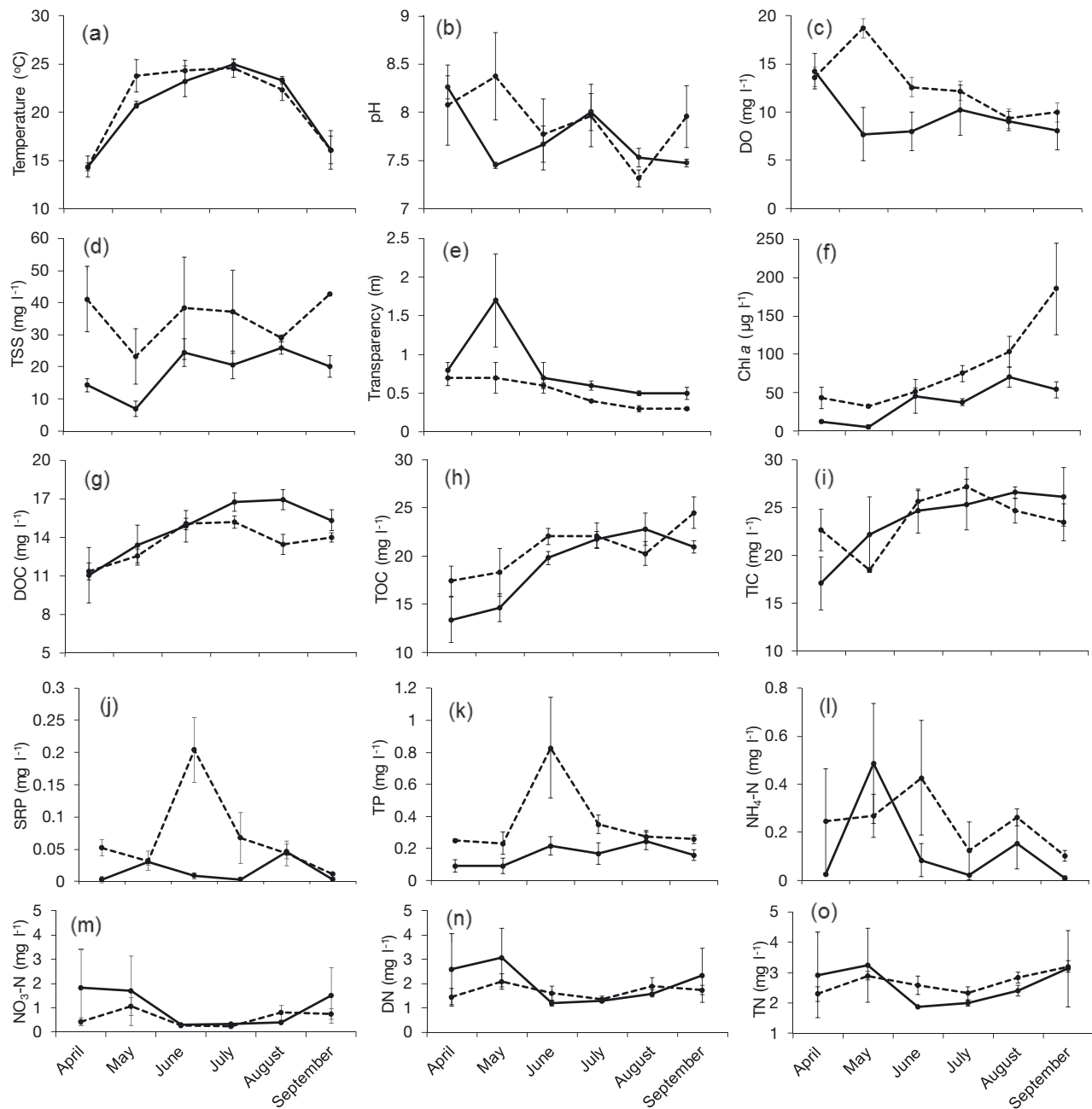


Fig. 1. Temporal dynamics of physico-chemical characteristics of water in main (dotted line) and nursery (continuous line) ponds. Variable abbreviations as in Table 2. Values are means \pm SE

black particles, whereas those collected in the shallower areas were sandy, coarse, and brownish.

