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CONTENT

CHAPTER 1

GENERAL INTRODUCTION

Fish farming in ponds

Fishponds are the types of water bodies mostly used in inland fish production (FAO, 2018). Currently, inland fish production in ponds contributes approximately 65% of the world's farmed fish production (FAO, 2018). Grass carp, silver carp, common carp, Nile tilapia and bighead carp are, in the descending order, the first five species raised in aquaculture worldwide. Because of the shortage of capture fisheries products, aquaculture continues to grow faster than other major food production sectors worldwide with an annual growth of 5.8% (FAO, 2018). Based on the way cultured fish obtain their food, aquaculture can be classified into three categories (van Dam et al., 2002). In extensive systems, fish feed solely on natural food produced in the pond whereas in semi-intensive systems, natural food production is enhanced by addition of nutrients in manure and often supplemented by feeds. In intensive systems, fish feed only on external high quality complete feed.

In extensive and semi-intensive fish culture, higher fish productivity is achieved when fish are able to utilize maximally the primary production either directly or via the food chain (Pokorný et al., 2005). Pond management aims at balancing production and decomposition processes in order to enhance the efficiency of energy flow in the food chain within fishponds (Bosma and Verdegem, 2011). The increase of aquaculture production involves the intensification of fishery management and the expansion of the area used for aquaculture (Adámek, 2014; Troell et al., 2014). Intensification measures include different pond management practices such as manuring, liming, polyculture farming, supplementary feeding, high stocking density, and selection of good and disease resistant brood stocks (Rahman et al., 2006; Adámek, 2014; Troell et al., 2014). However, such intensification may have significant drawbacks in the functioning of the pond ecosystem, fish productivity and ecological sustainability of fish farming in ponds. Eutrophication of fishponds has been one of the many drawbacks of intensifying fish production (Pechar, 2000).

Pond aquaculture in The Czech Republic

Pond aquaculture spread in the Czech Republic during the 14th century and fishponds covered an area of 75,000 ha at that time (Pokorný and Pechar, 2000). Fishpond increased in number until the 16th century when they covered an area of about 160,000 ha but declined afterwards and they only cover about 40,000 ha nowadays (Pokorný and Hauser, 2002). On the other hand, fish productivity did not depend on the size of the land used for fish farming. A production of 50 kg ha^{-1} of fish remained same over the first five centuries of pond aquaculture history in the Czech Republic (Pokorný and Pechar, 2000). Fish production increased ten times since the 1930s due to intensive fertilisation, nutrient loads from catchments as run-off or wastewaters, use of supplementary feeding, and high stocking density (Pokorný and Hauser, 2002). Nowadays, fish production varies between 500 and 1000 kg.ha^{-1} per year and polyculture extensive and semi-intensive production systems are the only systems used by fish farmers (Adámek, 2014). The main fresh water fish species cultured in ponds is the common carp *Cyprinus carpio* L. representing approximately 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 *Hypophthalmichthys nobilis* Richardson 1845, whitefish genus *Coregonus*, and tench *Tinca tinca* L. (Potužák et al., 2007).

Sources of organic matter and nutrients in fishponds

Primary producers

Primary production is the base of the production of natural food in extensive and semi-intensive temperate carp ponds. This applies particularly for the provision of organic carbon in ponds. Because of low transparency, primary production is carried out mainly by phytoplankton dominated by algae and cyanobacteria (Vanacker et al., 2015). In such conditions, phytobenthic primary production is insignificant (Adámek, 2014). Submerged and floating macrophytes are found in fishponds only during the clear water state with low nutrient loads and low fish biomass (Scheffer et al., 2001; Robin et al., 2014; Vanacker et al., 2015). Littoral emergent plants can survive in ponds even with higher fish biomass.

Nutrient levels and the grazing pressure are the most important factors regulating phytoplankton species richness. Increased nutrient levels boost selectively some phytoplankton taxonomic groups (Potužák et al., 2007). For instance, a phytoplankton community dominated by cyanobacteria is an indicator of fishpond eutrophication (Adámek, 2014; Robin et al., 2014). Nutrient stoichiometry also induces the same effect. At low N:P and C:P ratios indicating nitrogen deficiency, phytoplankton tend to be dominated by cyanobacteria that can use atmospheric nitrogen (Elser et al., 2000b).

Factors influencing primary production in fishponds

Algae, cyanobacteria and macrophytes require a supply of inorganic nitrogen (N), phosphorus (P), carbon (C), sufficient light and favourable temperatures to grow (Knud-Hansen, 1998). It is well established that increase in nutrient inputs, P in particular, induces correspondingly increase in phytoplankton production and standing stocks (Schindler, 1978). In addition, provision of nutrient in a balanced stoichiometric ratio is equally important. Most algae seem to require a N:P ratio of at least 10:1 (Elser et al., 2000b). Nutrients are supplied to ponds both from the catchment by natural and human-induced processes and from the addition of fertilisers and or/manure by fish farmers. Supplementary feeding supports indirectly primary production in ponds through nutrient leaching and the mineralisation of uneaten and undigested feed (Milstein, 1992).

Grazing, cell size, and sinking rate have also considerable effects on phytoplankton primary production (Pálffy et al., 2013). Grazing has a negative feedback on phytoplankton. Phytoplankton biomass is low in the presence of large zooplankton while it increases when the latter are heavily predated by fish (Pechar, 2000). Availability of photosynthetically active radiation is crucial for primary productivity in water column (Havens et al., 1998). It determines the water volume within which primary production takes place (Houser, 2006). The extent of light penetration in turn depends on water colour, turbidity, and trophic status (Houser, 2006). Suspended solids absorb light hence reducing primary productivity (Houser, 2006).

Fish farming restricts macrophyte growth. Common carp feeding behaviour reduces the abundance of submerged and emergent plants directly by their consumption and/or by damaging their roots or indirectly by increasing turbidity through bioturbation (Vanacker et al., 2015). Some pond management practices directed against macrophyte growth (Holdren et al., 2001), such as stabilization of pond banks and pond sediment dredging reduce habitat for littoral emergent plants (Broyer and Curtet, 2012).

Primary production vary highly in response to diel or seasonal variation of abiotic factors and extreme disturbances such as floods, storms, rapid flushing and variation in irradiance and temperature (Tsai et al., 2008). For instance primary production is low during storms and floods because of increased turbidity, terrestrial DOC and wash out of autotrophic organisms (Tsai et al., 2008). Although the primary production in ponds is primarily driven by abiotic factors (similarly to natural lakes, especially shallow), it is intentionally increased by pond management practices such as fertilisation, supplementary feeding and liming (Vanacker et al., 2015). There is a lack of updated rates of primary production in Czech fishponds. Chapter II and chapter III of this study were designed to measure ecosystem metabolic rates and compared them with other natural lakes.

Supplementary feeding

Supplementary feeding is the provision of feed to fish in order to obtain production levels that would have not been achieved with only natural food available in ponds (Ćirić et al., 2015). Cereals (wheat, triticale, rye, maize, and barley) are the main supplementary feeds used in semi-intensive carp farming system in the Czech Republic. They do not replace the natural food as they only constitute 25 to 30% of the total fish nutrition (Adámek, 2014). Daily feed addition is roughly 1-3% of fish biomass in conventional ponds (Kestemont, 1995).

Amounts of OC, N and P supplied in a feed depend on the feeding rates and its OC, N and P content. In turn, feeding rates depends on the age and density of reared animals, water temperature and the availability of natural food. In semi-intensive systems, supplementary feeding comes as the second source of OC after the primary production whereas it is the main input of N and. Feed can supply up to 23% of total OC inputs in tilapia ponds (Boyd et al., 2010). Feed can supply from 80% to 98% of total N and P in channel catfish ponds in the USA (Gross et al., 2000) and in polyculture of major Indian carps and scampi farms in India (Adhikari et al., 2012).

Fertilisation

The increase of primary production is the main purpose of fertilisation in aquaculture by supplying additional soluble N, P and C for algal uptake and growth (Knud-Hansen et al., 1991). Fertilisers can be supplied either in soluble or particulate form. They can further be divided according to their production into organic from animal manure or plant composting (green manure) or industrial fertilisers. Currently, industrial fertilisers are less used either for environmental concerns in developed countries or for affordability in developing countries. Fresh manure can be added directly from small livestock farms associated to fishponds (Adámek, 2014). Nutrient requirements and fertilisation frequency are two key factors to consider in order to maximize the fertilisation efficiency (Garg and Bhatnagar, 2000). Fertilisation management options can be selected based on inputs of N, P and C that correspond to phytoplankton demands (Knud-Hansen et al., 2003). These options are namely: (i) Fixed input strategy based on empirical relationship between algal productivity and net fish yield results generated through pond fertilisation trials; (ii) nutrient addition determined from a comparison between pond water nutrient concentrations and theoretical nutrients concentrations needed to attain the maximum potential primary productivity; and (iii) algal bioassay that uses nutrient enrichment test to identify the one that limits algal growth.

Supply water, inflows and atmospheric deposition

The background concentrations of C, N and P in water used to fill fishponds and their concentrations in inlet water are among factors taken into consideration during fertilisation programs (Knud-Hansen et al., 1991). C, N and P inputs from these two sources vary depending on the pond size, land use in the catchment, amount of rainfall and the exchange rate with the surrounding water. Atmospheric derived C, N and P inputs are another source to consider in nutrient balance of fishponds. They may play a considerable role in determining the trophic status of oligotrophic water bodies or supply significant inputs even in water bodies located in agricultural dominated catchments (Kopáček et al., 1997). The inputs of C, N and P from rain, inflow and water supply are relatively low in different aquaculture systems compared to other inputs (Gross et al., 2000; Sahu et al., 2013; Zhang et al., 2016).

Nitrogen fixation

Nitrogen fixation takes place mainly in P-rich but N-poor aquatic ecosystems. Heterocystous cyanobacteria are able to reduce atmospheric dinitrogen and use it during photosynthesis (Hargreaves, 1998). The quantity of atmospheric N fixed in aquaculture ponds depends upon species composition of the phytoplankton community and ammonia concentration (Gross et al., 2000). Atmospheric N fixation is inversely related to ammonia concentration in the upper layer receiving light (Hendzel et al., 1994). Nitrogen fixation is negligible in fishponds and is seldom included in fishpond nitrogen balances (El Samra and Oláh, 1979). In this study, nutrient and organic carbon balances were analysed in chapter II and chapter III to serve as a starting point for any measures that may aim at improving the water quality in semi-intensive fishponds.

Efficiency use of inputs in fishponds

The efficiency use of a given input expresses the fraction of its total amount used during the production cycle that was incorporated into the harvested fish biomass (Zhang et al., 2016). A pond aquaculture system that would have the highest efficiency requires to be managed in harmony with natural processes and would thus reduce negative environmental impacts (Bosma and Verdegem, 2011). In semi-intensive pond aquaculture, such efficiency depends on the food chain energy efficiency, the quality of supplementary feed and culture system.

Factors influencing input use efficiency in fishponds

Structure of the food web

Input use efficiency in semi-intensive aquaculture depends on food chain efficiency (FCE) and food conversion efficiency. The food chain energy efficiency is the proportion of energy fixed by primary producers that is transferred to higher trophic levels (Dickman et al., 2008). Because many fish species reared in ponds cannot feed directly on phytoplankton, zooplankton or macroinvertebrates are involved in converting phytoplankton into fish biomass (van Dam et al., 2002). Thus, the diversity and abundance of zooplankton and macroinvertebrates regulate the use of primary production in fish production. The utilisation efficiency of phytoplankton via zooplankton does not depend only on increase of zooplankton biomass but also on zooplankton size because most planktivorous fish generally prey upon large-bodied zooplankton (Carpenter et al., 1985). In ponds with high stocking density, smaller zooplankton dominate due to high predation pressure (Přikryl, 1996). This smaller zooplankton community cannot exert greater grazing pressure on phytoplankton and fish do not feed on them hence a reduced use of the primary production by fish in ponds (Potužák et al., 2007).

Efficiency use of food by herbivorous zooplankton often depends on food quality characterised by its edibility and nutritional quality (Dickman et al., 2008). The gross growth efficiency of herbivores decreases with increasing food carbon to nutrient ratio (Elser et al., 2000a). These nutrient limitations caused by the stoichiometry of aquatic primary producers act upwards through the food web and constrain energy transfer from primary producers to higher trophic levels even at intermediate trophic levels (Malzahn et al., 2007). Species composition of the phytoplankton in ponds may also be an indicator of their quality as food for herbivores. Species specific attributes such as morphological features (size, shape, presence of gelatinous sheaths) and biochemicals (e.g. protein, polyunsaturated fatty acids, sterols concentrations) determine the nutritional value and edibility of phytoplankton (Martin-Creuzburg et al., 2008). For instance cyanobacteria dominates in eutrophic conditions and are well known for their grazing resistance associated with the formation of long filaments or cell colonies that renders them inedible for zooplankton.

Macroinvertebrates play a central role in the fishpond ecosystem as a food for fish and form an important part of the carp's diet (Adámek et al., 2003). Fishponds have a relatively low diversity of macroinvertebrates compared to other water bodies because they are regularly fertilised and become nutrient-rich (Wezel et al., 2014). Only macroinvertebrates tolerant to low levels of dissolved oxygen that are common at the sediment water interface and in the pond sediment are the most abundant in ponds (Ságová-Marecková, 2002). Macroinvertebrates are more diverse and abundant in fishponds having a substantial macrophyte cover, but in such conditions macrophytes provide effective refuges against fish predation (Broyer and Curtet, 2011). Fish management practices reduce the abundance of macroinvertebrates. In fishponds with high fish stock density, fish predation affects negatively the biomass and composition of macroinvertebrate community. Pond fertilisation, scrapping of shallow areas to increase water volume, sediment removal and regular drainage for fish harvest indirectly affect macroinvertebrate biomass and diversity hence reducing their efficiency in fish production (Broyer and Curtet 2011; Sychra and Adámek, 2011).

Feed quality

Food conversion efficiency is commonly measured as the feed conversion rate (FCR) calculated as the ratio of feed intake to weight gain (Fry et al., 2018). FCR indicates the efficiency with which feed is converted to animal biomass and a low FCR reduces the amount of waste generated through feeding (Boyd et al., 2007). Feed acceptability, digestibility of its ingredients and nutrient composition are the main factors that affects waste outputs originating from supplementary feeding (Cho and Bureau, 2001). Whereas FCR rates varying between 1.5 and 2.0 are considered good growth for most fish species (Craig et al., 2017), FCR rates of different grains used as feed in temperate carp ponds range between 4 and 5 (Woynarovich et al., 2011). Thus, generation of wastes from supplementary feeding should be expected in these ponds.

Species combination

Fish polyculture is based on the assumption that stocked fish species have fully or partially separated feeding niches and do not compete for food (Rahman et al., 2006). Stocking multiple species together increases the use of space and natural food available in the fishpond thus enhancing resource utilisation more than it is in monoculture ponds (Pokorný and Pechar 2000). Adequate stocking densities play a role as well. Zhang et al. (2016) found that the utilisation efficiency of organic carbon was three times higher in polyculture systems of swimming crab *Portunus trituberculatus* with white shrimp *Litopaneus vannamei* and short-necked clam *Ruditapes philippinarum* at an optimum stocking density of 6 crabs, 45 shrimps and 30 to 60 clams than in monoculture of crabs. In polyculture, one species may also enhance food availability, food production for another species and improvement of environmental conditions (Milstein, 1992). For instance, in a polyculture system combining rohu and common carp, nutrients resuspension by common carp increased the food availability in the pond, food utilisation and rohu growth and production (Rahman et al., 2006). Grass carp improves the living conditions of other fish by reducing nocturnal oxygen consumption by controlling excessive growth of macrophytes (Milstein, 1992). Chapter II of this study dealt with Input use efficiency and controlling factors in a representative semi-intensive Czech fishpond.

Fishery management and environmental impacts

With the static production of capture fishery, aquaculture emerged as the alternative to meet the ever increasing demands of fishery products (FAO, 2018). Despite the positive socio-economic results associated with aquaculture farming, its impact on environment and its sustainability have raised concern (Naylor et al., 2000). The impacts on the environment depend on the cultivated species, production system (e.g. extensive, semi-intensive, or intensive), stocking density, feed quality and management practices (Naylor et al., 2000).

Fishpond eutrophication

Eutrophication of aquatic ecosystems, including ponds, refers to the increasing primary productivity as a result of increased nutrient inputs (Wetzel, 2001). These inputs result from the low assimilation of feed, manuring or and fertilisation and changes in the pond catchment land use pattern (Pokorný and Hauser, 2002). Eutrophication causes major changes in the composition and quantity of phytoplankton, zooplankton macroinvertebrates and such changes are likely to affect the overall food web structure and the pond ecosystem stability (Jeppesen et al., 2000). The most obvious changes in eutrophic conditions are in the phytoplankton community where a transition from small, edible algae to larger and less edible algal forms and filamentous or toxic bacteria, or both, become more frequent. These large algae and cyanobacteria are a poor food for most zooplankton species resulting in a reduced transfer efficiency to higher trophic levels (Jeppesen et al., 2000; Jeppesen et al., 2003; Potužák et al., 2007). This unutilized primary production sinks and accumulates at the bottom where its breakdown depletes oxygen near the pond bottom. Bottom sediment becomes enriched in organic matter and nutrients (Pokorný and Hauser, 2002). The settled organic matter and nutrients can be exchanged with water by mineralization, bioturbation, chemical reactions, sediment mixing and resuspension (Sondergaard et al., 2001; Rahman et al., 2008a).

Quality of fishponds effluent

Effluent discharged from fishponds can cause modifications in receiving water bodies. These changes are related to higher concentrations of nitrogen (N), phosphorus (P), organic matter (OM) and suspended solids (SS) in effluents from fishponds than in the receiving water bodies (Banas et al., 2008). Increased nitrogen N and P in fishpond effluents triggers the growth of undesirable algal blooms while that of OM depletes oxygen due to OM decomposition in receiving waters. Acute exposure of SS interferes with the growth and reproduction of fish, increase the drift and mortality of macroinvertebrates, and affects the habitat quality of benthic organisms (Dodds and Whiles 2004; Banas et al., 2008). The quality of the effluent water is determined by the quality of the inlet water, the input types and levels, stocking density, water exchange rate, the pond sediment processes and the stage of the production cycle (Burford et al., 2003; Banas et al., 2008; Bosma and Verdegem, 2011). Chapter III of this study assessed the pollution potential of a representative Czech semi-intesnsive fishpond and its ability to retain nutrients.

Greenhouse gas emissions

Carbon dioxide (CO_2), methane (CH_4), and nitrogen oxide (N_2O) are the three major greenhouse gases (GHGs) (Hu et al., 2012; Selvam et al., 2014). Currently, there is an effort to quantify the emissions of these GHGs from different sources due to their atmospheric concentrations increase (Musenze et al., 2014). In fishponds as in other aquatic ecosystems, CO_2 is produced during the decomposition of organic matter under aerobic conditions, whereas CH_4 is produced under anaerobic conditions (Bastviken et al., 2004). Recently, researchers pointed out that the supersaturation of dissolved CH_4 in large and deep lakes can result also from CH_4 production in oxic water column (Grossart et al., 2011; Bogard et al., 2014). N_2O can be produced during both microbial nitrification and denitrification processes (Hu et al., 2013). GHGs may be emitted from open water to atmosphere in different four pathways: ebullition flux, diffusive flux, and flux through aquatic vegetation (Bastviken et al., 2004).

Different factors influence the production and emission of GHGs from aquatic ecosystems and may be having same effects in fishponds although few studies have been conducted to quantify the contribution of aquaculture to the global GHGs budget. GHGs are likely to be produced and released at a high rate in aquatic ecosystems containing easily degradable organic matter. However, CO_2 production and release is quite variable fluctuating between net release and a net sink on a daily or seasonal basis (Balmer and Downing 2011; Yang et al., 2018b). Oligotrophic and mesotrophic lakes and fishponds are frequently source of CO_2 because they receive large subsidies of allochthonous carbon (C) from their catchments and from fishery management, respectively (Cole et al., 2000). On the other hand, eutrophic lakes and fishponds acts as sinks of CO_2 due to high photosynthetic rates and accumulation of the produced organic matter in sediments (Balmer and Downing, 2011). Depletion of oxygen due to the decomposition of excessive production of labile autochthonous C in eutrophic lakes and fishponds can increase the production and emission of CH_4 and N_2O (Huttunen et al., 2003). Temperature is an important parameter that affects GHGs production and emission because microbial processes (organic matter decomposition, nitrification and denitrification) leading to their production are temperature dependent (Huotari et al., 2011; Natchimuthu et al., 2016).