3.2. CH₄ concentrations and diffusive emissions

The mean (\pm SD) surface concentrations of dissolved CH₄ were 0.8 ± 0.8 and 1.3 ± 0.9 μ M in main and nursery ponds, respectively. In nursery ponds, a

2-peak pattern was observed, with the minimum in April and September, intermediate values in June and July, and maximum values in May and August (Fig. 3a). The main ponds showed a peak in May and low consistent values in the remaining months of the season (Fig. 3a). Dissolved CH₄ concentrations ranged from 0.06 to 4.8 μ M in all ponds. There was an effect of time of sampling ($F_{5,416} = 77.8$, $p < 0.001$, Fig. 3a) and an interaction of pond type and time of

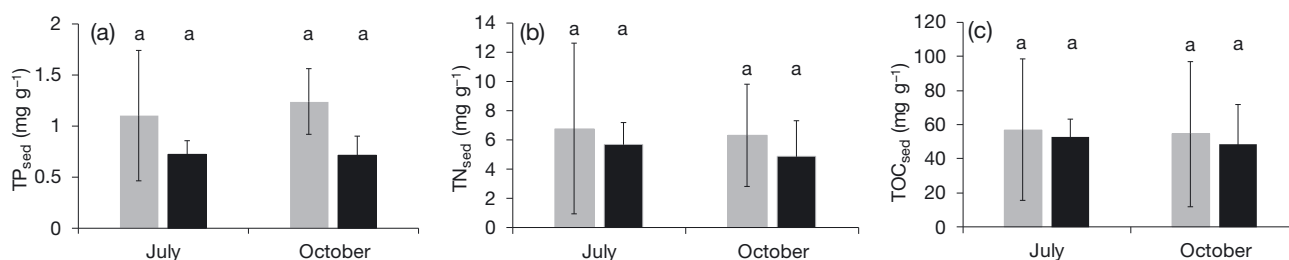


Fig. 2. Sediment composition in nursery (black bars) and main (grey bars) ponds. Variable abbreviations as in Table 2. Values are means \pm SE

sampling ($F_{5,416} = 14.1$, $p < 0.001$, Fig. 3a) influencing the surface CH_4 concentration. CH_4 concentration differed significantly between nursery and main ponds in June, July, and August (Fig. 3a). Nursery ponds exhibited higher dissolved CH_4 concentration than did main ponds throughout the monitored period. All investigated ponds were highly supersat-

urated with CH_4 . The mean saturation degree was $41\,824 \pm 28\,932\%$ and $20\,770 \pm 22\,791\%$ in nursery and main ponds, respectively (Fig. 3b). CH_4 supersaturation showed the same temporal trend in both pond types.

All ponds were sources of CH_4 in the atmosphere during the growing season. Diffusive emissions of CH_4 carbon ($\text{CH}_4\text{-C}$) ranged from 0.19 to $32\text{ mg m}^{-2}\text{ d}^{-1}$ in all ponds with a mean of $7.8 \pm 7.0\text{ mg m}^{-2}\text{ d}^{-1}$. CH_4 flux rates differed significantly over time ($F_{5,416} = 96.5$, $p < 0.001$, Fig. 3c), with a significant interaction between sampling time and pond type ($F_{5,416} = 27.9$, $p < 0.001$, Fig. 3c). However, the interaction was weak, as flux rates differed significantly between pond types only in August. Flux rates of diffusive $\text{CH}_4\text{-C}$ were slightly higher in nursery ponds ($9.1 \pm 6.8\text{ mg m}^{-2}\text{ d}^{-1}$) than in main ponds ($6.4 \pm 6.9\text{ mg m}^{-2}\text{ d}^{-1}$) throughout the growing season. Nursery ponds exhibited peaks in May and August, while main ponds peaked in May (Fig. 3c). Unlike the trends in dissolved CH_4 and CH_4 saturation, the highest peak, recorded in May, was in the main ponds (Fig. 3c).