Fishponds share processes and factors controlling GHGs production and emissions with other aquatic ecosystems but have particularities pertaining to the rearing system, shallowness, eutrophication, high fish stock, regular sediment perturbation and regular draining. The results are system specific and not unambiguous. For instance, addition of fish in rainfed rice fields increased the emission of CH_4 while it decreased that of N_2O (Frei et al., 2007; Datta et al., 2009). Contrarily, Liu et al. (2015) showed that the conversion of rice fields into ponds of crab and fish decreased the emissions of CH_4 and N_2O. Sediment bioturbation was the reason for the increase of CH_4 emissions from rice-fish integrated farms (Datta et al., 2009). Conversely, other studies showed that sediment bioturbation by benthic invertebrates increases CH_4 oxidation thus reducing CH_4 concentration and flux (Leal et al., 2007). Knowledge of the dynamics of GHGs and controlling factors in fishponds is important with respect to the development of sustainable aquaculture. The fourth chapter of this thesis was specifically designed to explore the production and emission of diffusive methane.

The aim of the thesis

Although fish productivity received attention in temperate carp ponds, there are still gaps in assessing the flow of energy and nutrient cycling in eutrophic carp ponds and their impact on greenhouse gases emissions. The overall aim of this thesis was to assess the efficiency use of inputs in temperate carp ponds. The specific objectives were:

I. to measure ecosystem metabolic rates in a hypereutrophic semi-intensive fishpond;
II. to measure carbon and nutrient balance in a hypereutrophic semi-intensive fishpond;
III. to determine and compare levels of dissolved CH_4 and diffusive CH_4 emission fluxes in nursery and main ponds and investigate their influencing factors.

References

Adámek, Z., 2014. Hydrobiology in Fisheries. In: Adámek, Z., Helešic, J., Maršálek, B., Rulík, M. (Eds), Applied Hydrobiology. FFPW USB, Vodňany, CZE, pp. 307–351.

Adámek, Z., Sukop, I., Rendón, P.M., Kouřil, J., 2003. Food competition between 2+ tench (*Tinca tinca* L.), common carp (*Cyprinus carpio* L.) and bigmouth buffalo (*Ictiobus cyprinellus* Val.) in pond polyculture. Journal of Applied Ichthyology 19: 165–169.

Adhikari, S., Sahu, B.C., Dey, L., 2012. Nutrients budget and effluents characteristics in polyculture of scampi (*Macrobrachium rosenbergii*) and Indian major carps ponds using organic inputs. Water Science and Technology 66: 1540–1548.

Balmer, M.B, Downing, J.A., 2011. Carbon dioxide concentrations in eutrophic lakes: undersaturation implies atmospheric uptake. Inland Waters 1: 125–132.

Banas, D., Masson, G., Leglize, L., Usseglio-Polatera, P., Boyd, C.E., 2008. Assessment of sediment concentration and nutrient loads in effluents drained from extensively managed fishponds in France. Environmental Pollution 152: 679–685.

Bastviken, D., Cole, J.J., Pace, M.L., Tranvik, L., 2004. Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. Global Biogeochemical Cycles 18: GB4009.

Bogard, M.J., Del Giorgio, P.A., Boutet, L., Chaves, M.C.G., Prairie, Y.T., Merante, A., Derry, A. M., 2014. Oxic water column methanogenesis as a major component of aquatic CH_4 fluxes. Nature Communications 5: 5350.

Bosma, R.H., Verdegem, M.C., 2011. Sustainable aquaculture in ponds: principles, practices and limits. Livestock Science 139: 58–68.

Boyd, C.E., Tucker, C., McNevin, A., Bostick, K., Clay, J., 2007. Indicators of resource use efficiency and environmental performance in fish and crustacean aquaculture. Reviews in Fisheries Science 15: 327–360.

Boyd, C.E., Wood, C.W., Chaney, P.L., Queiroz, J.F., 2010. Role of aquaculture pond sediments in sequestration of annual global carbon emissions. Environmental Pollution 158: 2537–2540.

Broyer, J., Curtet, L., 2011. The influence of fish farming intensification on taxonomic richness and biomass density of macrophyte-dwelling invertebrates in French fishponds. Knowledge and Management of Aquatic Ecosystems: 10.

Broyer, J., Curtet, L., 2012. Biodiversity and fish farming intensification in French fishpond systems. Hydrobiologia 694: 205–218.

Burford, M.A., Costanzo, S., Dennison, W., Jackson, C., Jones, A. McKinnon, A., Preston, N., Trott, L., 2003. A synthesis of dominant ecological processes in intensive shrimp ponds and adjacent coastal environments in NE Australia. Marine Pollution Bulletin 46: 1456-1469.

Carpenter, S., Kitchell, J., Hodgson, J., 1985. Cascad~ ng trophic Interactions and lake productivity. BioScience 35: 634–639.

Cho, C., Bureau, D., 2001. A review of diet formulation strategies and feeding systems to reduce excretory and feed wastes in aquaculture. Aquaculture Research 32: 349–360.

Ćirić, M., Subakov-Simić, G., Dulić, Z., Bjelanović, K., Ćičovački, S., Marković, Z., 2015. Effect of supplemental feed type on water quality, plankton and benthos availability and carp (*Cyprinus carpio* L.) growth in semi-intensive monoculture ponds. Aquaculture Research 46: 777–788.

Cole, J.J., Pace, M.L., Carpenter, S.R. Kitchell, J.F., 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnology and Oceanography 45: 1718–1730.

Craig, S., Helfrich, L.A., Kuhn, D., Schwarz, M.H., 2017. Understanding fish nutrition, feeds, and feeding. Page 4 PublicationVirginia State University, Yorktown, Virginia. No. 420–256.

Datta, A., Nayak, D., Sinhababu, D., Adhya, T., 2009. Methane and nitrous oxide emissions from an integrated rainfed rice-fish farming system of Eastern India. Agriculture, ecosystems & environment 129: 228–237.

Dickman, E.M., Newell, J.M., Gonzalez, M.J., Vanni, M.J., 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proceedings of the National Academy of Sciences of the United States of America 105: 18408–18412.

Dodds, W.K., Whiles, M.R., 2004. Quality and quantity of suspended particles in rivers: continent-scale patterns in the United States. Environmental Management 33: 355–367.

El Samra, M., Oláh, J., 1979. Significance of nitrogen fixation in fish ponds. Aquaculture 18: 367–372.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, S., Interlandi, A., Kilham, S.S., McCauley, E., Schulz, K.L., 2000a. Nutritional constraints in terrestrial and freshwater food webs. Nature 408: 578.

Elser, J.J., Sterner, R.W., Galford, A.E., Chrzanowski, T.H., Findlay, D.L., Mills, K.H., Paterson, M. J., Stainton, M. P., Schindler, D.W., 2000b. Pelagic C : N : P stoichiometry in a eutrophied lake: Responses to a whole-lake food-web manipulation. Ecosystems 3: 293–307.

FAO, 2018. The state of World fisheries and aquaculture. FAO, Rome, Italy.

Frei, M., Razzak, M., Hossain, M., Oehme, M., Dewan, S., Becker, K., 2007. Methane emissions and related physicochemical soil and water parameters in rice-fish systems in Bangladesh. Agriculture, Ecosystems & Environment 120: 391–398.

Fry, J. P., Mailloux, N.A., Love, D. C., Milli, M. C., Cao, L., 2018. Feed conversion efficiency in aquaculture: do we measure it correctly? Environmental Research Letters 13: 024017.

Garg, S., Bhatnagar, A., 2000. Effect of fertilization frequency on pond productivity and fish biomass in still water ponds stocked with *Cirrhinus mrigala* (Ham.). Aquaculture Research 31: 409–414.

Gross, A., Boyd, C.E., Wood, C., 2000. Nitrogen transformations and balance in channel catfish ponds. Aquacultural Engineering 24:1–14.

Grossart, H.-P., Frindte, K., Dziallas, C., Eckert, W., Tang, K.W., 2011. Microbial methane production in oxygenated water column of an oligotrophic lake. Proceedings of the National Academy of Sciences 108: 19657–19661.

Hargreaves, J.A., 1998. Nitrogen biogeochemistry of aquaculture ponds. Aquaculture 166: 181–212.

Havens, K.E., Phlips, E.J., Cichra, M.F., Li, B.L., 1998. Light availability as a possible regulator of cyanobacteria species composition in a shallow subtropical lake. Freshwater Biology 39: 547–556.

Hendzel, L., Hecky, R., Findlay, D., 1994. Recent changes of N2-fixation in Lake 227 in response to reduction of the N: P loading ratio. Canadian Journal of Fisheries and Aquatic Sciences 51: 2247–2253.

Holdren, C., Jones, B., Taggart, J., 2001. Managing lakes and reservoirs. North American Lake Management Society; Terrene Insitute, Madison.

Houser, J.N., 2006. Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. Canadian Journal of Fisheries and Aquatic Sciences 63: 2447–2455.

Hu, Z., Lee, J.W., Chandran, K., Kim, S., Khanal, S.K., 2012. Nitrous oxide (N_2O) emission from aquaculture: a review. Environmental Science & Technology 46: 6470–6480.

Hu, Z., Lee, J.W., Chandran, K., Kim, S., Sharma, K., Brotto, A.C., Khanal, S.K., 2013. Nitrogen transformations in intensive aquaculture system and its implication to climate change through nitrous oxide emission. Bioresource technology 130: 314–320.

Huotari, J., Ojala, A., Peltomaa, E., Nordbo, A., Launiainen, S., Pumpanen, J., Rasilo, T., Hari, P., Vesala, T., 2011. Long-term direct CO_2 flux measurements over a boreal lake: Five years of eddy covariance data. Geophysical Research Letters 38: L18401.

Huttunen, J.T., Alm, J., Liikanen, A., Juutinen, S., Larmola, T., Hammar, T., Silvola, J. Martikainen, P.J., 2003. Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. Chemosphere 52: 609–621.

Jeppesen, E., Peder Jensen, J., SØndergaard, M., Lauridsen, T., Landkildehus, F., 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology 45: 201–218.

Jeppesen, E., Jensen, J.P., Jensen, C., Faafeng, B., Hessen, D.O., Søndergaard, M., Lauridsen, T., Brettum, P. , Christoffersen, K., 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the arctic. Ecosystems 6: 313–325.

Kestemont, P., 1995. Different systems of carp production and their impacts on the environment. Aquaculture 129: 347–372.

Knud-Hansen, C.F., Batterson, T.R., McNabb, C.D., Harahat, I.S., Sumantadinata, K., Eidman, H. M., 1991. Nitrogen input, primary productivity and fish yield in fertilized freshwater ponds in Indonesia. Aquaculture 94: 49–63.

Knud-Hansen, C.F., Hopkins, K.D., Guttman, H., 2003. A comparative analysis of the fixed-input, computer modeling, and algal bioassay approaches for identifying pond fertilization requirements for semi-intensive aquaculture. Aquaculture 228: 189–214.

Kopáček, J., Prochazkova, L., Hejzlar, J., Blažka, P., 1997. Trends and seasonal patterns of bulk deposition of nutrients in the Czech Republic. Atmospheric Environment 31: 797–808.

Leal, J.J.F., dos Santos Furtado, A. L., de Assis Esteves, F., Bozelli, R.L., Figueiredo-Barros, M. P., 2007. The role of *Campsurus notatus* (Ephemeroptera: Polymitarcytidae) bioturbation and sediment quality on potential gas fluxes in a tropical lake. Hydrobiologia 586: 143–154.

Liu, S., Hu, Z., Wu, S., Li, S., Li, Z., Zou, J., 2015. Methane and nitrous oxide emissions reduced following conversion of Rice paddies to inland crab-fish aquaculture in Southeast China. Environmental Science & Technology 50: 633–642.

Malzahn, A.M., Aberle, N., Clemmesen, C., Boersma, M., 2007. Nutrient limitation of primary producers affects planktivorous fish condition. Limnology and Oceanography 52: 2062–2071.

Martin-Creuzburg, D., von Elert, E., Hoffmann, K.H., 2008. Nutritional constraints at the cyanobacteria–*Daphnia magna* interface: the role of sterols. Limnology and Oceanography 53: 456–468.

Milstein, A., 1992. Ecological aspects of fish species interactions in polyculture ponds. Hydrobiologia 231: 177–186.

Musenze, R.S., Grinham, A., Werner, U., Gale, D., Sturm, K., Udy, J., Yuan, Z., 2014. Assessing the spatial and temporal variability of diffusive metha,ne and nitrous oxide emissions from subtropical freshwater reservoirs. Environmental Science & Technology 48: 14499–14507.

Natchimuthu, S., Sundgren, I., Gålfalk, M., Klemedtsson, L., Crill, P., Danielsson, Å., Bastviken, D., 2016. Spatio-temporal variability of lake CH_4 fluxes and its influence on annual whole lake emission estimates. Limnology and Oceanography 61: S13–S26.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C., Clay, J., Folke, C., Lubchenco, J., Mooney, H., Troell, M., 2000. Effect of aquaculture on world fish supplies. Nature 405: 1017.

Pálffy, K., Présing, M., Vörös, L., 2013. Diversity patterns of trait-based phytoplankton functional groups in two basins of a large, shallow lake (Lake Balaton, Hungary) with different trophic state. Aquatic Ecology 47: 195–210.

Pechar, L., 2000. Impacts of long-term changes in fishery management on the trophic level water quality in Czech fish ponds. Fisheries Management and Ecology 7: 23–31.

Pokorný, J., Hauser, V., 2002. The restoration of fish ponds in agricultural landscapes. Ecological Engineering 18: 555–574.

Pokorný, J., Pechar, L., 2000. Development of fishpond ecosystems in the Czech Republic. Role of management and nutrient input (Limnological review). Sylvia 36: 8–15.

Pokorný, J., Prikryl, I., Faina, R., Kansiime, F., Kaggwa, R.C., Kipkemboi, J., Kitaka, N., Denny, P., Bailey, R., Lamtane, H., 2005. Will fish pond management principles from the temperate zone work in tropical fish ponds. Natural and constructed Wetlands: Nutrients, Metals and Management: 382–399.

Potužák, J., Hůda, J., Pechar, L., 2007. Changes in fish production effectivity in eutrophic fishponds-impact of zooplankton structure. Aquaculture International 15: 201–210.

Přikryl, I., 1996. Development of fishery management in ponds and its reflection in zooplankton structure as a possible criterion of pond's biological value in the Czech Republic. In: Flajšhans, M. (Ed.), Collection of scientific work to 75th anniversary of establishment of Research Institute of Fish Culture and Hydrobiology. USB, Vodňany, CZ, pp. 153–166.

Rahman, M., Verdegem, M., Nagelkerke, L., Wahab, M., Milstein, A., Verreth, J., 2006. Growth, production and food preference of rohu *Labeo rohita* (H.) in monoculture and in polyculture with common carp *Cyprinus carpio* (L.) under fed and non-fed ponds. Aquaculture 257: 359–372.

Rahman, M., Jo, Q., Gong, Y., Miller, S., Hossain, M., 2008. A comparative study of common carp (*Cyprinus carpio* L.) and calbasu (*Labeo calbasu* Hamilton) on bottom soil resuspension, water quality, nutrient accumulations, food intake and growth of fish in simulated rohu (Labeo rohita Hamilton) ponds. Aquaculture 285: 78–83.

Robin, J., Wezel, A., Bornette, G., Arthaud, F., Angelibert, S., Rosset, V., Oertli, B., 2014. Biodiversity in eutrophicated shallow lakes: determination of tipping points and tools for monitoring. Hydrobiologia 723: 63–75.

Ságová-Marecková, M., 2002. Distribution of benthic macroinvertebrates in relationship to plant roots, sediment type and spatial scale in fishponds and slow streams. Archiv für Hydrobiologie 156: 63–81.

Sahu, B.C., Adhikari, S., Mahapatra, A. S., Dey, L., 2013. Carbon, nitrogen, and phosphorus budget in scampi (*Macrobrachium rosenbergii*) culture ponds. Environmental Monitoring and Assessment 185: 10157–10166.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walkerk, B., 2001. Catastrophic shifts in ecosystems. Nature 431: 591–596.

Schindler, D., 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnology and Oceanography 23: 478–486.

Selvam, P.B., Natchimuthu, S., Arunachalam, L., Bastviken, D., 2014. Methane and carbon dioxide emissions from inland waters in India–implications for large scale greenhouse gas balances. Global Change Biology 20: 3397–3407.

Sondergaard, M., Jensen, P.J., Jeppesen, E., 2001. Retention and internal loading of phosphorus in shallow, eutrophic lakes. The Scientific World Journal 1: 427–442.

Sychra, J., Adámek, Z., 2011. The impact of sediment removal on the aquatic macroinvertebrate assemblage in a fishpond littoral zone. Journal of Limnology 70: 129–138.

Troell, M., Naylor, R.L., Metian, M., Beveridge, M., Tyedmers, P.H., Folke, C., Arrow, K.J., Barrett, S., Crépin, A.-S., Ehrlich, P.R., 2014. Does aquaculture add resilience to the global food system? Proceedings of the National Academy of Sciences 111: 13257–13263.

Tsai, J.-W., Kratz, T.K., Hanson, P.C., Wu, J.-T., Chang, W.Y.B., Arzberger, P.W., Lin, B.-S., Lin, F.-P., Chou, H.-M., Chiu, C.-Y., 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. Freshwater Biology 53: 1929–1941.

van Dam, A.A., Beveridge, M.C.M., Azim, M.E., Verdegem, M.C.J., 2002. The potential of fish production based on periphyton. Reviews in Fish Biology and Fisheries 12: 1–31.

Vanacker, M., Wezel, A., Payet, V., Robin, J., 2015. Determining tipping points in aquatic ecosystems: The case of biodiversity and chlorophyll alpha relations in fish pond systems. Ecological Indicators 52: 184–193.

Wetzel, R.G. 2001. Limnology: lake and river ecosytems. 3rd edition. Academic Press, San Diego.

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

Woynarovich, A., Bueno, P. B., Altan, O., Jeney, Z., Reantaso, M., Xinhua, Y., Van Anrooy, R., 2011. Better management practices for carp production in Central and Eastern Europe, the Caucasus and Central Asia. FAO Fisheries and Aquaculture Technical Paper 566. FAO, Ankara.

Yang, P., Zhang, Y., Lai, D.Y., Tan, L., Jin, B., Tong C., 2018. Fluxes of carbon dioxide and methane across the water–atmosphere interface of aquaculture shrimp ponds in two subtropical estuaries: The effect of temperature, substrate, salinity and nitrate. Science of The Total Environment 635: 1025–1035.

Zhang, K., Tian, X.-l., Dong, S.-l., Feng, J., He, R.-p., 2016. An experimental study on the budget of organic carbon in polyculture systems of swimming crab with white shrimp and short-necked clam. Aquaculture 451: 58–64.

CHAPTER 2

CARBON METABOLISM AND NUTRIENT BALANCE IN A HYPEREUTROPHIC SEMI-INTENSIVE FISHPOND

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RESEARCH PAPER — OPEN ACCESS

Carbon metabolism and nutrient balance in a hypereutrophic semi-intensive fishpond

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Abstract – Eutrophication and nutrient pollution is a serious problem in many fish aquaculture ponds, whose causes are often not well documented. The efficiency of using inputs for fish production in a hypereutrophic fishpond (Dehtář), was evaluated using organic carbon (OC), nitrogen (N) and phosphorus (P) balances and measurement of ecosystem metabolism rates in 2015. Primary production and feeds were the main inputs of OC and contributed 82% and 13% to the total OC input, respectively. Feeds and manure were the major inputs of nutrients and contributed 73% and 86% of the total inputs of N and P, respectively. Ecosystem respiration, accumulation in water and accumulation in sediment were the main fates of OC, N and P, respectively. They accounted for 79%, 52% and 61% of OC, N and P inputs. The efficiency of using OC, N and P inputs to produce fish biomass was very low and represented 0.9%, 25% and 23% of total OC, N, and P inputs, indicating an excessive phytoplankton production and overdosing of fish feeds and manure. Dehtář pond was slightly autotrophic and phosphorus availability did not limit the phytoplankton growth. The low efficiency of using inputs was attributed to the low digestibility of raw cereals grain used as feed and the inability of planktonic food webs to transfer the primary production to fish due to high predatory pressure of fish stock on zooplankton. The primary production is an important input of OC in semi-intensive fishponds and should be considered in evaluations of fish production efficiency.

Keywords: Aquaculture pond / input use efficiency / metabolism / organic carbon / nitrogen / phosphorus / primary production / freshwater fish production

Résumé – Métabolisme du carbone et équilibre des nutriments dans un étang eutrophe d'aquaculture semi-intensive. L'eutrophisation et la pollution par les nutriments constituent un grave problème dans de nombreux étangs piscicoles, dont les causes sont souvent mal documentées. L'efficacité de l'utilisation des intrants pour la production de poissons dans un étang hypertrophique (Dehtář) a été évaluée à l'aide des bilans du carbone organique (CO), de l'azote (N) et du phosphore (P) et de la mesure des taux du métabolisme des écosystèmes en 2015. La production primaire et les aliments pour animaux étaient les principaux intrants de CO et contribuaient respectivement à 82 % et 13 % de l'intrant total en CO. Les aliments du bétail et le fumier étaient les principaux intrants d'éléments nutritifs et contribuaient à 73 % et 86 % des intrants totaux d'azote et de phosphore, respectivement. La respiration de l'écosystème, l'accumulation dans l'eau et l'accumulation dans les sédiments étaient les principaux devenirs du CO, du N et du P, respectivement. Ils représentaient 79 %, 52 % et 61 % des intrants du CO, de l'azote et du phosphore. L'efficacité de l'utilisation des intrants de CO, N et P pour produire de la biomasse de poisson était très faible et représentait 0,9 %, 25 % et 23 % des intrants totaux de CO, N et P, ce qui indique une production excessive de phytoplancton et un surdosage des aliments pour poissons et du fumier. L'étang Dehtář était légèrement autotrophe et la disponibilité du phosphore n'a pas limité la croissance du phytoplancton. La faible efficacité de l'utilisation des intrants a été attribuée à la faible digestibilité des céréales brutes utilisées comme aliments pour animaux et à l'incapacité des réseaux alimentaires planctoniques à transférer la production

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primaire aux poissons en raison de la forte pression prédatrice des stocks de poissons sur le zooplancton. La production primaire est un intrant important du CO dans les étangs semi-intensifs et devrait être prise en compte dans les évaluations de l'efficacité de la production piscicole.

Mots-clés : Bassin aquacole / efficacité d'utilisation des intrants / métabolisme / carbone organique / azote / phosphore / production primaire / production de poissons d'eau douce

1 Introduction

Fish production in semi-intensive aquaculture depends, in addition to the natural productivity of ponds, on manuring and supplementary feeding (Broyer and Curtet, 2012; Wezel *et al.*, 2013). Manure is added in fishponds in order to increase fish yields by supporting primary production and feed is added to sustain high density of fish stock that can no longer rely on the food produced naturally in the fishpond (Adámek, 2014; Knud-Hansen *et al.*, 1991). The efficiency of using inputs in semi-intensive fishpond management depends on the flow of energy in the food chain towards fish, either through the grazing or the detritus food chains (Pokorný *et al.*, 2005). The availability of abundant zooplankton and macroinvertebrates throughout the growing season plays a key role in maintaining this efficiency in carp ponds. However, the intensification of fish production, together with inputs of nutrients and organic residues from wastewater and agricultural areas, has often resulted in fishpond eutrophication (Nhan *et al.*, 2006; Pokorný and Hauser, 2002). In summer months, hypereutrophic water bodies (Vollenweider and Kerekes, 1982) are characterised by a primary producer community dominated by planktonic cyanobacteria and a low biomass of zooplankton (Pálffy *et al.*, 2013; Scheffer *et al.*, 2001; Sommer *et al.*, 2012). Increased turbidity and availability of nutrients favour the growth of cyanobacteria while fish grazing pressure and lack of edible phytoplankton limit the growth of zooplankton. Fish in hypereutrophic ponds and lakes are threatened by phytoplankton die off followed by drops in dissolved oxygen levels that can even reach lethal values for fish (Jeppesen *et al.*, 1990; Schindler *et al.*, 2008). Such states indicate that the planktonic primary production of the pond exceeds the capacity of the food chain to exploit the produced phytoplankton biomass (Pechar, 2000; Potužák *et al.*, 2007). In addition, the hypereutrophic condition of water bodies is a sign that the system receives nutrients in excess, especially phosphorus, which is considered a limiting factor for the primary production in freshwater ecosystems (Reynolds and Davies, 2001; Schindler *et al.*, 2008).

Improvement of pond water quality and pond effluent is crucial to achieve an ecological sustainable aquaculture (Alongi *et al.*, 2009). A balance between the amount of supplemented nutrients and organic matter added and that used to produce fish biomass is required to avoid excessive fishpond eutrophication (Bosma and Verdegem, 2011). Prior to taking actions to try to improve the water quality in fishponds, it is important to understand the sources, sinks and transformation of nutrients and organic matter in fishponds. The magnitude of total primary production and respiratory processes in the aquatic ecosystem and the use of nutrients can be determined by measuring diurnal changes in dissolved oxygen (DO) concentrations and nutrient balance (Adhikari *et al.*, 2012; Staehr *et al.*, 2010). Using these methods, it is also possible to show how effective the fertilization and application of fish feed is for the growth and the production of fish in ponds.

The aim of this study was to assess the effective utilisation of organic carbon (OC) and nutrient inputs for the production of fish in the Dehtář pond, a typical representative of semi-intensive, hypereutrophic fishponds in the Czech Republic (Pechar, 2000). Specific objectives were to determine ecosystem metabolic rates, carbon and nutrient balance and to compare the inputs to the amount of nutrients that were really needed to attain the produced fish biomass. In addition, phosphorus regeneration in the fishpond and the amount of phosphorus needed to counterbalance its limitation in the system were also measured. We hypothesise that the inefficient use of nutrients, mainly P, its overdosing and then its re-cycling within the aquatic ecosystem lead to hypereutrophic conditions observed in semi-intensive fishponds.

2 Methodology

2.1 Study area

The Dehtář pond (49.0083N, 14.3058E; 406.4 m above sea level) is situated in the upper Vltava River basin and is the last and lowest water body in the system of fishponds in the upper basin of the Dehtářský stream (Fig. 1). It ranks among the ten largest Czech fishponds, having a surface area of 2.28 km^2, maximum and mean depths of 5.5 and 2.2 m, respectively, and a catchment area of 91.4 km^2 (Potužák *et al.*, 2016). It is used as a polyculture semi-intensive fishpond. Manure and supplementary feed, mainly wheat, rye or barley grains, are added to increase fish production over natural productivity, which is between ca 100 and 200 $kg\,ha^{-1}\,yr^{-1}$ in this region (Kestemont, 1995; Pechar, 2000). Common carp (*Cyprinus carpio* L.) usually represents 95% of stocked fish biomass and the remaining 5% are composed of grass carp (*Ctenopharyngodon idella* Valenciennes 1844), bighead carp (*Hypophthalmichthys nobilis* Richardson 1845), pike-perch (*Sander lucioperca* L.), and northern pike (*Esox lucius* L.). It is one of the fishponds called main ponds as it is stocked with two-year-old carp that are harvested at the end of a two-year growing cycle. Ponds in which younger fish are kept are known as nursery ponds (Pokorný and Pechar, 2000). This study was carried out during the first year of the fish production cycle.

2.2 Sampling and data used

Three platforms equipped with high frequency stations for recording water temperature (T_w) and dissolved oxygen (DO) (M4016, Fiedler AMS) were installed in the Dehtář pond at three sites (Fig. 1), *i.e.* at the dam (D), Dehtářský bay (DB), and Babický bay (BB). T_w and DO were recorded in 10 minute

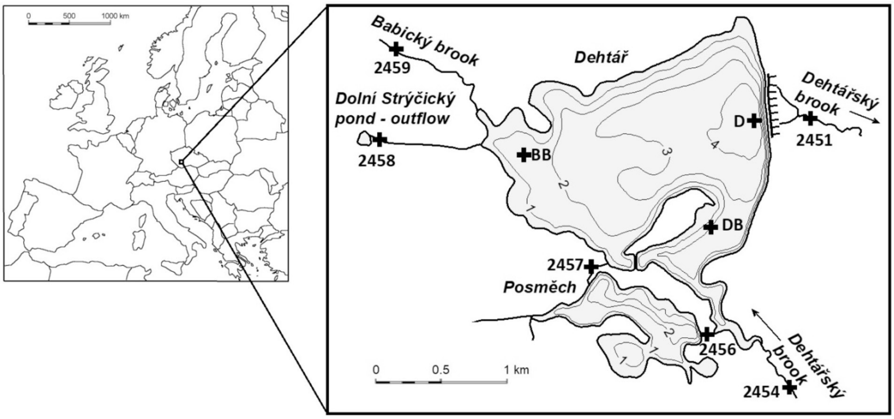

Fig. 1. Location of the Dehtář pond. The crosses indicate the metabolism measurements and water sampling sites. The isobaths in the Dehtář and Posměch ponds show the depths in meters at the water level at maximum filling.

intervals at 0.3-m and 1.5-m depths at the dam (site D) and at 0.3-m depth at sites DB and BB. Site D was also equipped with a meteorological station (M4016-A-G3, Fiedler AMS) to record air temperature, wind speed at 2-m height, and shortwave incident radiation at the same intervals as above. The stations were operated from April to November 2015. Maintenance, checking and re-calibration of the stations were performed at weekly or two-week intervals based on algal growth on the sensors.

For the evaluation of water quality and nutrient balance, water samples were taken from the pond, its tributaries, and the outflow. On days of the maintenance of stations, integrated water samples were taken from the top 2-m layer at all three sites and grab samples from the 3-m depth and 0.5 m above the bottom at site D using a Friedinger sampler. All five tributaries (*i.e.*, sites No. 2454, 2456, 2457, 2458, 2459; Fig. 1) and the outflow (No. 2451; Fig. 1) were sampled and their flow was measured once a month from December 2014 to March 2015, and every two weeks from April to November 2015. The samples were analysed for concentrations of nutrients, namely total carbon (TC), total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total nitrogen (TN), nitrate nitrogen ($N\text{-}NO_3^-$), ammonium nitrogen ($N\text{-}NH_4^+$), total phosphorus (TP), dissolved phosphorus (DP), soluble reactive phosphorus (SRP), and chlorophyll *a* (Chl*a*). The analyses are specified in Supplementary Material, Table S1. The flow was measured using a hydrometric probe (FlowTracker, Sontek, USA). In the pond at sites D, DB and BB, water transparency was measured with a Secchi disc and a multiparametric probe (YSI 6600 V2-4) was used to record vertical profiles of T_w and DO at 0.5 m depth intervals. Water level in the pond was read out at a gauge fixed at the dam structure weekly or more frequently from January to December 2015.

The hydrological characteristics of the Dehtář pond, namely its inflows, outflows, volume of stored water and water level changes, were reconstructed in a daily time step. First, the two-weekly measured data in the inflows were completed by the hydrological analogy from the recorded daily flow data in a nearby stream (the Zlatý potok) and information on the timing of filling up and/or emptying of the ponds situated upstream in the catchment. Then the water balance of the Dehtář pond was calculated as the difference between water inputs (the reconstructed daily inflows plus daily precipitation on the pond surface) and losses of water (evaporation, outflow and seepage). The loss of water by seepage was calculated by subtracting the inputs from the other losses and was positively correlated with the level of pond filling. The precipitation data originated from the climatic station of the Czech Hydrometeorological Institute at České Budějovice (48.9518N, 14.4698E; distance from the Dehtář pond ca 13 km). Daily evaporation from the pond was calculated using the Penman-Montheith formula based on daily average temperature, air humidity, radiation and wind speed data (Wetzel, 2001). The theoretical water residence time was calculated by dividing the average water volume of the Dehtář pond by the average inflow (George and Hurley, 2003).

2.3 Metabolism measurements, phosphorus regeneration and phosphorus demand

Ecosystem metabolic rates in the pond were calculated using a model developed for lakes (Hanson *et al.*, 2003; Staehr *et al.*, 2010) expressed in the equation: $\Delta O_2/\Delta t = GPP - ER - F - A$. In this formula, $\Delta O_2/\Delta t$ is the change in dissolved oxygen over time, GPP the gross primary production, ER the total ecosystem respiration, F the oxygen exchange with the atmosphere, and A includes other processes affecting the concentration of dissolved oxygen such as inflow, outflow, leakage or photochemical decomposition of humic substances. $\Delta O_2/\Delta t$ was determined from measured dissolved oxygen concentrations that were area and volume weighted at each of the three sites. The F values were modelled as a function of the concentration gradient between the actual and saturation values of dissolved oxygen concentration at a given temperature and the coefficient of wind and temperature dependent reaction according to Staehr *et al.* (2010). The values of A were neglected as insignificant for the conditions present at the Dehtář pond (Coloso *et al.*, 2011; Staehr *et al.*, 2010). Since the primary production is zero at night, the ecosystem respiration was calculated from the decrease of dissolved oxygen in the pond during the night and from exchange with the atmosphere (Lauster *et al.*, 2006; Sadro *et al.*, 2011). Furthermore, assuming that ecosystem respiration is the same during the day and night, the hourly average respiration was multiplied by 24 hours to obtain total daily ecosystem respiration (ER). Daily net ecosystem production (NEP) was obtained by summing the change in oxygen concentration from all time steps from dawn to dawn. Gross primary production (GPP) was obtained by summing daily NEP and daily ER.

Regeneration and demand of orthophosphate phosphorus by the planktonic community were calculated from the monthly metabolic rates (Kamarainen *et al.*, 2009; Knoll *et al.*, 2016). First, the values of the GPP, ER and NEP were converted from oxygen units ($mg\,m^{-2}\,d^{-1}\,O_2$) to carbon units ($mg\,m^{-2}\,d^{-1}C$) multiplying them by 0.33 (*i.e.*, mass ratio of O_2 and C assuming a photosynthetic quotient of 1.15 (Knoll *et al.*, 2016). Then, the net planktonic production (NPP) was calculated as the difference between GPP and autotrophic respiration (R_{auto}), where R_{auto} was assumed to be 70% of ER according to previous studies in eutrophic lakes (Biddanda *et al.*, 2001; del Giorgio and Peters, 1993; Staehr *et al.*, 2010). Heterotrophic respiration (R_{hetero}) was assumed to be 30% of ER according to the same studies. Phosphorus regeneration was then obtained by dividing R_{hetero} by seston C/P ratio and phosphorus demand was obtained by dividing the NPP by seston C/P ratio (Kamarainen *et al.*, 2009; Knoll *et al.*, 2016).

2.4 Balance of organic carbon and nutrients

The balance of organic carbon, nitrogen and phosphorus in the Dehtář pond was calculated from May to October 2015 using the equation: $\Delta M/\Delta t = \mathrm{GPP} + \mathrm{IN} + \mathrm{AD} + \mathrm{FF} + \mathrm{M} - \mathrm{ER} - \mathrm{OUT} - \mathrm{FISH} - \mathrm{RET}$. In this equation, $\Delta M/\Delta t$ is the change in the quantity of organic carbon or nutrients in the pond water between the beginning and the end of the balance period, GPP is the gross primary production (applicable for organic carbon only), IN, AD, FF, and M are the inputs from inflows, atmospheric deposition, fish feed, and manure, respectively, ER is the loss of organic carbon by ecosystem respiration, OUT and FISH are the outputs from the system by outflow plus seepage and by the uptake into the produced fish biomass, respectively, and RET is the calculated residual of the balance and represents retention in the sediment and/or loss to the atmosphere. The inputs by the inflows and atmospheric deposition and the outputs by the outflow and seepage were calculated for each month as the product of the monthly averaged measured concentrations and the corresponding monthly volumes of water entering or leaving the pond. Afterwards the monthly values were summed over the study period. The concentrations in the atmospheric deposition used were from the measurements of bulk precipitation at the Slapy reservoir. It is a long term project monitoring atmospheric

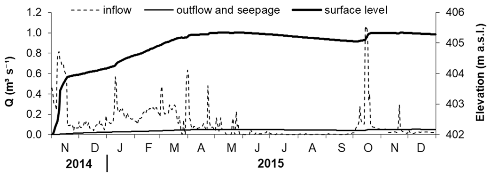

Fig. 2. Water inflow, outflow and losses by seepage, and trend of surface water level in the Dehtář pond during the period from November 2014 to December 2015.

deposition carried out by researchers from the Institute of Hydrobiology (Biology Centre of the Czech Academy of Sciences) (Kopáček *et al.*, 1997). The volume-weighted means in the atmospheric deposition collected from May to October 2015 and used in the balance were 3.1 $mg\,l^{-1}$, 1.34 $mg\,l^{-1}$ and 42 $\mu g\,l^{-1}$ for TOC, TN and TP, respectively, and the depth of precipitation was 307 mm over the same period. The concentrations of TOC, TN and TP in manure, feed and fish were obtained from the literature. The TOC, TN and TP inputs in manure, feed and output in harvested fish were estimated by multiplying their quantity with their respective concentrations. The mean concentrations of TOC, TN and TP in manure (cattle straw manure) were 100, 5.0 and 1.3 $g\,kg^{-1}$ (MA-CR, 1998) whereas those for the feed (wheat grain) were 420, 15 and 4.0 $g\,kg^{-1}$ (Čermák *et al.*, 2008; Hlaváč *et al.*, 2015; Rachon *et al.*, 2015), respectively. Concentrations of TOC, TN and TP in fish biomass were considered to be 150, 40 and 7 to 9 $g\,kg^{-1}$ (specifically for each species), respectively (Rothschein, 1983). The fish growth was estimated by empirical growth models for each species based on their stocked size and weight, and considering mortality losses that were calibrated for the Dehtář pond on six previous 2-year production periods with available data for stocking and harvest.

3 Results

3.1 Fishpond management

The Dehtář pond started refilling just after autumn fish harvest in November 2014 but the surface level did not reach the level planned for the 1st year of the production cycle (*i.e.*, 405.85 m a.s.l.) due to dry weather conditions and little inflow (Fig. 2). The average pond morphological parameters during the balance period May–October 2015 were significantly smaller than its nominal values (*i.e.*, volume 2.56 hm^3, flooded area 1.57 km^2; maximum and mean depths 4.7 and 1.6 m, respectively). The water renewal in the pond was minimal during the May–October period, with a theoretical water residence time of 1.6 years. The outflow from the pond occurred only through seepage, except at the end of October when a small amount of water was discharged through the main pond outlet at the dam.

Fish were stocked in November 2014 and in March 2015 (20% and 80% of the stocked biomass, respectively). The total biomass of the stocked fish was 390 $kg\,ha^{-1}$ and consisted of 97% of common carp, 2.3% of grass carp, 0.6% of pikeperch, 0.1% of pike, and 0.1% of bighead carp. The body weight of the stocked common carp was 360 g on average and increased

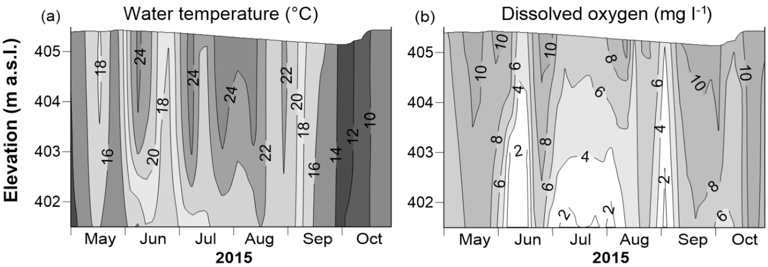

Fig. 3. Stratification of (a) water temperature (°C) and (b) dissolved oxygen (mg l^{-1}) in the Dehtář pond at site D during the period from May to October 2015 plotted using weekly or two-weekly measured profiles.

to ca 1.1 kg at the end of the growing season, according to our fish growth model. As in many Czech fishponds, also weed fish, dominated mainly by topmouth gudgeon (*Pseudorasbora parva* Temminck & Schlegel, 1846) and including roach (*Rutilus rutilus* L.), common bream (*Abramis brama* L.), silver bream (*Abramis bjoerkna* L.), rudd (*Scardinius erythrophthalmus* L.), and Prussian carp (*Carassius gibelio* Bloch, 1782) (Musil *et al.*, 2007), were present in the Dehtář pond. Their biomass and time of pond invasion were not recorded in this study but were noticed later, at the fish harvest in 2016 (J. Potužák, pers. commun.). The biomass of stocked fish nearly doubled by the end of the study period, when it was 750 kg ha^{-1}, according to the fish growth model. Cattle manure was used in the pond at the beginning of the growing season from March to April in the amount of 2200 kg ha^{-1}. Wheat grain was used as supplementary feed with 4, 13, 26, 37 and 20% of total feed applied in May, June, July, August and September, respectively. The amounts of fish feed took into account water temperature, visually assessed zooplankton biomass and increasing biomass of fish stock. Fish were fed twice a week in May and three times a week in the remaining months. The total amount of supplementary feed used over the study period was 1900 kg ha^{-1}. The food conversion ratio (FCR) that was calculated by dividing the feed amount (kg) by the live weight gain (kg) of the fish was 5.7.