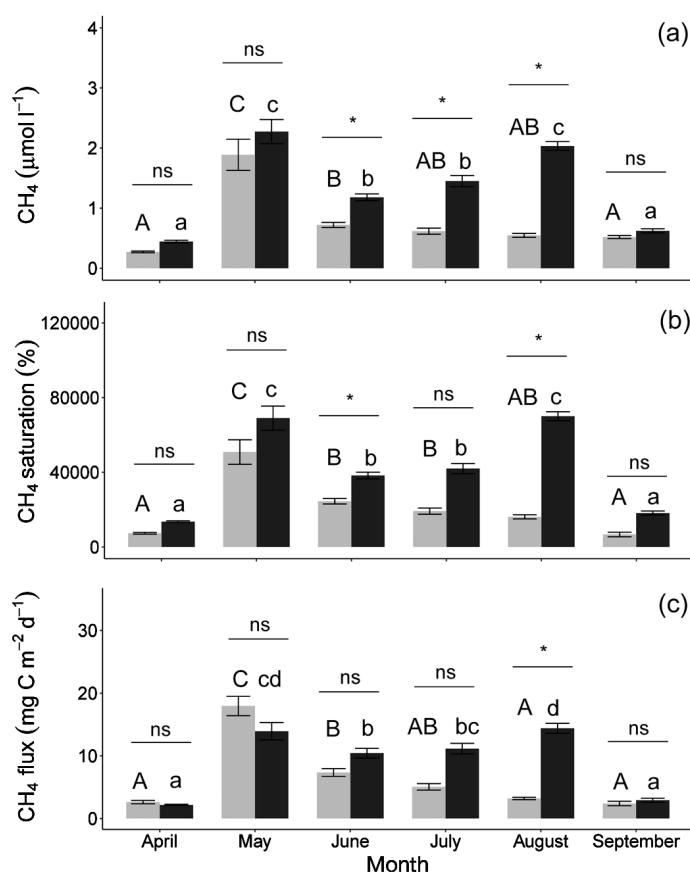


Fig. 3. Temporal variability of (a) CH_4 concentration, (b) CH_4 saturation, and (c) diffusive flux of CH_4 in nursery (black bars) and main (grey bars) ponds. Data are means \pm SE. Different letters denote significant ($p < 0.05$) differences in the same pond type over time (uppercase letters = main ponds, lowercase letters = nursery ponds). Horizontal bars with asterisks show significant differences between pond types at a given sampling time, and horizontal bars with 'ns' show non-significant differences

3.3. Factors affecting CH_4 concentration and diffusive emissions

The PLSR was used to reveal whether physico-chemical properties of water and sediment composition can explain CH_4 concentration and diffusive emissions. The results indicated that 3 components explained 55% of the variation in CH_4 concentration in the investigated ponds (Table 3). The first component explained 40% of the total variance, and its information content was positively associated with water temperature and negatively associated with pond type. The second component, also positively associated with water temperature, and the third component, negatively associated with DOC, ac-

Table 3. Results of the partial least square regression analysis, extracted components and weights of associated explanatory variables. COMP: component; other variable abbreviations as in Table 2. R²Y: explained variability of dependent variables (CH₄ concentration or CH₄ diffusive flux); R²X: explained variability in independent variables. Significant correlations ($p < 0.05$) are highlighted in **bold**

Parameters	Dissolved methane			Methane flux
	COMP1	COMP2	COMP3	COMP1
Water temp	0.55	0.52	0.19	0.76
DO	-0.17	0.29	0.13	-0.04
Chl <i>a</i>	-0.24	0.07	-0.42	-0.34
DOC	0.26	-0.14	-0.46	0.23
POC	0.28	0.25	-0.32	0.06
TN	0.03	0.43	0.32	-0.14
TP	-0.16	0.14	-0.3	-0.05
TN _{sed}	0.09	0.38	-0.29	-0.07
TP _{sed}	-0.15	0.29	-0.41	-0.25
Pond type	-0.45	0.26	0.08	-0.28
R ² Y	0.4	0.11	0.04	0.34
R ² X	0.25	0.23	0.15	0.24

counted for 11 and 4 % of the total variance, respectively (Table 3). The PLSR analysis also indicated that only 1 component explained 37 % of the variation in diffusive CH₄ flux (Table 3). This component was positively associated with water temperature, but the association was not significant.

4. DISCUSSION

The increase in CH₄ concentration and flux that occurred from April to May suggests that the increase in CH₄ concentration was primarily related to the increase in water temperature (Table 3). Water temperature influences CH₄ production in aquatic ecosystems as it stimulates activity of methanogenic bacteria (Hofmann et al. 2010, Musenze et al. 2014, Natchimuthu et al. 2014, Borges et al. 2018). In temperate regions, CH₄ concentration in water increases at the beginning of spring, triggered by the increase in sediment temperature and water temperature (Descloux et al. 2017). The peak of CH₄ flux recorded in the main ponds in May can be explained by sediment bioturbation by carp along with wind speed. At the beginning of the growing season, the feeding behaviour of carp enhances the release of CH₄ accumulated in sediment during the previous growing season and winter (Bhattacharyya et al. 2013, Xiong et al. 2017). The average wind speed in May was higher over the main ponds ($2.3 \pm 0.5 \text{ m s}^{-1}$) than above nursery ponds ($1.0 \pm 0.5 \text{ m s}^{-1}$).