3.2 Stratification and water quality

Thermal and oxygen stratification in the water column at site D during May–October 2015 showed a general polymictic pattern (Fig. 3). Nevertheless, during periods of warm and still weather, the water column stratified and DO rapidly exhausted above the bottom, leading to hypoxia. Largely depleted DO in such temporarily formed hypolimnion was measured in the first half of June, during almost the whole of July until early August, and in the beginning of September. In late summer and autumn, stratification became unstable with frequent mixing of the entire water column. Nevertheless, a temporary mild stratification was observed in September and early October, when differences in *Tw* in the water column were low (usually <0.5 °C) but DO concentrations at the surface and above the bottom differed significantly from the middle layers of the water column.

Dissolved and particulate fractions of OC, N and P concentrations increased gradually in the Dehtář pond during the May–October period (Fig. 4b, e, h). The DOC and POC concentrations increased approximately twofold: DOC from about 11 to 20 mg l^{-1} and POC from about 4 to 9 mg l^{-1}. Inorganic carbon (TIC) increased relatively less from about 21 to 30 mg l^{-1}. A similar seasonal pattern of C concentrations also occurred in the inflow into the pond (Fig. 4a), but its effect on concentrations in the Dehtář pond was minimal due to a very low flow during the summer (Fig. 2). Phytoplankton was present in the pond at a high concentration all year, with a drop in spring and then a gradual increase during the growing season, as evidenced by an increase in Chl*a* concentration from approximately 30 μg l^{-1} in spring to more than 100 μg l^{-1} at the end of summer (Fig. 4c) and from the transparency of water decreasing from 0.65 m in May to 0.4 m in summer (Fig. 4f). TN concentration in the pond gradually increased from ca 1 to 2.5 mg l^{-1} concurrent with an accumulation of organic N (ON), while inorganic forms of nitrogen (N-NO_3^- and N-NH_4^+) were low during the whole season (<0.05 mg l^{-1}). TP concentration also increased throughout the growing season to nearly 200 μg l^{-1} in the later summer and autumn, while SRP was relatively low (10–40 μg l^{-1}). Despite low concentrations of inorganic N and P forms, biomass of seston increased during the whole growing season with a sestonic molar C/P ratio ranging from 100 to 150 (Fig. 4i).

3.3 Metabolic rates and phosphorus regeneration

High-frequency measurement of the DO concentration at depths of 0.3 to 1.5 m showed large fluctuations of their daily values from hypersaturation to deeply hypoxic values (Fig. 5a). The DO concentrations in these layers were always higher than the critical survival concentration of about 2 mg l^{-1} for cyprinid fish (Svobodova *et al.*, 1993). The metabolic rates showed very dynamic changes characterized by frequent alternations between periods of autotrophy and periods of heterotrophy (Fig. 5b, c). The number of autotrophic days (NEP $>$ 0) was almost equal to the number of heterotrophic days (NEP $<$ 0) with a proportion of 53% and 47%, respectively. Daily rates of NEP ranged between -6.8 and 7.8 g O_2 m^{-2} d^{-1} with an average of 0.2 g O_2 m^{-2} d^{-1} (Fig. 5c) and the Dehtář pond was therefore slightly autotrophic. GPP

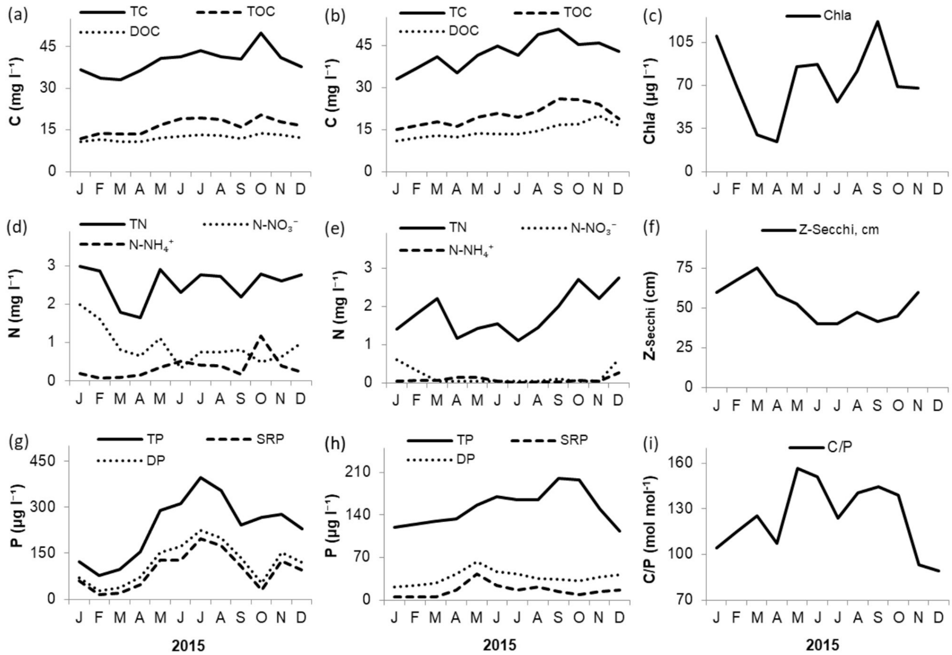

Fig. 4. Water quality in the Dehtář pond at site D and its inflow in 2015: (a) total carbon (TC), total organic carbon (TOC) and dissolved organic carbon (DOC) in the total volume-weighted inflow to the pond, (b) TC, TOC and DOC in the pond, (c) chlorophyll-a (Chl*a*) in the pond, (d) total nitrogen (TN), nitrate nitrogen (N-NO_3^-) and ammonium nitrogen (N-NH_4^+) in the total volume-weighted inflow to the pond, (e) TN, N-NO_3– and NH_4^+ in the pond, (f) water transparency (Z-Secchi), (g) total phosphorus (TP), dissolved phosphorus (DP) and soluble reactive phosphorus (SRP) in total volume-weighted inflow to the pond, (f) TP, DP and SRP in the pond, (i) C/P ratio in the pond.

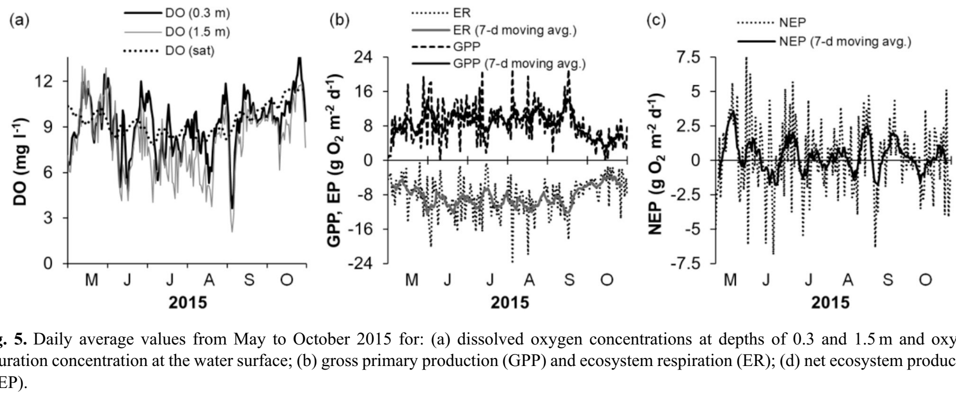

Fig. 5. Daily average values from May to October 2015 for: (a) dissolved oxygen concentrations at depths of 0.3 and 1.5 m and oxygen saturation concentration at the water surface; (b) gross primary production (GPP) and ecosystem respiration (ER); (d) net ecosystem production (NEP).

Table 1. Monthly metabolic rates of C (g m^{-2} d^{-1}), C/P ratio of seston (mol mol^{-1}), P regeneration (mg m^{-2} d^{-1}) and P demand (mg m^{-2} d^{-1}) in the Dehtář pond water from May to October 2015.

	GPP	ER	NEP	NP	C/P	P regeneration	P demand
May	2.4	2.1	0.3	0.9	123	13	19
June	3.3	3.2	0.1	1.0	149	17	17
July	3.0	3.0	0.0	0.9	124	17	17
August	3.4	3.2	0.2	1.2	138	17	22
September	3.1	3.0	0.1	1.0	149	16	17
October	1.5	1.6	–0.1	0.5	152	8	8
Average	*2.8*	*2.7*	*0.1*	*0.9*	*139*	*15*	*17*

Table 2. Balance of OC, N and P in the Dehtář pond from May to October 2015 in metric tons and percentages related to total inputs.

Variable	Organic carbon		Nitrogen		Phosphorus	
	(t)	(%)	(t)	(%)	(t)	(%)
			Inputs			
GPP	836	82	–	–	–	–
Inflow water	18	1.7	2.48	27	0.27	13
Rainfall	2.6	0.3	0.01	0.1	0.01	0.5
Feed	133	13	4.75	53	1.27	63
Manure	36	3.5	1.8	20	0.47	23
Total inputs	*1025*	*100*	*9.04*	*100*	*2.02*	*100*
			Outputs			
ER	807	79	–	–	–	–
Outflow and seepage	17	1.7	1.27	14	0.13	6
Fish production	8.8	0.9	2.3	25	0.46	23
Total outputs	*833*	*81*	*3.57*	*40*	*0.59*	*29*
Accumulation in water	30	2.9	4.66	52	0.2	10
Retention and/or losses	162	15.8	0.81	9	1.23	61

rates varied between 0.1 and 21.1 g O_2 m^{-2} d^{-1} with an average of 8.5 g O_2 m^{-2} d^{-1} (Fig. 5b). ER rates varied between 0.4 and 24 g O_2 m^{-2} d^{-1} with an average of 8.2 g O_2 m^{-2} d^{-1} (Fig. 5b). Monthly averages values of GPP and ER were higher from June to September while NEP increased moderately in May and August (Tab. 1). The rate of P regeneration in the planktonic community was in the range of 8–19 mg m^{-2} d^{-1} while P demand ranged between 8 and 22 mg m^{-2} d^{-1} (Tab. 1).

3.4 Organic carbon and nutrient balance

Total inputs of OC into the Dehtář pond during the 2015 growing season were 1025 t (Tab. 2). GPP, fish feeds and manure were the pond's main sources with a contribution of 82, 13 and 3.5% of all OC inputs, respectively. Manure was included in the balance because, although it was used before the beginning of the balance period, its decomposition is slow and its effect persists during the growing season. Ecosystem respiration was the main pathway of OC output from the system and accounted for 79% of all OC inputs. A small amount of OC (1.7%) left the system through the outflow and seepage, and an even smaller fraction (0.9% of OC inputs) was assimilated in the produced fish biomass. The fraction of OC that accumulated in the pond water, the calculated retention in the sediment, and/or loss of OC to the atmosphere represented 2.9 and 15.8% of all OC inputs, respectively.

Inputs of N and P into the Dehtář pond during the growing season of 2015 were 9.0 t and 2.0 t, respectively (Tab. 2). The main source for both nutrients was aquaculture: feed and manure applications contributed 73% of N inputs and 86% of P inputs. Inflows were the second most important source of nutrients into the pond and contributed 27 and 13% to TN and TP inputs, respectively. Unlike OC, relatively higher percentages of nutrients inputs were incorporated in the biomass of produced fish, namely 25 and 23% for TN and TP, respectively. The outflow and seepage accounted for 14% of TN and 6% of TP inputs in the pond. A significant proportion of N accumulated in the pond water during the growing season (*i.e.*, 52% of TN inputs), whereas only 9% of TN was retained in the sediment and/or lost from the system. In contrast, the accumulation of P in pond water and P retention were 10 and 61% of TP inputs, respectively, indicating that P is more susceptible to sedimentation than N.

Table 3. Example values of metabolic rates in some selected lakes. Z_{mean} (m): mean depth of the lake, GPP (mmol O_2 m^{-2} d^{-1}): gross primary production, ER (mmol O_2 m^{-2} d^{-1}): ecosystem respiration, NEP (mmol O_2 m^{-2} d^{-1}). International country codes based on the ISO 3166 standard published by the International Organization for Standardization (https://www.iso.org/iso-3166-country-codes.html) are in parentheses.

Lake	Z_{mean}	Trophic status	Major source of OC	GPP	ER	NEP	Reference
Yuan-Yang (TWN)	1.5	Oligotrophic/dystrophic	Allochthonous	0.03	0.09	–0.06	Tsai *et al.* (2008)
Northgate Bog (USA)	1.5	Oligotrophic/dystrophic	Allochthonous	11	116	–105	Hanson *et al.* (2003)
Hummingbird (USA)	1.5	Mesotrophic/dystrophic	Allochthonous, phytoplankton	23	219	–196	Hanson *et al.* (2003)
Võrstjär (EST)	2.8	Eutrophic	Phytoplankton	97	94	3	Laas *et al.* (2012)
Apopka (USA)	1.7	Hypereutrophic	Phytoplankton, sediment	104	198	–94	Bachmann *et al.* (2000)
Albardiosa (ESP)	0.26	Hypereutrophic	Macrophytes	175	152	23	Florín and Montes (1998)
Dehtář (CZE)	1.7	Hypereutrophic	Phytoplankton	265	257	8	This study
Santa Olalla (ESP)	0.37	Hypereutrophic	Phytoplankton, wild animals	285	308	−23	López-Archilla *et al.* (2004)
Frederiksborg Slotssø (DNK)	3.5	Hypereutrophic	Phytoplankton	366	357	9	Staehr and Sand-Jensen (2007)

4 Discussion

4.1 Structure of fishpond ecosystem, trophic conditions and metabolism

The ecosystem structure of Dehtář pond reflected the effect of reared fish that were stocked at high density. The phytoplankton community were dominated by colonial, filamentous algae and cyanobacteria during the summer months (Fránková *et al.*, 2017), submersed aquatic plants were absent whereas emergent macrophytes were sparse in the littoral zone (K. Šumberová *et al.*, unpubl. data). The zooplankton community was composed mainly of small-sized zooplankton species (*e.g. Bosmina longirostris*, nauplii, cyclopoid copepods, rotifers) and macroinvertebrates were rare (Potužák *et al.*, 2007). These results are comparable to those of Iglesias *et al.* (2011) who found that small-sized zooplankton were inversely related to fish density in lakes. This ecosystem structure may be explained by the spectrum of the natural food of common carp and the present weed fish. Adult common carp are primarily bottom feeders and prefer macroinvertebrates but they are also water column feeders and consume larger zooplankton (Adámek *et al.*, 2003). High predation pressure by intentionally over-stocked fish eliminates large zooplankton individuals and macroinvertebrates at a high rate (Rahman *et al.*, 2006). Weed fish compete with common carp for macroinvertebrates and large zooplankton, especially *Daphnia*, further reducing zooplankton and macroinvertebrate biomass (Musil *et al.*, 2014). The zooplankton community is thus dominated by small individuals that cannot control the growth of larger and colonial species of phytoplankton (Matsuzaki *et al.*, 2009). The abundance and diversity of macroinvertebrates were further reduced in Dehtář pond by frequent hypoxic conditions above the pond bottom and low biomass of macrophytes (Lemmens *et al.*, 2015). This alteration of the grazing food web structure leads to autochthonous organic matter being accumulated and not being used in the food chain and subsequent fish biomass production, but instead sinking to the pond bottom and being degraded by microbial loop communities (Deines *et al.*, 2015; Přikryl, 1996).

TOC, TN and TP concentrations in the Dehtář pond increased during the study period, mainly due to the accumulation of sestonic (or particulate) organic matter, nitrogen and phosphorus in water. The reason was apparently the increasing phytoplankton biomass as evidenced by the increase of Chl*a*. The increase in the total amount of nutrients during the growing season was obviously due to feed addition rather than to inputs from the surrounding catchment, since the inflow and outflow were negligible. The low water exchange rate and small precipitation observed during this study further supported nutrient accumulation and growth of phytoplankton biomass in the Dehtář pond. These results are consistent with the results of Hopkins *et al.* (1993), who found that Chl*a*, nutrients and organic matter concentrations were negatively correlated with water exchange and positively correlated with pond production.

N-NO_3^-, N-NH_4^+ and SRP were low during the whole season. These low concentrations may be explained by denitrification and nutrient uptakes by the growing phytoplankton. Despite the relatively low concentrations of SRP throughout the growing season, phosphorus availability was clearly not a factor limiting the growth of phytoplankton. This is apparent from the molar *C*/*P* ratio of seston that varied between 100 and 150 (Fig. 4i), hence not differing much from the Redfield ratio (*i.e.*, 106) in phytoplankton not limited by phosphorus (Hecky and Kilham, 1988; Vrba *et al.*, 1995). There are two plausible explanations of this continuous growth and increase of phytoplankton biomass at such low inorganic nutrient levels: (i) Biotic recycling of organic P in the water column may explain this sustained growth of phytoplankton (Kamarainen *et al.*, 2009; Knoll *et al.*, 2016). Indeed, the calculated P needs for the planktonic community were the same as the P regeneration rate (Tab. 1). In addition, common carp excrete substantial amounts of nutrients that favour phytoplankton growth (Chumchal and Drenner, 2004). (ii) Sediment-bound P could have been released during the study period in the deepest parts of the pond where anoxic conditions were prevailing at the sediment water interface (Sondergaard *et al.*, 2003).

In this study, the Dehtář pond can be classified as slightly autotrophic, based on the calculated metabolic rates. This indicates that the production of organic matter by phytoplankton was higher than its aerobic degradation by various living components of the Dehtář ecosystem. GPP and ER in Dehtář were comparable to lakes with similar trophic status (Tab. 3) where production of organic matter by phytoplankton and/or macrophytes was the source of OC that fuelled ER (Laas *et al.*, 2012). On the other hand, GPP and NEP in the Dehtář pond were higher compared to those from heterotrophic lakes with lower trophic status (Tab. 3). In such lakes, various living components of the ecosystem breakdown organic matter by respiration at rates that exceed its production by photosynthesis. This occurs mainly in clear-water, humic and mesotrophic lakes receiving substantial terrestrial organic matter to fuel respiration (Duarte and Prairie, 2005). However, heterotrophy is not always supported by allochthonous OC in lakes. It can also be supported by autochthonous OC accumulated in lake sediment over time. Lake Apopka is an example of a heterotrophic lake in which excess respiration is supported by organic matter originating from a massive burial of macrophytes in the lake sediment. An irreversible ecological disturbance caused by hurricanes switched the community of primary producers from a macrophyte dominated one to a phytoplankton dominated (Bachmann *et al.*, 2000). Despite substantial external OC inputs (feed and manure), the ecosystem metabolism was not heterotrophic in the Dehtář pond. A part of these inputs and GPP were respired while another part was retained in the sediment or metabolised anaerobically by methanogenesis and released into the atmosphere as carbon dioxide (CO_2) or methane (CH_4) (Oliveira Junior *et al.*, 2019). Based on the findings of Rutegwa *et al.* (2019), Dehtář pond may have released 2 tons of diffusive CH_4-C corresponding to 0.2% of total OC inputs to the pond over six months of this study in 2015. Total CH_4 emission can be even higher if bubble flux of CH_4-C is accounted for.