CH₄ concentration and flux in the main ponds decreased in summer and became lower than in

nursery ponds. Other studies have shown CH₄ emissions to be highly correlated with temperature throughout the growing season (Natchimuthu et al. 2014, Wik et al. 2014). The observed low CH₄ concentration and flux in the main ponds may be explained by CH₄ oxidation and the behaviour of carp over 1 kg body weight burrowing in search of food at the bottom of the ponds. CH₄ oxidation is an important pathway that reduces surface water CH₄ concentration and its emission from water bodies (Bastviken et al. 2008, Juutinen et al. 2009). Oxidation probably plays an important role in CH₄ dynamics in carp ponds as well, despite its short time exposure due to shallowness of the ponds (Table 1). In shallow lakes, CH₄ bubbles escape oxidation due to short travel time from sediment through a well-mixed water column to the surface (Bastviken et al. 2004, 2008, Juutinen et al. 2009, Natchimuthu et al. 2014). However, low concentrations of NO₃ (Table 2) may be a limiting factor in CH₄ oxidation occurring in deeper areas near pond outlets (Bastviken et al. 2008, Deutzmann et al. 2014, Roland et al. 2017). CH₄ oxidation rates are positively correlated to consumption of NO₃ under anoxic conditions (Roland et al. 2017). Bioturbation of the top sediment layer by carp may reduce CH₄ production by improving aerobic conditions of top sediment or by reducing the concentration of easily oxidised organic matter through the exposure of older sediment (Ritvo et al. 2004).

CH₄ concentration was negatively related to DOC (Table 3), implying that DOC was not the primary source of, or a factor strongly associated with, CH₄ production. The increase in CH₄ concentration and flux in the nursery ponds in August probably followed maturation and decomposition of fresh plant biomass rather than originating from old settled detritus (Kelly et al. 1997). CH₄ production in lakes of temperate and boreal regions might differ substantially depending on the chemical composition of sediments (Emilsson et al. 2018). Sediments containing organic matter from macrophytes and aquatic plants produce more CH₄ than sediments containing organic matter of terrestrial origin. Nursery ponds had littoral zones largely covered by emergent macrophytes in addition to floating and submerged aquatic plants that could supply fresh organic matter for methanogenesis. Additionally, water bodies with higher abundance of macrophytes usually have significantly higher CH₄ concentration and flux than those without, or with low abundance, of macrophytes (Selvam et al. 2014). Similarly, Ma et al. (2018) reported higher CH₄ flux from crab ponds with macrophytes than from those without. Macrophytes

were rare in main ponds due to eutrophication, as indicated by low water transparency, as an effect of nutrient overload. Moreover, aquatic plants cannot establish in densely stocked fishponds due to carp feeding behaviour (Scheffer et al. 2001). Common carp, especially larger individuals, are known to interfere with aquatic plant growth both directly by mechanical uprooting and consumption and indirectly by increasing water turbidity causing reduction in photosynthesis (Miller & Crowl 2006). Diffusive CH_4 flux was not significantly related to any measured environmental factor, indicating that wind speed was the main factor regulating diffusive flux (Musenze et al. 2014).

Our findings of CH_4 concentration and diffusive flux were in general agreement with those obtained in other aquatic bodies worldwide (Table 4), although they deviated from some observations. CH_4 concentrations and flux were reported to be lower in Lake Erssjön in Sweden and higher in Indian ponds compared to our findings (Table 4). The primary difference between our ponds and the Indian ponds was higher organic matter supply and higher water temperature recorded in Indian ponds than in our ponds (Selvam et al. 2014). Lake Erssjön had lower nutrient concentrations and lower mean temperature compared to our ponds (Natchimuthu et al. 2016). Recent studies have reported very diverse values for emissions of greenhouse gases from aquaculture systems (Yang et al. 2015, Ma et al. 2018). In agreement with our study, these authors confirmed that temperature and aquaculture management strongly influ-