4.2 Use efficiency of nutrient inputs

The efficiency of using OC, N and P inputs in the production of fish biomass in the Dehtář pond was 0.9, 25 and 23% of all OC, TP and TN inputs. The assimilation of OC by fish in this study is comparable to the results of Boyd *et al.* (2010) who reported the efficiency of OC use in the range of 0.86 to 3.44% in tilapia ponds. Our value is lower than the OC use efficiency reported by Zhang *et al.* (2016) who observed higher values, ranging from 4.5 to 8.3%, in polyculture ponds of swimming crab, white shrimp and short necked clam in China. This higher efficiency of OC use apparently resulted from a better use of OC inputs by the reared species exploiting different feeding niches. The efficiency of N and P use reported in our study is also in the range of the values reported in other studies of polyculture fishponds. On average, produced fish utilise ca 25 and 20% of N and P, respectively, of all N and P inputs (Hargreaves, 1998; Rahman *et al.*, 2008).

This comparison shows that in general the efficiency of using OC, N and P inputs is relatively small in the current practice of managing semi-intensive fishponds. A large proportion of inputs (more than 95% of OC and three quarters of N and P) in this type of ponds is not used by the reared animals. In the Dehtář pond, there are two obvious reasons for this low efficiency: (i) high predation pressure on zooplankton due to high fish biomass, which causes poor transfer of C from phytoplankton via zooplankton and/or benthic macroinvertebrates to fish; and (ii) low digestibility of the wheat grain used as fish feed. Under such conditions, the fish must be fed by supplementary feed. The low share of zooplankton as a source of food for fish in Czech semi-intensive ponds can be further demonstrated by the fatty acid (FA) composition of the produced common carp. The FA composition in fish muscles reflects the diet (Steffens, 1997). Zooplankton and macroinvertebrates that feed on algae are rich in omega-3 (n-3) and omega-6 (n-6) polyunsaturated fatty acids (PUFA) while cereals are carbohydrate rich and poor in n-3 PUFA (Böhm *et al.*, 2014). The contents of n-3 and n-6 PUFA and the ratio n-3/n-6 PUFA are several times lower in carp which feed mostly on cereals in densely stocked ponds than in extensive ponds, where conditions are favourable for large zooplankton (Steffens and Wirth, 2007). Similarly, Mráz *et al.* (2012) showed that fish produced in semi-intensive Czech fishponds supplemented with cereals have low levels of n-3 and n-6 PUFA and low n-3/n-6 PUFA ratios suggesting the low contribution of zooplankton and macroinvertebrates in their diet and demonstrating low efficiency of using algal primary production in fish biomass production.

The low ability of reared fish to digest cereals is another reason that may explain the low efficiency of using OC, N and P inputs in the Dehtář pond (Degani, 2006; Fagbenro, 1999). The absence of phytase in the carp digestive tract and the presence of digestive enzyme-resistant compounds in cereals (*e.g.* phytates) is a reason that has been suggested to explain this low cereal digestibility (Fagbenro, 1999). The low digestibility of cereals increases FCR leading to an accumulation of wastes from feed in the fishpond. The FCR in our study was 5.7, which is higher than the average FCR of 4.7 in carp ponds using cereals as supplementary feed (Woynarovich *et al.*, 2011). Thus, partially digested grain promotes primary production by releasing nutrients (P and N) instead of serving as direct feed for fish. They end up becoming part of the pond bottom and may be ingested again along with plant detritus by carp after being partially degraded by bacteria. Detritus may contribute approximately 70% of the natural food of common carp in extensively managed ponds (Adámek *et al.*, 2003). However, more research is needed to understand this pathway of nutrient use from feed. The poor quality of supplementary feed used in the Dehtář pond may also be used to explain the contribution of supplied feed to fish production. Fish biomass production in this study ($370\,kg\,ha^{-1}$) was lower than the expected production of $565\,kg\,ha^{-1}$, which should be achieved with an average FCR value for carp ponds that use wheat as a supplementary feed (Woynarovich *et al.*, 2011). The FCR of grain is lower than the optimal one that ranges between 1.5 and 2 (Craig *et al.*, 2017).

5 Conclusion

The use efficiency of OC, TN and TP inputs in the produced fish biomass was low, indicating an overloading of OC, N and P in the Dehtář pond, similar to other polyculture carp ponds with comparable fishery management practices. Respiration was the main output of OC from the pond, while accumulation in water and sediment were the main routes for N and P, respectively. This overloading by inputs impairs pond water quality, and primary production does not contribute much to fish production. The main reasons are high fish density and the disruption of the natural food chain in the pond. This also increases the pollution potential of effluents from fish farming activities and emissions of greenhouse gases. Unused inputs represent avoidable production costs. Our results from the Dehtář pond, which were obtained under low flow hydrological conditions when many pond processes were well recognizable, call for more research into pond management practices that will help to improve fish production efficiency while minimizing pollution risks in Dehtář pond and other hypereutrophic carp ponds. These practices include the decrease of fish stock density, stopping the use of manure and replacing cereals by draff or mechanically treated cereals.

Supplementary Material

Supplementary material provided by the author.
The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2019043/olm.

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References

Adámek Z. 2014. Hydrobiology in Fisheries. In: Adámek Z, Helešic J, Maršálek B, Rulík, M. (ed.), Applied Hydrobiology. Vodnany, CZ: USB, 376.

Adámek Z, Sukop I, Rendón PM, Kouřil J. 2003. Food competition between 2+ tench (*Tinca tinca* L.), common carp (*Cyprinus carpio* L.) and bigmouth buffalo (*Ictiobus cyprinellus* Val.) in pond polyculture. *J Appl Ichthyol* 19: 165–169.

Adhikari S, Sahu BC, Dey L. 2012. Nutrients budget and effluents characteristics in polyculture of scampi (Macrobrachium rosenbergii) and Indian major carps ponds using organic inputs. *Water Sci Technol* 66: 1540–1548.

Alongi DM, McKinnon AD, Brinkman R, Trott LA, Undu MC. 2009. The fate of organic matter derived from small-scale fish cage aquaculture in coastal waters of Sulawesi and Sumatra, Indonesia. *Aquaculture* 295: 60–75.

Bachmann RW, Hoyer MV, Canfield DE. 2000. Internal heterotrophy following the switch from macrophytes to algae in Lake Apopka, Florida. *Hydrobiologia* 418: 217–227.

Biddanda B, Ogdahl M, Cotner J. 2001. Dominance of bacterial metabolism in oligotrophic relative to eutrophic waters. *Limnol Oceanogr* 46: 730–739.

Böhm M, Schultz S, Koussoroplis A-M, Kainz MJ. 2014. Tissue-specific fatty acids response to different diets in common carp (*Cyprinus carpio* L.). *PLOS ONE* 9: e94759.

Bosma RH, Verdegem MC. 2011. Sustainable aquaculture in ponds: principles, practices and limits. *Livestock Sci* 139: 58–68.

Boyd CE, Wood CW, Chaney PL, Queiroz JF. 2010. Role of aquaculture pond sediments in sequestration of annual global carbon emissions. *Environ Pollut* 158: 2537–2540.

Broyer J, Curtet L. 2012. Biodiversity and fish farming intensification in French fishpond systems. *Hydrobiologia* 694: 205–218.

Čermák B, Cempírková R, Jeroch H, *et al*. 2008. Krmiva konvenční a ekologická/Feedstuffs conventional and ecological : vědecká monografie. Jihočeská univerzita v Českých Budějovicích, Zemědělská fakulta, 326 s., České Budějovice.

Chumchal MM, Drenner RW. 2004. Interrelationships between phosphorus loading and common carp in the regulation of phytoplankton biomass. *Archiv für Hydrobiol* 161: 147–158.

Coloso JJ, Cole JJ, Pace ML. 2011. Difficulty in discerning drivers of lake ecosystem metabolism with high-frequency data. *Ecosystems* 14: 935.

Craig S, Helfrich LA, Kuhn D, Schwarz MH. 2017. Understanding fish nutrition, feeds, and feeding. Publication 420-256. Yorktown, Virginia: Virginia State University, 4.

Degani G. 2006. Digestible energy in dietary sorghum, wheat bran, and rye in the common carp (*Cyprinus carpio* L.).

Deines AM, Bunnell DB, Rogers MW, Beard TD Jr., Taylor WW. 2015. A review of the global relationship among freshwater fish, autotrophic activity, and regional climate. *Rev Fish Biol Fish* 25: 323–336.

del Giorgio PA, Peters RH. 1993. Balance between phytoplankton production and plankton respiration in lakes. *Can J Fish Aquatic Sci* 50: 282–289.

Duarte CM, Prairie YT. 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. *Ecosystems* 8: 862–870.

Fagbenro O. 1999. Apparent digestibility of various cereal grain by-products in common carp diets. *Aquacult Int* 7: 277–281.

Florín M, Montes C. 1998. Which are the relevant scales to assess primary production of Mediterranean semiarid salt lakes. *Int J Ecol Environ Sci* 24: 161–177.

Fránková M, Šumberová K, Potužák J, Vild O. 2017. The role of plant substrate type in shaping the composition and diversity of epiphytic diatom assemblages in a eutrophic reservoir. *Fund Appl Limnol/Arch Hydrobiol* 189: 117–135.

George DG, Hurley MA. 2003. Using a continuous function for residence time to quantify the impact of climate change on the dynamics of thermally stratified lakes. *J Limnol* 21–26.

Hanson PC, Bade DL, Carpenter SR, Kratz TK. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnol Oceanogr* 48: 1112–1119.

Hargreaves JA. 1998. Nitrogen biogeochemistry of aquaculture ponds. *Aquaculture* 166: 181–212.

Hecky R, Kilham P. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment 1. *Limnol Oceanogr* 33: 796–822.

Hlaváč D, Másílko J, Hartman P, *et al*. 2015. Effects of common carp (*Cyprinus carpio* Linnaeus, 1758) supplementary feeding with modified cereals on pond water quality and nutrient budget. *J Appl Ichthyol* 31: 30–37.

Hopkins JS, Hamilton RD, Sandier PA, Browdy CL, Stokes AD. 1993. Effect of water exchange rate on production, water quality, effluent characteristics and nitrogen budgets of intensive shrimp ponds. *Journal of the World Aquaculture Society* 24: 304–320.

Iglesias C, Mazzeo N, Meerhoff M, *et al*. 2011. High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments. *Hydrobiologia* 667: 133–147.

Jeppesen E, Søndergaard M, Sortkjær O, Mortensen E, Kristensen P. 1990. Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study of phytoplankton collapses in Lake Søbygård, Denmark. Trophic Relationships in Inland Waters. Springer, 149–164.

Kamarainen AM, Penczykowski RM, Van de Bogert MC, Hanson PC, Carpenter SR. 2009. Phosphorus sources and demand during summer in a eutrophic lake. *Aquat Sci* 71: 214–227.

Knoll LB, Morgan A, Vanni MJ, Leach TH, Williamson TJ, Brentrup JA. 2016. Quantifying pelagic phosphorus regeneration using three methods in lakes of varying productivity. *Inland Waters* 6: 509–522.

Knud-Hansen CF, Batterson TR, McNabb CD, Harahat IS, Sumantadinata K, Eidman HM. 1991. Nitrogen input, primary productivity and fish yield in fertilized freshwater ponds in Indonesia. *Aquaculture* 94: 49–63.

Kopáček J, Prochazkova L, Hejzlar J, Blažka P. 1997. Trends and seasonal patterns of bulk deposition of nutrients in the Czech Republic. *Atmos Environ* 31: 797–808.

Laas A, Noges P, Koiv T, Noges T. 2012. High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. *Hydrobiologia* 694: 57–74.

Lauster GH, Hanson PC, Kratz TK. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. *Can J Fish Aquat Sci* 63: 1130–1141.

Lemmens P, Mergeay J, Van Wichelen J, De Meester L, Declerck SA. 2015. The impact of conservation management on the community composition of multiple organism groups in eutrophic interconnected man-made ponds. *PLOS ONE* 10: e0139371.

López-Archilla AI, Molla S, Coleto MC, Guerrero MC, Montes C. 2004. Ecosystem metabolism in a mediterranean shallow lake (Laguna de Santa Olalla, Donana National Park, SW Spain). *Wetlands* 24: 848–858.

MA. 1998. Decree no 274/1998 on storage and use of fertilisers. In: Agriculture (ed.). Czech Ministry of Agriculture, Prague.

Matsuzaki SS, Usio N, Takamura N, Washitani I. 2009. Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia* 158: 673–686.

Mráz J, Máchová J, Kozák P, Pickova J. 2012. Lipid content and composition in common carp–optimization of n-3 fatty acids in different pond production systems. *J Appl Ichthyol* 28: 238–244.

Musil J, Adámek Z, Baranyi C. 2007. Seasonal dynamics of fish assemblage in a pond canal. *Aquacul Int* 15: 217–226.

Musil M, Novotná K, Potužák J, Huda J, Pechar L. 2014. Impact of topmouth gudgeon (*Pseudorasbora parva*) on production of common carp (*Cyprinus carpio*)—question of natural food structure. *Biologia* 69: 1757–1769.

Nhan DK, Milstein A, Verdegem MC, Verreth JA. 2006. Food inputs, water quality and nutrient accumulation in integrated pond systems: a multivariate approach. *Aquaculture* 261: 160–173.

Oliveira Junior ES, Temmink RJ, Buhler BF, *et al*. 2019. Benthivorous fish bioturbation reduces methane emissions, but increases total greenhouse gas emissions. *Freshw Biol* 64: 197–207.

Pálffy K, Présing M, Vörös L. 2013. Diversity patterns of trait-based phytoplankton functional groups in two basins of a large, shallow lake (Lake Balaton, Hungary) with different trophic state. *Aquat Ecol* 47: 195–210.

Pechar L. 2000. Impacts of long-term changes in fishery management on the trophic level water quality in Czech fish ponds. *Fish Manag Ecol* 7: 23–31.

Pokorný J, Hauser V. 2002. The restoration of fish ponds in agricultural landscapes. *Ecol Eng* 18: 555–574.

Pokorný J, Pechar L. 2000. Development of fishpond ecosystems in the Czech Republic. Role of management and nutrient input (Limnological review). *Sylvia* 36: 8–15.

Pokorný J, Prikryl J, Faina R, *et al*. 2005. Will fish pond management principles from the temperate zone work in tropical fish ponds. *Nat Construc Wetlands* 382–399.

Potužák J, Duras J, Drozd B. 2016. Mass balance of fishponds: are they sources or sinks of phosphorus? *Aquacult Int* 24: 1725–1745.

Potužák J, Huda J, Pechar L. 2007. Changes in fish production effectivity in eutrophic fishponds-impact of zooplankton structure. *Aquacult Int* 15: 201–210.

Přikryl I. 1996. Development of fishery management in ponds and its reflection in zooplankton structure as a possible criterion of pond's biological value in the Czech Republic. In: Flajšhans, M. (ed.), Collection of scientific work to 75th anniversary of establishment of Research Institute of Fish Culture and Hydrobiology. Vodnany, CZ: USB, 153–166.

Rachon L, Szumilo G, Brodowska M, Wozniak A. 2015. Nutritional value and mineral composition of grain of selected wheat species depending on the intensity of a production technology. *J Elementol* 20.

Rahman M, Verdegem M, Nagelkerke L, Wahab M, Milstein A, Verreth J. 2006. Growth, production and food preference of rohu *Labeo rohita* (H.) in monoculture and in polyculture with common carp *Cyprinus carpio* (L.) under fed and non-fed ponds. *Aquaculture* 257: 359–372.

Rahman MM, Nagelkerke LA, Verdegem MC, Wahab MA, Verreth JA. 2008. Relationships among water quality, food resources, fish diet and fish growth in polyculture ponds: a multivariate approach. *Aquaculture* 275: 108–115.

Reynolds C, Davies P. 2001. Sources and bioavailability of phosphorus fractions in freshwaters: a British perspective. *Biolog Rev* 76: 27–64.

Rothschein J. 1983. Kolobeh fosforu a ryp vo vodárenských nádřziach. *Vodní hosp* B33: 9–13.

Rutegwa M, Gebauer R, Veselý L, *et al*. 2019. Diffusive methane emissions from temperate semi-intensive carp ponds. *Aquacult Environ Interact* 11: 19–30.

Sadro S, Melack JM, MacIntyre S. 2011. Depth-integrated estimates of ecosystem metabolism in a high-elevation lake (Emerald Lake, Sierra Nevada, California). *Limnol Oceanogr* 56: 1764–1780.

Scheffer M, Carpenter S, Foley JA, Folke, C, Walkerk B. 2001. Catastrophic shifts in ecosystems. *Nature* 431: 591–596.

Schindler DW, Hecky R, Findlay D, *et al*. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. *Proc Natl Acad Sci* 105: 11254–11258.

Sommer U, Adrian R, De Senerpont Domis L, *et al*. 2012. Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. *Annu Rev Ecol Evol Syst* 43: 429–448.

Sondergaard M, Jensen JP, Jeppesen E. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506: 135–145.

Staehr PA, Bade D, Van de Bogert MC, *et al*. 2010. Lake metabolism and the diel oxygen technique: State of the science. *Limnol Oceanogr Methods* 8: 628–644.

Staehr PA, Sand-Jensen K. 2007. Temporal dynamics and regulation of lake metabolism. *Limnol Oceanogr* 52: 108–120.

Steffens W. 1997. Effects of variation in essential fatty acids in fish feeds on nutritive value of freshwater fish for humans. *Aquaculture* 151: 97–119.

Steffens W, Wirth M. 2007. Influence of nutrition on the lipid quality of pond fish: common carp (*Cyprinus carpio*) and tench (*Tinca tinca*). *Aquac Int* 15: 313–319.

Svobodova Z, Lloyd R, Baddow L, Essex C, Machova J, Vykusova B. 1993. Water quality and fish health. *EIFAC Technical paper* 54: 59.

Tsai J-W, Kratz TK, Hanson PC, *et al*. 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. *Freshw Biol* 53: 1929–1941.

Vollenweider RA, Kerekes JJ. 1982. Eutrophication of waters. Monitoring assessment and control. Environment Directorate OECD, Paris. 154 p.

Vrba J, Vyhnálek V, Hejzlar J, Nedoma J. 1995. Comparison of phosphorus deficiency indices during a spring phytoplankton bloom in a eutrophic reservoir. *Freshw Biol* 33: 73–81.

Wetzel RG. 2001. Limnology: Lake and River Ecosystems, 3rd edn. ed. Elsevier, San Diego: Academic Press.

Wezel A, Robin J, Guerin M, Arthaud F, Vallod D. 2013. Management effects on water quality, sediments and fish production in extensive fish ponds in the Dombes region, France. *Limnologica* 43: 210–218.

Woynarovich A, Bueno PB, Altan O, *et al*. 2011. Better management practices for carp production in Central and Eastern Europe, the Caucasus and Central Asia. FAO, Rome: FAO Fisheries and Aquaculture Technical Paper.

Zhang K, Tian X-l, Dong S-l, Feng J, He R-p. 2016. An experimental study on the budget of organic carbon in polyculture systems of swimming crab with white shrimp and short-necked clam. *Aquaculture* 451: 58–64.

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CHAPTER 3

NUTRIENT RETENTION EFFICIENCY IN A HYPEREUTROPHIC FISHPOND

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Nutrient retention efficiency in a hypereutrophic fishpond

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Abstract

The maximisation of fish production may reduce non-production functions including nutrient and organic matter retention in earthen fishponds. Water quality of inflow, pond water and outflow were monitored from 2015 to 2018 in a Central Europe semi-intensive fishpond. In addition, balances of nutrients and ecosystem metabolic rates calculation were used to investigate phosphorus and nitrogen retention in the pond during these two-year fish production cycles. The phytoplankton trophic index (44±2 µg TP l^{-1}), the average of Secchi depth (0.7±0.1 m), total phosphorus (0.2±0.1 $mg.l^{-1}$), chlorophyll *a* concentrations (87±9 $µg.l^{-1}$) and phytoplankton: zooplankton ratio (0.18±0.05) reflected a state of high eutrophication. Such eutrophication pressure was caused mainly by fisheries management in the pond. The utilisation efficiency of organic carbon, nitrogen and phosphorus inputs was low and accounted for 1.3, 20 and 28% of the total inputs, respectively. This low efficiency was due to overgrazing of large zooplankton by high fish stocks, a high proportion of primary production not transferred to higher level of the food chain, and poor quality of supplementary feed. The pond retained nitrogen and phosphorus in a range comparable to other lakes and artificial waterbodies with comparable hydrology and morphology. High loads of nutrients combined with a low rate of water exchange allow for high phytoplankton growth and accumulation of organic matter in the water, long-term accumulation of phosphorus in sediments even during its high internal cycling in the pond, and nitrogen losses by denitrification. On the other hand, high input loads of nutrients exceeded the assimilation capacity of the pond ecosystem. Thus, the outflow from the pond was still rich in nutrients and organic matter, which can cause pollution in lower water bodies. We recommend a revision of the fishery management practices (fish stock density, use of manure, quality and amount of fish feed needed) in order to improve the pond water quality and maintain its non-production functions.