ence CH_4 emissions from ponds. However, they did not relate CH_4 emissions from ponds to the behaviour of cultured animals. We did not compare CH_4 flux rates from these studies to our results, since they did not distinguish diffusive flux from ebullitive flux. Our results represent only a portion of the CH_4 flux from the ponds because our study does not include ebullitive flux. The contribution of ebullitive CH_4 to total CH_4 emission ranges from 10 to more than 90 % of total CH_4 emissions in temperate and boreal aquatic systems (Casper et al. 2000, Bastviken et al. 2004), hence it is not possible to make a reliable estimate of total emissions based on diffusive fluxes only. The level of ebullitive CH_4 from carp ponds remains uncertain until temporal and spatial data of ebullitive fluxes from them are available, as ebullitive CH_4 is system specific. In this study, the main ponds did not diffuse more CH_4 than the nursery ponds, possibly due to sediment disturbance by carp. This indicates that organic matter in the sediment of the main ponds might be processed more through oxic pathways than anoxic-methanogenic pathways.

5. CONCLUSIONS

Both the nursery ponds and the main carp ponds were significant sources of diffusive CH_4 into the atmosphere. Contrary to our expectations, the main ponds had lower CH_4 concentration and lower diffuse CH_4 flux m^{-2} than the nursery ponds, despite the higher loadings of organic matter they receive

Table 4. Methane (CH_4) concentration and flux (means \pm SD or range of values) in lentic water bodies worldwide. Conc: concentration; Dif: diffusive; Ebul: ebullitive; nm: not measured. International country codes based on the ISO3166 standard published by the International Organisation for Standardisation (www.iso.org/iso-3166-country-codes.html) are in parentheses

Site	Climate	CH_4 conc (μM)	Dif CH_4 ($\text{mg l}^{-1}\text{d}^{-1}$)	Ebul CH_4 ($\text{mg l}^{-1}\text{d}^{-1}$)	Reference
Nursery ponds (CZE)	Temperate	1.3 ± 0.9	12.2 ± 9.1	nm	This study
Main ponds (CZE)	Temperate	0.8 ± 0.8	8.5 ± 9.3	nm	This study
MT Lake (W Siberia, RUS)	Boreal	0.3 ± 0.3	8.1 ± 8.7	12.9	Repo et al. (2007)
MT Pond (W Siberia, RUS)	Boreal	2.6 ± 2.6	41 ± 41	23	Repo et al. (2007)
Erssjön (SWE)	Boreal	0.33 ± 0.23	1.9 ± 1.3	3.0 ± 5.9	Natchimuthu et al. (2016)
Weir impoundments (CZE)	Temperate	1.1 ± 0.1	15.8 ± 6.7	1086 ± 413	Bednařík et al. (2017)
Priest Pot Lake (GBR)	Temperate	1.3	6.0 ± 5.5	155 ± 277	Casper et al. (2000)
Paul Lake (USA)	Temperate	0.5–2.6	14.4	9.8	Bastviken et al. (2008)
Peter lake (USA)	Temperate	0.5–2.6	9.3	16.3	Bastviken et al. (2008)
Hummingbird Lake (USA)	Temperate	0.5–2.6	3.5	4.3	Bastviken et al. (2008)
Římov reservoir (CZE)	Temperate	nm	nm	266 ± 381	Tušer et al. (2017)
Lakes (IND)	Tropical	0.9 ± 1.0	11.2	52.9 ± 9.4	Selvam et al. (2014)
Ponds (IND)	Tropical	12.4 ± 26.9	49.7	237 ± 247	Selvam et al. (2014)
Reservoirs (IND)	Tropical	0.6 ± 0.4	3.2	48 ± 53	Selvam et al. (2014)
Lake Kivu (RWA)	Tropical	0.06 ± 0.02	0.6 ± 0.2	nm	Borges et al. (2011)

through fishery management. Common carp, being a benthic feeder in the main ponds, may reduce CH₄ production and release by disturbing sediment and maintaining the upper layer in oxic conditions. The CH₄ emissions from the carp ponds in our study are within the range found in other freshwater lentic water bodies. However, more studies are required to quantify ebullitive and other pathways of CH₄ release into the atmosphere in order to define the local and global role of carp ponds in CH₄ emissions.

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