Key words: *Aquaculture pond; input use efficiency; nutrient retention; organic carbon, nitrogen and phosphorus balance; primary production*

Introduction

With the reduction in catches of sea fish, more farmed fish have been produced to meet the world market demand thanks to inland aquaculture, which is mainly practised in freshwater man-made earthen ponds (FAO, 2018). In the Czech Republic, fish farming in earthen ponds is a long tradition that started in the Middle Ages (Pechar, 1995). For centuries fish production remained modest, using primarily autochthonous nutrient sources and primary production in the pond. The trophic state of the ponds was oligotrophy with a varied biocenosis of aquatic plants (Pokorný and Pechar, 2000). The modern fish farming system dates back to the end of the 19th century, when Šusta (1898) introduced methods based on understanding the role of natural food chains in fish production and recommended liming and manuring to increase pond productivity. The period of intensification of fish production began in the first half of the 20th century, when fertilization of ponds and fish feeding became a common practice. Since then, annual fish production has increased from ca 50 to > 500 kg per hectare (Pokorný and Pechar, 2000). The main cultivated species of fish is traditionally common carp, *Cyprinus carpio* L. Higher stocking densities of fish in this semi-intensive production requires the use of supplementary feed, especially grain, and trophic conditions in ponds has changed to eutrophy or hypereutrophy (Pechar, 2000). Fisheries management efforts aims at maintaining or increasing this level of fish production while following more or less traditional practices, but less attention has been paid to environmental impacts and possible pollution of the river network by the discharge of water from ponds (Potužák et al., 2007).

Semi-intensive production fishponds not only produce fish but also provide other ecosystem services and functions. Fishponds contribute to local and regional biodiversity and may sometimes shelter rare and endangered species (Wezel et al., 2014; Francová et al., 2019). They regulate flood and local climate and can be used as recreation sites in countries where natural lakes are sparse. Semi-intensive fishponds, like other aquatic ecosystems, are able to remove or retain nutrients, organic substances, thereby improving the quality of the water flowing through them (Boyd et al., 2010; Gaillard et al., 2016; Four et al., 2017; Koschorreck et al., 2020). This ability results from the predominant use of natural food produced within the pond and fewer feed inputs compared to intensive aquacultures (Boyd et al., 2010).

The mechanisms of retention and removal of nutrients include settling of particles and sediment accumulation, incorporation in organisms and loss to the atmosphere (Sondergaard et al., 2001; Kalff 2002). The processes of nutrient loss to the atmosphere include respiration that releases organic carbon as carbon dioxide (CO_2) (Cole et al., 2007) or methane (CH_4) (Bastviken et al., 2004) and denitrification that releases nitrogen as a gas (N_2) (Hargreaves, 1998). A number of studies have focussed on the role of water bodies on nutrients and organic matter retention (Seitzinger et al., 2006; Pacheco et al., 2014; Coppens et al., 2016). According to these studies, nutrient retention in aquatic ecosystems depends on different factors such as hydraulic residence time, water depth, nutrient inflow concentration, temperature, water pH, phytoplankton and macrophyte abundance, sediment organic content, oxygen concentrations and trophic conditions. Other factors such as fish feeding behaviour (Rahman et al., 2008a; Rahman et al., 2008b), water discharge during fish harvest and harvesting technique (Lin et al., 2001), and water discharge from surface or bottom layers (Duras and Hejzlar, 2001) influence the retention of nutrients and organic matter in fishponds and other artificial water bodies.

With the rise of environmental concerns and from the socio-economic reasons, fish farmers are nowadays facing conflicting goals: increasing or at least maintaining current fish production in terms of economic profit while better ensuring non production functions. Low-efficiency in use of natural food, over-fertilization and supplementary feeding may impede non production pond functions, including recreational use due to eutrophication, biodiversity loss and limited nutrient retention.

Good fertilisation practice is the one that meets demands of phytoplankton, zooplankton and produced fish for nitrogen (N) and phosphorus (P) (Knud-Hansen et al., 1991). These demands are usually set by experimental trials in given regional conditions and a fixed-input rate of N and P inputs is advised to fish farmers. These recommendations are then followed as a routine for decades without major adjustments. However, when high doses of fertilisers and manure are used for a long time, this inevitably results in pond eutrophication. Negative effects such as loss of biodiversity and enhanced ecosystem productivity have been associated with eutrophication. Moreover, eutrophication reduces the natural ability to assimilate nutrients and organic matter inputs in aquatic ecosystems. But on the other hand, organic burial rates increase with increasing lake productivity (Anderson et al., 2014). Another constraint is the proportion of primary production that is used for produced biomass of fish. It often depends on food quality attributes such as digestibility of supplementary feed, its nutritional quality and length of food chains (Dickman et al., 2008).

Small water bodies, and especially artificial ones including ponds, play an important role in biogeochemical cycles (Selvam et al., 2014). However they are not regularly monitored even in countries where major inland waters are managed by integrated river basin catchment management program under the European Union Water Framework Directive (WFD) (Koschorreck et al., 2020). The lack of knowledge of their status and functioning in the river network may therefore interfere with the achieving of good ecological status of all inland water bodies. In our first paper, based on metabolic rates, input use efficiency, trophic levels and high fish stock pressure on zooplankton, we conclude that primary production and various wastes such as fish excrement and unconsumed food can increase the pollution potential of the Dehtář pond (Rutegwa et al., 2019). In this work, we extended our study to two complete production cycles to assess the nutrient retention efficiency in the Dehtář pond. A study of seasonal changes in phytoplankton and zooplankton biomass was included to be used as bioindicators and to gain insight into their role in nutrient cycles in the Dehtář pond.

The objectives of this study were: (i) to assess the quality of inflow, effluent and pond waters of Dehtář pond, using zooplankton and phytoplankton as bioindicators of pond conditions and processes, (ii) assess the interannual variability of nutrients and organic matter retention, (iii) identify drivers of observed trends in water quality, nutrient and organic matter retention.

Materials and methods

Study area

The Dehtář pond (49.0083N, 14.3058E; 406.4 m above the sea level; area 2.28 km^2; maximum and mean depths 5.5 and 2.2 m, respectively) is located in the upper Vltava River Basin in South Bohemia, the Czech Republic (Figure 1). It is the last pond of the system of ponds in the upper part of the catchment of Dehtářský stream, which has an area of 91.4 km^2. Details on its geographic location and description were given in Rutegwa et al. (2019). It is a polyculture semi-intensively managed fishpond used in a two-year production cycle. Common carp (*Cyprinus carpio* L.) usually represents 95% of stocked fish biomass and the remaining 5% are composed of grass carp (*Ctenopharyngodon idella* Valenciennes 1844), bighead carp (*Hypophthalmichthys nobilis* Richardson 1845), pike-perch (*Sander lucioperca* L.), and northern pike (*Esox lucius* L.). Two year old carp are stocked and harvested after two growing seasons for market sales. Manure and supplementary feed, in particularly wheat, rye or barley grains, are used. The water level and pond filling are maintained at a lower elevation in the first year of the production cycle (405.85 m a.s.l.) than in the second year (406.4 m a.s.l.).

Water quality and biology

This study was conducted during two two-year fish production cycles in the period from autumn 2014 to autumn 2018. Water parameters including temperature (T_w), dissolved oxygen (DO), pH, suspended solids, water transparency, chlorophyll *a* (Chl*a*), total carbon (TC), total inorganic carbon (TIC), total organic carbon (TOC), dissolved carbon (DC), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), total nitrogen (TN), ammonium (NH_4^+), nitrate (NO_3^-), total phosphorus (TP), soluble reactive phosphorus (SRP) and particulate phosphorus (PP) were measured at all sampling sites on the tributaries, the pond and its outflow. The summary of all standard methods and their corresponding method numbers used in the analyses are detailed in Supplementary material, Table S1. Water samples were collected monthly during the winter months and biweekly during summer and autumn months. Grab water samples were collected from inlets and outlets of the pond. Pond water was sampled at three sites (the dam, Dehtářský bay and Babický bay (BB)). Depth integrated water samples were taken from the top 2-m layer from all the sites and additional samples were taken at 3 m below the water surface and at 0.5 m above the pond bottom at the dam with a Friedinger sampler (Rutegwa et al., 2019). During the pond harvesting period, samples were taken daily four days before the harvesting day and hourly on the harvesting day using a portable automated sampler (Sigma 900 MAX). The hourly samples were mixed proportionally to flow and a subsample was used for laboratory analysis.

Three platforms equipped with high frequency stations (M4016, Fiedler AMS) installed at the three sites of the pond (Figure 1) were used to record in 10 minute intervals DO and T_w at 0.3-m and 1.5-m depths at the dam (site D) and at 0.3-depth at sites DB and BB in period May–October. In addition, the station at the dam (site D) was equipped with a meteorological station that measured air temperature, light intensity and wind speed. At site D, water transparency and vertical profiles of T_w and DO were measured monthly or biweekly with a Secchi disc and a multiparametric probe (YSI 6600 V2-4), respectively. The profiles of T_w and DO were recorded at 0.5-m depth intervals.

Phytoplankton were analysed in composite samples taken from the top 2-m water layer in the period May–October. Samples were fixed with the Lugol's solution. The phytoplankton were identified, counted and their biomass calculated microscopically using the relative distribution of size-biomass for the major taxonomic groups (Utermöhl, 1958). The phytoplankton biovolume ($mm^3.l^{-1}$) was converted into dry weight ($\mu g\ l^{-1}$) using the following formula according to Reynolds (1984): $W_D = 0.47*V^{0.99}$, where W_D stands for dry weight and V for biovolume. The phytoplankton trophic index (PTI) was calculated from the composition of phytoplankton taxa present in the samples according to Phillips et al. (2013).

Zooplankton was collected by vertical hauls of Apstein plankton nets with 80 µm mesh net size in the period May–October. The net was thrown three times from the dam and the entire water column was sampled without disturbing the bottom sediments. The average sampling length was about 5 m. The zooplankton samples were preserved in 4% formalin solution and stored for subsequent identification and quantitative counting. The zooplankton were identified up to species level and counted in Sedgewick-Rafter chamber under microscope (Wetzel and Likens 2000). The biomass of cladocerans and copepods was calculated from length-weight allometric relationships based on published regressions (Bottrell et al., 1976; Culver et al., 1985; Vuille, 1991). The mean body sizes from the year 2017 were used for cladocerans and copepods. The individual biomass of nauplii was set to 0.25 µg of dry weight (Culver et al., 1985). For rotifers, the typical individual wet weight reported by Bielanska-Grajner et al. (2015) was used. Their dry weight (DW) was estimated to be 4% and 10% of the wet weight for the genus *Asplanchna* and all other rotifers, respectively (Bottrell et al., 1976). The zooplankton : phytoplankton biomass ratio (dry weight basis) was used to indicate the trophic level of the Dehtář pond (Jeppesen et al., 2000; Haberman and Laugaste, 2003).

Hydrology

The water discharge was measured twice a month during water sampling in all tributaries and outlets of the Dehtář pond using the area-velocity method. The water velocity was measured using a hydrometric probe (FlowTracker, Sontek, USA). The water level in the pond was measured manually with a gauge fixed at the outlet opening until January 2016. Afterwards it was continuously recorded with a pressure probe (Fiedler AMS). From the two-week measured flow data, the daily time series of flow was reconstructed using hydrological analogy with daily flow data records in a nearby stream (the Zlatý potok) and information about filling and emptying of the ponds situated upstream of the Dehtář pond. For more details on how the water balance was subsequently calculated, see Rutegwa et al. (2019).

Ecosystem metabolism rates, nutrients balance and efficiency of input use

Ecosystem metabolic rates in the Dehtář pond were calculated using the diel dissolved oxygen concentration changes (Staehr et al., 2010). By this technique net ecosystem production (NEP), ecosystem respiration (ER) and gross primary production were calculated by measuring changes in DO concentration over 24 hours at a 10-minute intervals. The equations used $\Delta O_2/\Delta t$ = GPP − ER − F − A takes into account that the measured DO concentration at a given time is a balance between the DO produced by the primary production (GPP), the DO consumed by the respiration processes (ER), the net exchange between the atmosphere and the water (F) and other physical processes (A) (Staehr et al., 2010; Laas et al., 2012).

The balance of organic carbon (OC), nitrogen (N) and phosphorus (P) was calculated by subtracting the outputs of OC, N and P from their inputs with considering the change in mass between the beginning and the end of the balanced period using the equation: $\Delta M/\Delta t$ = GPP + IN + AD + FF + M − ER − OUT − FISH − RET. In this equation, $\Delta M/\Delta t$ is the change in the quantity of organic carbon or nutrients in the pond water between the beginning and the end of the balance period, GPP is the gross primary production (applicable for OC only), IN, AD, FF, and M are the inputs from inflows, atmospheric deposition, fish feed, and manure, respectively, ER is the loss of OC by ecosystem respiration, OUT and FISH are the outputs from the system by outflow plus seepage and by the uptake into the produced fish biomass, respectively, and RET is the calculated residual of the balance and represents retention in the sediment and/or loss to the atmosphere. As the continuous measurements were recorded only from middle April of each year, ecosystem metabolic rates and OC balance were calculated from May to October and from May to the pond harvesting day during each first year and second year of the fish production cycle, respectively. The N and P balances were calculated for the whole hydrological years (November–October). Details of the calculations and all parameters used were described in Rutegwa et al. (2019). The efficiency use of inputs was calculated as the ratio of fish gain biomass and total inputs of OC, N and P in percentages. The utilisation efficiency of inputs was calculated as the ratio of the nutrient gain in harvested fish to the total inputs. The fish growth was estimated by empirical growth models for each species based on their stocked size and weight, and considering also the real harvested amounts in 2016 and 2018 and mortality losses. The models were also calibrated for the Dehtář pond on six previous two-year production periods with data available for stocking and harvesting.

Retention and apparent removal rate of P and N

The nutrient retention coefficient was calculated by dividing the difference between the inputs and outputs of P and N with their respective inputs according to the equation: RET = (IN + AD + FF + M – OUT – FISH)/ (IN + AD + FF + M) where RET is N and P retention, IN, AD, FF, and M are the inputs of N and P from inflows, atmospheric deposition, fish feed, and manure, respectively, OUT and FISH are the outputs of N and P from the system by outflow plus seepage and by the uptake into the produced fish biomass, respectively. The apparent removal rates of P (vP) and N (vN) in m year^{-1} were calculated using the following formula: vP or vN = q_w*RET/OUT, where q_w is the areal water load (m year^{-1}), RET (kg) is the retention of N or P that include losses by sedimentation and/or transfer to atmosphere and OUT (kg) is the output of P or N with outflow.

Statistical analyses

Prior to statistical analyses, the data were subjected to normality testing using Shapiro-Wilk test. Since the dataset did not match normal distribution, non-parametric tests were used. The Mann-Whitney test was used to test difference between the concentrations of OC and nutrients in inflow and outflow water. The Mann-Whitney test was also used to test any difference among metabolic rates between the growing seasons. All statistical analyses were carried out using R software version 3.6.1 (R Core Team, 2019).

Results

Pond hydrology and fishery management

The Dehtář pond was refilled gradually since each autumn fish harvest at the end of October 2014 and 2016 (Figure 2). The first fish production cycle was characterised by a water level decrease in the summer months of 2015 due to low inflows and less precipitation. The water level has been increasing since November 2015, but did not reach the required level in the second year of the fish production cycle until June 2016. The course of pond refilling was normal during the second fish production cycle. The overall average inflow, outflow discharge and water level were similar in both cycles. The average inflow was 0.14±0.01 (maximum 1.63) and 0.15±0.01 (maximum 2.29) m^3.s^{-1} in the first and second cycle, respectively. The mean outflow was 0.13±0.01 (maximum 2.68) m^3.s^{-1} in the first cycle and 0.15±0.01 (maximum 1.76) m^3.s^{-1} in the second cycle. The average water level was 405.2 (maximum 406.3) and 405.4 (maximum 406.2) m a.s.l in the first and second cycle, respectively. The average water retention time was 0.65 years in 2015–2016 and 0.7 years in 2017–2018.

During the first cycle, fish were stocked in November 2014 and in March 2015 with a stocking density of 390 kg.ha^{-1}. The relative biomass of stocked species was as follows: common carp 97%, grass carp 2.3%, pikeperch 0.6%, and pike 0.1%. During the second cycle, fish were stocked in October, November 2015, in March and in April 2016. The total biomass of stocked fish was 220 kg ha^{-1} and consisted of 94.2 % of common carp, 2.7% of grass carp, 1.9% of pike perch, 0.8% of European catfish and 0.4% of pike. Cattle manure was added in the pond and less was used in the second cycle than in the first cycle. The amount of applied manure was 2200, 3800, 2900 and 2200 kg.ha^{-1} in 2015, 2016, 2017 and 2018, respectively. Wheat grains were used to feed the fish and the feeding rates were reduced in the second cycle. They were 1970, 2300, 1370, and 1300 kg.ha^{-1} in 2015, 2016, 2017 and 2018, respectively. The fish yield was 360, 860, 320 and 970 kg.ha^{-1} in 2015, 2016, 2017 and 2018. The values of corresponding food conversion ratio (FCR) that was calculated by dividing the feed amount (kg) by the live weight gain (kg) of the fish were 5.7, 2.6, 4.1 and 2.3, respectively. The FCR was lower in the first years than in the second years of the production cycle.

Seasonal changes in pond water quality, biology and metabolism

Water quality. Most of the pond water quality variables showed seasonal patterns throughout the two fish production cycles (Figure 3). Water temperature and DO (Figure 3a, b) indicated a general polymictic pattern. However, during the warm part of the year (May–September), temporary stratification was formed. In stagnant water above the bottom, hypoxic conditions occurred, with the concentration of DO decreasing to zero. The duration of anoxia above the bottom was longer in the second years of the production cycle, when the pond was filled to a higher level.

Chla, TOC, DOC, TN and TP showed an increase during the growing season and a decrease at the onset of cold months (Figure 3c, d, e, f). In contrast, water transparency expressed as the Secchi depth had the opposite trend to the concentration of Chl*a* and decreased during the warm months (Figure 3c). Dehtář pond was classified as hypereutrophic based on the three water quality indicators of OECD (1982), i.e. TP, Chl*a* and Secchi depth. The pond was highly productive. The average concentration of TP was 0.20±0.01 mg.l^{-1}. The average concentration of Chl*a* was 87±9 µg.l^{-1} and the seasonal Chl*a* maximum value reached values of 110–330 µg.l^{-1}. The average Secchi depth was 0.7±0.1 m. Changes in TC concentrations were mainly associated with the seasonal TOC pattern, while TIC (difference between TC and TOC) was relatively stable in all seasons (mean seasonal values 20–26 mg.l^{-1}; Figure 3d). Concentrations of N-NH_4^+ and N-NO_3^- showed maximum values in winter and spring (Figure 3e), apparently due to inflow of water into the pond and / or release from mineralized organic matter and low phytoplankton uptake in the pond, while in the summer months they were low. Concentrations of SRP and DP were relatively low, indicating their uptake by phytoplankton (Figure 3e, f), but some peaks, especially during the period of high DO depletion above the bottom, indicate their release from sediments. Despite relatively low concentrations of inorganic N and P forms, no phosphorus limitation of phytoplankton occurred.

Phytoplankton. Representative phytoplankton species in the 2015–2016 production cycle were from the genera *Aphanizomenon, Oocystis, Closterium* and *Dolichospermum*. During the 2017–2018 cycle, species from the genera *Coelastrum, Dolichospermum, Planktothrix* and *Closterium*. The average biovolume of phytoplankton was 37±5 and 32±1 mm^3.l^{-1} in the first and the second fish production cycle, respectively (Figure 4). The phytoplankton biovolume was higher during the July-October period (Figure 4). During this period the average algal biovolume was above 46 mm^3.l^{-1}. The Chlorococcales were present in all month but dominant in May and June with a relative biomass of 50%. The Cyanophytes were rare in May but present in the remaining months and were dominant from July to October and represented 50% of the total phytoplankton biomass. The phytoplankton were more diverse in June and July during all four growing seasons and in September during the three growing seasons except in 2018. Chrysophytes, Cryptophytes, Desmids, diatoms, Dinoflagellates, Euglenophytes and Volvocales were also present but with a low biomass. Phytoplankton was dominated by eutrophication-tolerant species, as indicated by the average PTI of 44±2 µg.l^{-1} P. During the season, the proportion of highly eutrophic taxa increased, as shown by the PTI values, which increased from 33 µg.l^{-1} P in June to 48 µg.l^{-1} P in August.

Zooplankton. The average biomass of zooplankton was 192±7 and 162±3 µg.l^{-1} DW during the first and second fish production cycle, respectively (Figure 5). The zooplankton assemblage was dominated by the cladocerans (≈85 % of biomass). The majority of the recorded taxa are characteristic of eutrophic waters. The rotifers were present in all months. *Brachionus, Keratella, Polyarthra,* and *Filinia* were the dominant rotifer genera. Larger size classes of zooplankton represented mainly by *Daphnia galeata* were present only at the beginning of the growing season. In the other months, small sized Daphnia *species* (e.g. *Daphnia cucullata),* and other small cladocerans *(Ceriodaphnia* spp., *Bosmina longistris, Bosmina coregoni)* were present in all months but decreased from May to October. *Chydorus* species were substantially present only in July. Other cladocerans (mainly *Leptodora*) were present with a low abundance in summer months. The copepods were mainly represented by the nauplii and were present in all months.

The zooplankton: phytoplankton biomass ratio decreased from May to October in both fish production cycles. The overall average of zooplankton: phytoplankton biomass ratio was 0.18±0.05. It was higher in the first fish production cycle (0.30±0.10) than in the second fish production cycle (0.09±0.02).

Metabolic rates. Over the four growing seasons, there was a balance between the GPP and the ER (Table 1). The monthly average GPP ranged from 3.1 to 5 g C m^{-2}.d^{-1}, and the monthly average ER ranged between 3.1 and 5.1 g C m^{-2}.d^{-1}. The monthly average NEP ranged from -0.9 to 0.8 g C m^{-2}.d^{-1}. The Dehtář pond was slightly autotrophic with an NEP nearly in balance during the first three growing seasons covered by this study. In 2018, however, ER was higher and the pond was net heterotrophic. A comparison of GPP, ER and NEP between the two growing seasons showed that they did not differ during the first fish production cycle but they differed significantly during the second fish production cycle (Mann-Whitney U test, $p<0.05$).

Balances

Inflow – outflow concentrations. The concentrations of OC and nutrients in the inflow and outflow varied widely and sharp peaks corresponded to fishpond draining periods (Figure 6). The concentrations of TOC, DOC, N-NH_4^+ and PP were significantly higher (Mann-Whitney U test, $p<0.05$) in the outflow than in the inflow indicating net production of organic carbon in the pond (Figure 6b, c, f, h). The average differences of flow and time-weighted concentrations of TOC, DOC, N-NH_4^+ and PP between inflow and outflow were -3.4±0.7, -2.1±0.2, -0.17±0.19 mg.l^{-1} and -9.9 µg.l^{-1}, respectively. The concentrations of TSS, TN, N-NO_3^-, TP and SRP were higher in the inflow than in the outflow (Figure 6a, d, e, g, i). The average difference between inflow and outflow TSS, TN, N-NO_3^-, TP and SRP concentrations were 6.5±12.6, 0.6±0.3, 1.05±0.1, 0.1±0.06, 0.12±0.03 mg l^{-1}, respectively. However, inflow and outflow differed significantly only for TSS, N-NO_3^- and SRP concentrations (Mann-Whitney U test, $p<0.05$).

OC balance. The GPP, supply water, rainfall, feed and manure were the sources of OC in the Dehtář pond (Table 2). The GPP and feed were the main sources of OC and contributed on average 80.6% and 11.6% of all OC inputs. Inflow water and manure contributed on average equal amount of 3.7% of all OC inputs. The inputs from rainfall were less than 1% of all OC inputs. The ER was the main output of OC and accounted on average 91.6% of all OC outputs. The outflow and seepage accounted for 6.8% in average of all OC outputs and was higher in the second year of the fish reproduction cycle. Harvested fish biomass accounted only for 1.6% of all OC outputs. The accumulation of OC in water was observed only in each first year of the fish production cycle and accounted for less than 1% of all OC inputs. The retention or losses of OC was on average 12% of all OC inputs and was higher during the 2015–2016 fish production cycle than in the 2017–2018 fish production cycle.

N and P balance. Inflow water, rainfall, feed and manure were the sources of N and P in Dehtář pond (Table 3 & Table 4). Inflow water was the main source of N with an average contribution of 62.5% of all N inputs whereas the feed were the main source of P and accounted for 45.2%

of all P inputs. Feed, manure and rainfall accounted for 22.4, 10.4 and 4.7% of all N inputs. Inflow water, manure and rainfall accounted for 38.1, 15.8 and 0.9% of all P inputs. Seepage and outflow accounted for 76% and 64% of N and P outputs, respectively. Fish production represented 24 and 36% of N and P outputs, respectively. N and P accumulated in water column only during the first growing season of the production cycle but more N and P were released from the pond compared to inputs in the second year of the production cycle which includes the harvesting time. On average, Dehtář pond retained 17.9 and 44% of N and P inputs, respectively.

In addition to commercially important fish, weed fishes were harvested in 2016 (7,626 kg of mainly *Abramis brama*) and in 2018 (22,700 kg comprising *Abramis brama* and *Carassius gibelio*). However, it was not possible to determine their productivity as they were not stocked intentionally. The utilisation efficiency of OC, N and P inputs was higher in the second year of the reproduction cycle. The utilisation efficiency of OC input was similar in both production cycles and amounted to 1.3%. The utilisation efficiency of N and P inputs varied slightly between the two cycles. It was 18 and 22% for N in 2015–2016 and 2017–2018, respectively while it was 25 and 36% for P. The overall utilisation efficiency of OC, N and P inputs in fish production for both cycles was 1.3, 20 and 28%, respectively.

The retention coefficient and apparent removal rates of N and P. Dehtář pond was a sink of nutrients during this study period. The TP and TN retention and the apparent P and N removal rates similar in 2015–2016 but TP showed lower retention and apparent removal rate compared to TN in 2017–2018. TP retention coefficient was 0.70 in 2015–2016 whereas it was 0.58 in 2017–2018. TN retention coefficient was 0.63 in 2015–2016 whereas it was 0.72 in 2017–2018. The apparent P and N removal rates in 2015-2016 were 6.5 and 4.8 m year^{-1}, while in 2017–2018, they were 3.9 and 7.4 m year^{-1}, respectively.

Discussion

Pond characteristics

The results of our study revealed that the fishery management practices affected the trophic status, the ecosystem structure and carbon metabolism of the Dehtář fishpond. Based on water quality indicators of OECD (1982), the Dehtář pond falls in the category of a hypereutrophic water body. The average concentration of TP (0.2 mg.l^{-1}) and water transparency (0.7 m) were similar in both production cycles. The concentrations of Chl*a* differed slightly and were higher in the first production cycle (90 µg.l^{-1}) than the second cycle (84 µg.l^{-1}). Both cycles were characterised in summer by excessive growth of phytoplankton biomass that zooplankton were not able to control through consumption (Figure 3c). Similar high peaks usually followed by a remarkable decrease in phytoplankton biomass are common in eutrophic lakes. This rapid decline in phytoplankton biomass is mainly due to the die off of the dominant species of the poorly diverse phytoplankton community, which lacks alternative species to replace them (Jeppesen et al., 1990). This degradation of water quality was partly caused by an increase in the amount of nutrients added to these historically oligotrophic ponds in order to increase their ability to produce more natural food (Pokorný and Pechar, 2000). Nitrogen loads increased from 0.1 kg.ha^{-1} in the 1930s to 46 kg.ha^{-1} in the 1990s while those of P increased from 0.3 kg.ha^{-1} to 10 kg.ha^{-1} in the same period (Pechar 1995). Our results are in agreement with those reported by Lemmens et al. (2013) who found that intensification of fishery management increases TP, TN, Chl*a* levels and reduces water transparency. There have been some efforts to reduce the nutrient loads by banning the use of industrial fertilisers and the combination of fishponds with pig and duck farms (Adámek, 2014) but the fishpond systems did not recover from the old burden of overfertilisation. Since then, no other measure were taken to curb nutrient addition in ponds. The average loads of P (13 $kg.ha^{-1}$) and N (47 $kg.ha^{-1}$) originating from manure and feeds during the period of this study are comparable to those from the 1990s. Pokorný and Pechar (2000) suggested that the eutrophication of fishponds was a combination of fishery management and the changes in the land use. In this study, inflows contributed substantially to nutrient loads in Dehtář pond suggesting that manuring campaign should also consider all the potential sources of nutrients. The elevated nutrient concentrations in the tributaries can be explained by the water passage through the cascades and systems of upstream fishponds.

Phytoplankton and zooplankton species composition also reflected the eutrophication pressure. The majority of the phytoplankton species belonged to species indicating highly eutrophic conditions. Eutrophy-tolerant species (mainly cyanobacteria) (Phillips et al., 2013) were dominant in the summer months and in autumn. Their dominance may be explained by their ability to adapt to high turbidity, which limits the photic zone, their ability to fix dinitrogen, their resistance to sinking due to buoyancy, forming colonies and large filaments, or their tolerance to carbon dioxide depletion (Reynolds et al., 2002; Nixdorf et al., 2003). Species belonging to the groups with variable trophic tolerance (Phillips et al., 2013) were dominant in spring (chlorophytes) or were present throughout the study period (dinoflagellates, cryptophytes, desmids, chlorococcales and diatoms). The presence of these species may be explained their properties, which allow them to survive in turbid waters such as being small sized to avoid sinking, highly motile and able to regulate their position in the water column (Reynolds et al., 2002). The above properties allow them also to resist the zooplankton grazing pressure. The mean ratio of zooplankton biomass and phytoplankton biomass was less than 0.5. This ratio decreases with increasing eutrophic levels characterised by a high production of phytoplankton cohabiting with small-sized zooplankton (Jeppesen et al., 2000). This concurs with findings from other studies on the effects of eutrophication on zooplankton communities (Jeppesen et al., 2000; Oltra et al., 2001; Haberman and Laugaste, 2003). These researchers concluded that in eutrophic water bodies zooplankton communities are dominated by small-sized zooplankton species that feed mainly on detritus and able to adapt to low levels of dissolved oxygen. The type and quantity of available food are not the only factors shaping the size structure of zooplankton community in lakes and fishponds. The grazing pressure from the fish that selectively feed on larger individuals (e.g. larger *Daphnia*) was the main reason of the zooplankton size decrease noted in summer in our study. Similar zooplankton size decrease was observed to occur in other Czech ponds by Potužák et al. (2007).

The structure of the plankton community affected both the ecosystem metabolism and the flow of energy through the food web in Dehtář. The metabolic rates showed that there was an equilibrium between the gross primary production and the ecosystem respiration rates apart from 2018 when the system was slightly heterotrophic. Ecosystem respiration was the main fate of the primary production. This may be explained by the lack of phytoplankton grazers, as both the composition of the zooplankton and the fish populations were not able to significantly reduce phytoplankton production. Unused phytoplankton biomass is then decomposed both in the water column and pond sediment by heterotrophic bacteria. This implies that the carbon fixed by the primary producers passes into microbes, then into zooplankton and may eventually go to fish if the species of appropriate size were present. Although we did not measure this pathway, the results of Šimek et al., (2019) in ten eutrophic fishponds including the Dehtář pond showed that the microbial food web was an important pathway of the autochthonous organic matter. On the contrary, the same authors found that the microbial food web was not so important to transfer the primary biomass to zooplankton in fishponds with low fish stock density.

The efficiency of using OC inputs we calculated was lower compared to the values reported in other aquaculture systems (Olah et al., 1986; Zhang et al., 2016). The bottleneck was the low utilisation of the primary production although it was the main source of OC in the system. Common carp do not feed directly on phytoplankton and need intermediate level in the food chain (zooplankton or macroinvertebrates) to utilise primary production (Adámek et al., 2003). The latter were subject to a high grazing pressure and to bad environmental conditions especially during the summer months. Only small zooplankton, that are neither able to graze efficiently on the phytoplankton nor good food for adult common carp, was abundant in the period when carp were feeding actively. The utilisation efficiency of N and P inputs was comparable to results from other studies (Hargreaves, 1998) but still about 70% of these inputs are not harvested in fish biomass. This results probably from the poor digestibility of cereals used in the Dehtář pond (Fagbenro, 1999; Degani, 2006). The second reason is overloading of nutrients in inflow and manure as discussed in the first paragraph of this section.

Nutrient retention efficiency

To assess the ability of the Dehtář pond to retain nutrients, we compared the relationship between nutrient removal and water load and found that these values in the Dehtář are comparable to those from other temperate lakes and reservoirs (Figure 7, Tables S2, S3). The retention ability we observed may be explained by high external nutrient loads (Saunders and Kalff, 2001b; Coppens et al., 2016). The Dehtář pond, being a hypereutrophic fishpond in which manure and fish feed are in use, receives high nutrient loads that increase the potential for N and P retention through algal uptake, fish production, sedimentation of this algal biomass and denitrification. This retention may also be explained by the long water residence time and low depth of the pond. The low water depth and the long water residence time allow interactions and contact of water column with sediments, thereby enhancing nutrient uptake by the sediment and their recycling when soluble nitrogen and phosphorus fraction are released by mineralisation of organic compounds. Slower water flushing rates allow algae to extract nutrients from the whole water column (Salvia-Castellvi et al., 2001). Nitrogen is permanently lost from the water bodies through denitrification which contributes substantially to N loss from lentic ecosystems (Seitzinger et al., 2006). Although we did not measure directly the denitrification rates, we assume it was an important pathway of N retention in this study, based on the availability of labile organic matter from high phytoplankton biomass, low DO concentration at the bottom of the pond and low N-NO_3^- levels. It has been proved that organic matter influences denitrification rates because its mineralisation supplies ammonia and nitrates to denitrifying bacteria (Saunders and Kalff, 2001a). Besides, denitrification takes place when DO concentrations are reduced (Seitzinger et al., 2006). The retention was higher in years during which the pond was not drained. The retention decreased substantially in years during which the pond was drained for fish harvest. Longer water residence time and absence of outflow were the main reasons of a higher retention during the years the fishpond was not drained.

Despite the retention of N and P we measured, we also observed that the outflow was of poor quality. The quality of outflow was affected by high loads of nutrients that were above the assimilatory capacity of the pond. More nutrients were added through manure and fish feed, although pond sediment and water were already enriched in nutrients. Furthermore, inefficient use of the feed and the primary production reduce the self-purification capacity of the pond as discussed in the previous section. Therefore, waste is generated, which settles to the pond bottom or remains suspended in water column temporarily. Unused nutrients and organic matter are eventually released with the outflow during the water level control. Our results are in agreement with the findings of Bosma and Verdegem (2011) who found that in the early stages of pond draining, unsettled phytoplankton and dissolved nutrients are released to downstream water bodies. We noticed also that total suspended solids, nutrients and organic matter concentrations were higher in the outflow during the harvesting time. This increase was caused by the techniques and activities associated with fish harvesting. Banas et al. (2008) noticed in France that in the last phase of fish harvesting, sediments are resuspended by fish concentrated in a small area, outflowing water, seining and the movement of fishermen. Similar activities occur during fish harvesting in Czech Republic and may also explain the degradation of the outflow from the pond.

Conclusion

According to our results, the Dehtář pond is a fishpond under a pressure of eutrophication as indicated by water quality variables, phytoplankton trophic indices and zooplankton: phytoplankton biomass ratio. The Dehtář pond does not have a reduced ability to retain nutrients and its retention coefficients are comparable to those from other lakes and reservoirs. However, high loads of nitrogen, phosphorus and organic matter, the low efficiency use of inputs in fish production, and fish harvesting techniques that mobilize sediment reduce the pond ability to assimilate a significant fraction of inputs. Inflow water, fish feed and manure were the cause of high load of nutrients and organic matter in Dehtář pond. Observation of limnological and fish production changes in the Dehtář pond and also similar semi-intensive fishponds after a revision of some fishery management practices will obviously require further research, in particular on digestibility of feed, the use of natural food chains in fish stock nutrition and the role of accompanying species in fish stock polyculture. The management practices to consider include fish stock density, use of manure, quality and amount of fish feed.

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Authors' contributions

MR contributed to data analysis and manuscript writing. JH contributed to the analysis of the data and writing of the manuscript. JP contributed to study design, collection of field data, and laboratory analyses. JR contributed to data analysis. MŠ contributed to data analyses and manuscript writing. BD contributed to data acquisition and the writing of the manuscript. All authors discussed the results and contributed to the final manuscript.

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References

Adámek, Z., 2014. Hydrobiology in Fisheries. In: Adámek, Z., Helešic, J., Maršálek, B., Rulík, M. (Eds), Applied Hydrobiology. FFPW USB, Vodňany, CZE, pp. 307–351.

Adámek, Z., Sukop, I., Rendón, P.M., Kouři, J., 2003. Food competition between 2+ tench (*Tinca tinca* L.), common carp (*Cyprinus carpio* L.) and bigmouth buffalo (*Ictiobus cyprinellus* Val.) in pond polyculture. Journal of Applied Ichthyology 19: 165–169.

Anderson, N.J., Bennion, H., Lotter, A.F., 2014. Lake eutrophication and its implications for organic carbon sequestration in Europe. Global Change Biology 20: 2741–2751.

Banas, D., Masson, G., Leglize, L., Usseglio-Polatera, P., Boyd, C.E., 2008. Assessment of sediment concentration and nutrient loads in effluents drained from extensively managed fishponds in France. Environmental Pollution 152: 679–685.

Bastviken, D., Cole, J.J., Pace, M.L., Tranvik, L., 2004. Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. Global Biogeochemical Cycles 18: GB4009.

Bielarnska-Grajner, I., Ejsmont-Karabin, J., Radwan, S., 2015. Rotifers (Rotifera). Freshwater Fauna of Poland. Jagiellonian University Press, Wyda, p. 578.

Bosma, R.H., Verdegem, M.C., 2011. Sustainable aquaculture in ponds: principles, practices and limits. Livestock Science 139: 58–68.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., Weglenska, T., 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24: 419–456.

Boyd, C.E., Wood, C.W., Chaney, P.L., Queiroz, J.F., 2010. Role of aquaculture pond sediments in sequestration of annual global carbon emissions. Environmental Pollution 158: 2537–2540.

Chapra, S.C., 1975. Comment on 'An empirical method of estimating the retention of phosphorus in lakes' by WB Kirchner and PJ Dillon. Water Resources Research 11: 1033–1034.

Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10: 171–184.

Coppens, J., Hejzlar, J., Šorf, M., Jeppesen, E., Erdoğan, Ş., Scharfenberger, U., Mahdy, A., Nõges, P., Tuvikene, A., Baho, D.L., 2016. The influence of nutrient loading, climate and water depth on nitrogen and phosphorus loss in shallow lakes: a pan-European mesocosm experiment. Hydrobiologia 778: 13–32.

Culver, D.A., Boucherle, M.M., Bean, D.J., Fletcher, J.W., 1985. Biomass of freshwater crustacean zooplankton from length–weight regressions. Canadian Journal of Fisheries and Aquatic Sciences 42: 1380–1390.

Degani, G., 2006. Digestible energy in dietary sorghum, wheat bran, and rye in the common carp (*Cyprinus carpio* L.). Journal of Aquaculture – Bamidgeh 58: 71–77.

Dickman, E.M., Newell, J.M., Gonzalez, M.J., Vanni, M.J., 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proceedings of the National Academy of Sciences of the United States of America 105: 18408–18412.

Duras, J., Hejzlar, J.,2001. The effect of outflow depth on phosphorus retention in a small, hypertrophic temperate reservoir with short hydraulic residence time. International Review of Hydrobiology 86: 585–601.

Fagbenro, O., 1999. Apparent digestibility of various cereal grain by-products in common carp diets. Aquaculture International 7: 277–281.

FAO, 2018. The state of World fisheries and aquaculture. FAO, Rome, Italy.

Four, B., Arce, E., Danger, M., Gaillard, J., Thomas, M., Banas, D., 2017. Catchment land use-dependent effects of barrage fishponds on the functioning of headwater streams. Environmental Science and Pollution Research 24: 5452–5468.

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

Gaillard, J., Thomas, M., Lazartigues, A., Bonnefille, B., Pallez, C., Dauchy, X., Feidt, C., Banas, D., 2016. Potential of barrage fish ponds for the mitigation of pesticide pollution in streams. Environmental Science and Pollution Research 23: 23–35.

Haberman, J., Laugaste, R., 2003. On characteristics reflecting the trophic state of large and shallow Estonian lakes (L. Peipsi, L. Võrtsjärv). Hydrobiologia 506: 737–744.

Hargreaves, J.A., 1998. Nitrogen biogeochemistry of aquaculture ponds. Aquaculture 166: 181–212.

Hecky, R., Kilham, P., 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnology and Oceanography 33: 796–822.

Jeppesen, E., Søndergaard, M., Sortkjær, O., Mortensen, E., Kristensen, P., 1990. Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study of phytoplankton collapses in Lake Søbygård, Denmark. In: Trophic Relationships in Inland Waters, Springer, pp. 149–164.

Jeppesen, E., Peder, Jensen, J., SØndergaard, M., Lauridsen, T., Landkildehus, F., 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology 45: 201–218.

Kalff, J., 2002. Limnology: Inland Water Ecosystems. Prentice Hall, Upper Saddle River.

Kelly, C., Rudd, J., Hesslein, R., Schindler, D., Dillon, P., Driscoll, C.T., Gherini, S., Hecky, R., 1987. Prediction of biological acid neutralization in acid-sensitive lakes. Biogeochemistry 3: 129–140.

Knud-Hansen, C.F., Batterson, T.R., McNabb, C.D., Harahat, I.S., Sumantadinata, K., Eidman, H.M., 1991. Nitrogen input, primary productivity and fish yield in fertilized freshwater ponds in Indonesia. Aquaculture 94: 49–63.

Koschorreck, M., Downing, A.S., Hejzlar, J., Marcé, R., Laas, A., Arndt, W.G., Keller, P.S., Smolders, A.J., van Dijk, G., Kosten, S., 2020. Hidden treasures: Human-made aquatic ecosystems harbour unexplored opportunities. Ambio 49: 531–540.

Laas, A., Noges, P., Koiv, T., Noges, T., 2012. High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694: 57–74.

Lemmens, P., Mergeay, J., De Bie, T., Van Wichelen, J., De Meester, L., Declerck, S.A.J., 2013. How to maximally support local and regional biodiversity in applied conservation? Insights from Pond Management. Plos One 8.

Lin, C.K., Shrestha, M.K., Yi, Y., Diana, J.S., 2001. Management to minimize the environmental impacts of pond effluent: harvest draining techniques and effluent quality. Aquacultural Engineering 25: 125–135.

Nixdorf, B., Mischke, U., Rücker, J., 2003. Phytoplankton assemblages and steady state in deep and shallow eutrophic lakes – an approach to differentiate the habitat properties of Oscillatoriales. In: Phytoplankton and Equilibrium Concept: The Ecology of Steady-State Assemblages. Springer, pp. 111–121

OECD, 1982. Eutrophication of Waters, Monitoring, Assessment and Control. Final Report., OECD, Paris.

Olah, J., Sinha, V., Ayyappan, S., Purushothaman, C., Radheyshyam, S., 1986. Primary production and fish yields in fish ponds under different management practices. Aquaculture 58: 111–122.

Oltra, R., Alfonso, M. T., Sahuquillo, M., Miracle, M. R., 2001. Increase of rotifer diversity after sewage diversion in the hypertrophic lagoon, Albufera of Valencia, Spain. In: Rotifera IX. Springer, pp. 213–220

Pacheco, F.S., Roland, F., Downing, J.A., 2014. Eutrophication reverses whole-lake carbon budgets. Inland Waters 4: 41–48.

Pechar, L., 1995. Long-term changes in fish pond management as' an unplanned ecosystem experiment': Importance of zooplankton structure, nutrients and light for species composition of cyanobacterial blooms. Water Science and Technology 32: 187–196.

Pechar, L., 2000. Impacts of long-term changes in fishery management on the trophic level water quality in Czech fish ponds. Fisheries Management and Ecology 7: 23–31.

Phillips, G., Lyche-Solheim, A., Skjelbred, B., Mischke, U., Drakare, S., Free, G., Järvinen, M., de Hoyos, C., Morabito, G., Poikane, S., 2013. A phytoplankton trophic index to assess the status of lakes for the Water Framework Directive. Hydrobiologia 704: 75–95.

Pokorný, J., Pechar, L., 2000. Development of fishpond ecosystems in the Czech Republic. Role of management and nutrient input (Limnological review). Sylvia 36: 8–15.

Potužák, J., Hůda, J., Pechar, L., 2007. Changes in fish production effectivity in eutrophic fishponds-impact of zooplankton structure. Aquaculture International 15: 201–210.

Rahman, M., Jo, Q., Gong, Y., Miller, S., Hossain, M., 2008a. A comparative study of common carp (*Cyprinus carpio* L.) and calbasu (Labeo calbasu Hamilton) on bottom soil resuspension, water quality, nutrient accumulations, food intake and growth of fish in simulated rohu (Labeo rohita Hamilton) ponds. Aquaculture 285: 78–83.

Rahman, M.M., Nagelkerke, L.A., Verdegem, M.C., Wahab, M.A., Verreth J.A., 2008b. Relationships among water quality, food resources, fish diet and fish growth in polyculture ponds: A multivariate approach. Aquaculture 275: 108–115.

Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L., Melo, S., 2002. Towards a functional classification of the freshwater phytoplankton. Journal of Plankton Research 24: 417–428.

Rutegwa, M., Potužák, J., Hejzlar, J., Drozd, B., 2019. Carbon metabolism and nutrient balance in a hypereutrophic semi-intensive fishpond. Knowledge & Management of Aquatic Ecosystems: 49.

Salvia-Castellvi, M., Dohet, A., Vander Borght, P., Hoffmann, L., 2001. Control of the eutrophication of the reservoir of Esch-sur-Sûre (Luxembourg): Evaluation of the phosphorus removal by predams. Hydrobiologia 459: 61–71.

Saunders, D., Kalff, J., 2001a. Denitrification rates in the sediments of Lake Memphremagog, Canada – USA. Water Research 35: 1897–1904.

Saunders, D., Kalff, J., 2001b. Nitrogen retention in wetlands, lakes and rivers. Hydrobiologia 443: 205–212.

Seitzinger, S., Harrison, J. A., Böhlke, J., Bouwman, A., Lowrance, R., Peterson, B., Tobias, C., Drecht, G.V., 2006. Denitrification across landscapes and waterscapes: a synthesis. Ecological applications 16: 2064–2090.

Selvam, P.B., Natchimuthu, S., Arunachalam, L., Bastviken, D., 2014. Methane and carbon dioxide emissions from inland waters in India – implications for large scale greenhouse gas balances. Global Change Biology 20: 3397–3407.

Šimek, K., Grujčić, V., Nedoma, J., Jezberová, J., Šorf, M., Matoušů, A., Pechar, L., Posch, T., Bruni, E.P., Vrba, J., 2019. Microbial food webs in hypertrophic fishponds: *Omnivorous ciliate* taxa are major protistan bacterivores. Limnology and Oceanography 64: 2295–2309.

Sondergaard, M., Jensen, P.J., Jeppesen, E., 2001. Retention and internal loading of phosphorus in shallow, eutrophic lakes. The Scientific World Journal 1: 427–442.

Staehr, P.A., Bade, D., Van de Bogert, M.C., Koch, G.R., Williamson, C., Hanson, P., Cole, J.J., Kratz, T., 2010. Lake metabolism and the diel oxygen technique: State of the science. Limnology and Oceanography-Methods 8: 628–644.

Šusta, J., 1898. Fünf Jahrhunderte der Teichwirtschaft zu Wittingau. Herrke und Lebeling, Stettin.

Utermöhl, H., 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik: mit 1 Tabelle und 15 abbildungen im Text und auf 1 Tafel. Internationale Vereinigung für theoretische und angewandte Limnologie: Mitteilungen 9: 1–38.

Vuille, T., 1991. Abundance, standing crop and production of microcrustacean populations (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. Archiv für Hydrobiologie 123: 165–185.

Wetzel, R.G., Likens, G.E., 2000. Limnological Analyses. Springer-Verlag, New York.

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

Zhang, K., Tian, X.-l., Dong, S.-l., Feng, J., He, R.-p., 2016. An experimental study on the budget of organic carbon in polyculture systems of swimming crab with white shrimp and short-necked clam. Aquaculture 451: 58–64.

Table 1. *Monthly metabolic rates (g.m^{-2}.d^{-1}) during the growing season (May–October) in the Dehtář pond over two fish production cycles (2015–2016 and 2017–2018). GPP: gross primary production; ER: ecosystem respiration; NEP: net ecosystem respiration.*

Month	2015			2016			2017			2018		
	GPP	ER	NEP	GPP	ER	NEP	GPP	ER	NEP	GPP	ER	NEP
May	2.4	2.1	0.3	4.4	4.7	-0.3	2.3	1.5	0.8	4.4	5.1	-0.7
June	3.3	3.2	0.1	5	4.4	0.6	3.7	3.8	-0.1	4.5	4.1	0.4
July	3	3	0	2.7	2.6	0.1	4.3	4.2	0.1	2.7	2.5	0.2
August	3.4	3.2	0.2	3.3	3.7	-0.4	4.6	4.6	0	1.9	2.8	-0.9
September	3.1	3	0.1	3.6	3.5	0.1	3.5	3.6	-0.1	2.9	3	-0.1
October	1.5	1.6	-0.1	1.2	1.3	-0.1	1.9	2.4	-0.5	0.4	0.5	-0.1
Average	*2.8*	2.7	0.1	3.4	3.4	0.0	3.4	3.4	0.0	2.8	3.0	-0.2

Table 2. *Balance of OC in tonnes (t) during the growing season in the Dehtář pond during two fish production cycles (2015–2016 and 2017–2018).*

Variable	2015	2016	2015–2016		2017	2018	2017–2018		Average	
	(t)	(t)	(t)	(%)	(t)	(t)	(t)	(%)	(t)	(%)
Inputs:										
GPP	836	1181	2017	79	1075	982	2057	82	1019	80.6
Inflow water	18	89	107	4	65	15	79	1	47	3.7
Rainfall	2.6	3.7	6.7	0.3	4.8	7.8	13	0.7	5	0.4
Feed	133	185	318	12.4	105	165	270	14	147	11.6
Manure	36	74	110	4.3	53	23	76	2	47	3.7
Total inputs	***1025***	***1532***	***2558***	***100***	***1302***	***1193***	***2495***	***100***	***1265***	***100***
Outputs:										
ER	807	1171	1978	91.7	1064	1038	2013	91.2	1020	91.6
Outflow and seepage	17	127	144	6.7	27	133	167	7.3	76	6.8
Fish production	9	25	34	1.6	9	26	35	1.5	17	1.6
Total outputs	***833***	***1324***	***2156***	***29***	***1100***	***1197***	***2306***	***100***	***1113***	***100***
Accumulation in water	30	-7.9	22.1	1	28	-43	-15	-0.6	1.8	0.1
Retention and/or losses	162	217	379	14.8	174	38	212	8.5	148	12

Table 3. *Balance of N in the Dehtář pond during two fish production cycles (2015–2016 and 2017–2018)*

Variable	2015	2016	2015–2016		2017	2018	2017–2018		Average	
	(t)	(t)	(t)	(%)	(t)	(t)	(t)	(%)	(t)	(%)
Inputs:										
Inflow water	10.7	18.8	29.5	60.7	18.6	9.7	28.3	64.9	14.5	62.5
Rainfall	1.1	1.1	2.2	4.5	0.9	1.2	2.1	4.8	1.2	4.7
Feed	4.8	6.6	11.4	23.5	3.4	5.9	9.3	21.4	5.9	22.4
Manure	1.8	3.7	5.5	11.3	2.7	1.2	3.9	8.9	1.2	10.4
Total inputs	***18.3***	***30.2***	***48.6***	***100***	***25.5***	***17.9***	***43.6***	***100***	***23.2***	***100***
Outputs:										
Outflow and seepage	1.9	23.2	25.1	75	6.7	25.5	32.2	77	14.3	76
Fish production	2.3	6.5	8.8	25	2.4	7.0	9.4	23	4.6	24
Total outputs	***4.2***	***29.7***	***33.9***	***100***	***9.1***	***32.5***	***41.6***	***100***	***18.9***	***100***
Accumulation in water	6.0	-6.0	0	0	13.1	-13.1	0	0	0	0
Retention and/or losses	8.2	6.5	14.7	30	3.3	-1.4	1.9	4.4	4.2	17.9

Table 4. *Balance of P in the Dehtář pond during two fish production cycles (2015–2016 and 2017–2018)*

Variable	2015	2016	2015–2016		2017	2018	2017–2018		Average	
	(t)	(t)	(t)	%	(t)	(t)	(t)	(%)	(t)	(%)
Inputs:										
Inflow water	1.1	1.7	2.8	38	1.3	0.7	2	38	1.2	38.1
Rainfall	0.03	0.03	0.06	0.8	0.02	0.03	0.05	0.9	0.03	0.9
Feed	1.3	1.8	3.1	42.1	1.0	1.6	2.6	49.6	1.4	45.2
Manure	0.4	1.0	1.4	19.1	0.3	0.3	0.6	11.5	0.5	15.8
Total inputs	***2.8***	***4.4***	***7.36***	***100***	***3.0***	***2.6***	***5.3***	***100***	***3.2***	***100***
Outputs:										
Outflow and seepage	0.2	2.0	2.2	55	0.7	1.7	2.4	56	1.6	64
Fish production	0.5	1.3	1.8	45	0.5	1.4	1.9	44	0.9	36
Total outputs	***0.7***	***3.3***	***4***	***100***	***1.2***	***3.1***	***4.3***	***100***	***2.5***	***100***
Accumulation in water	0.4	-0.4	0	0	0.5	-0.5	0	0	0	0
Retention and/or losses	1.8	1.5	3.3	45	1.3	0.04	1.34	25	1.2	44

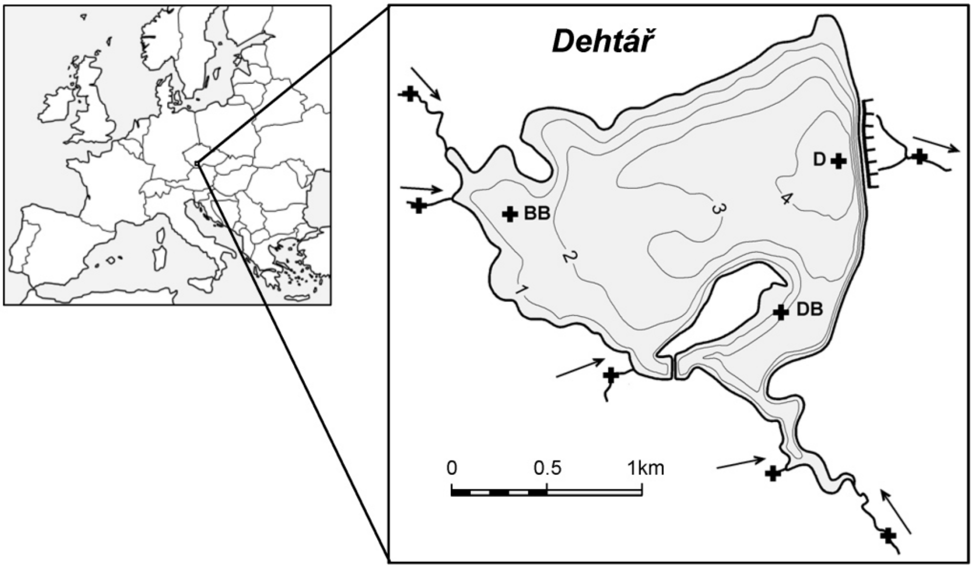

Figure 1. *Map of the Dehtář pond and its tributaries and outflow with sampling sites (crosses). The isobaths in the pond show the depth in meters at the water level at maximum filling.*

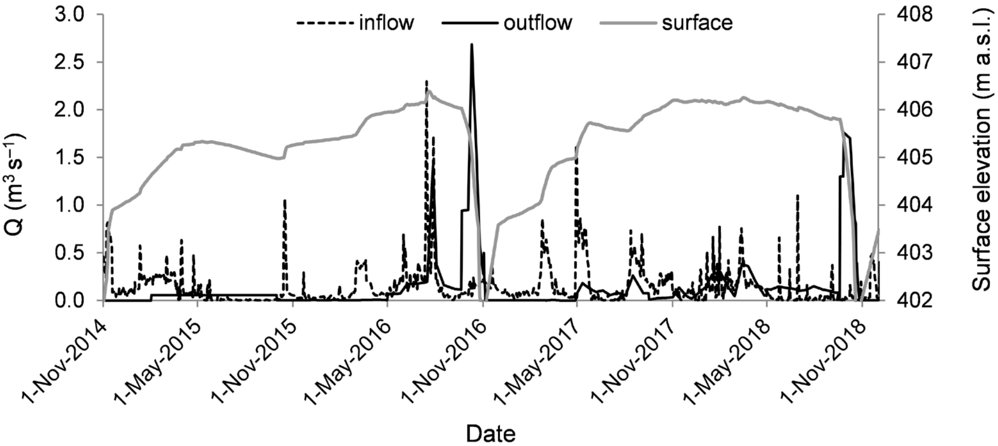

Figure 2. *Water level, inflow and outflow discharge in the Dehtář pond from November 2014 to November 2018.*

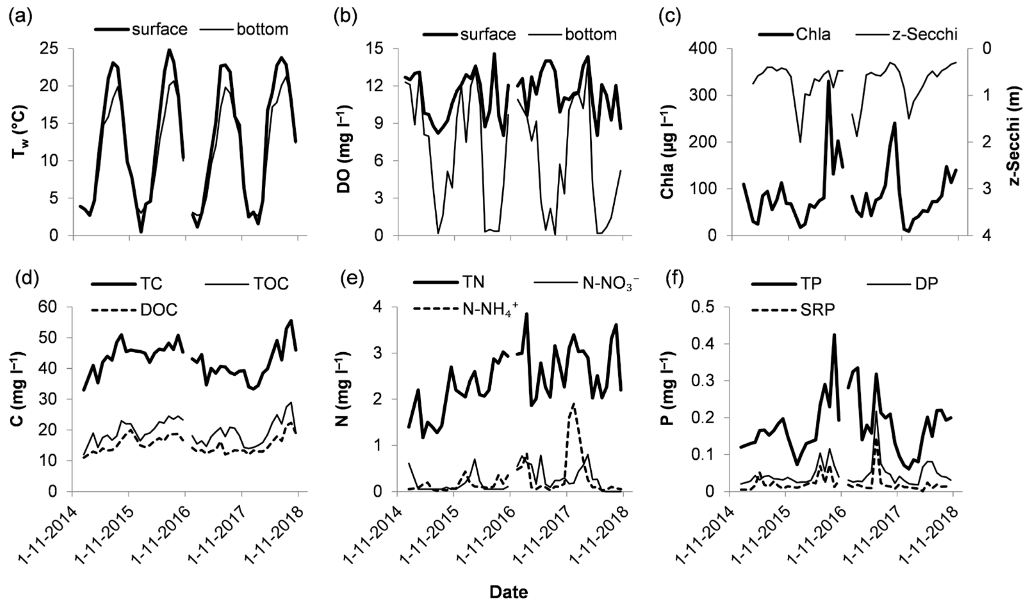

Figure 3. *Average monthly variables of water quality in the Dehtář pond at the dam site (site D): (a) surface and bottom water temperature, (b) dissolved oxygen (DO) concentration at the surface (0.3 m) and above the bottom, (c) chlorophyll a (Chla) and water transparency (z-Secchi), (d) concentrations of total carbon (TC), total organic carbon (TOC) and dissolved organic carbon (DOC), (e) concentrations of total nitrogen (TN) and mineral nitrogen fractions (N-NO_3^-, N-NH_4^+), (f) concentrations of total phosphorus (TP), dissolved phosphorus (DP) and soluble reactive phosphorus (SRP).*

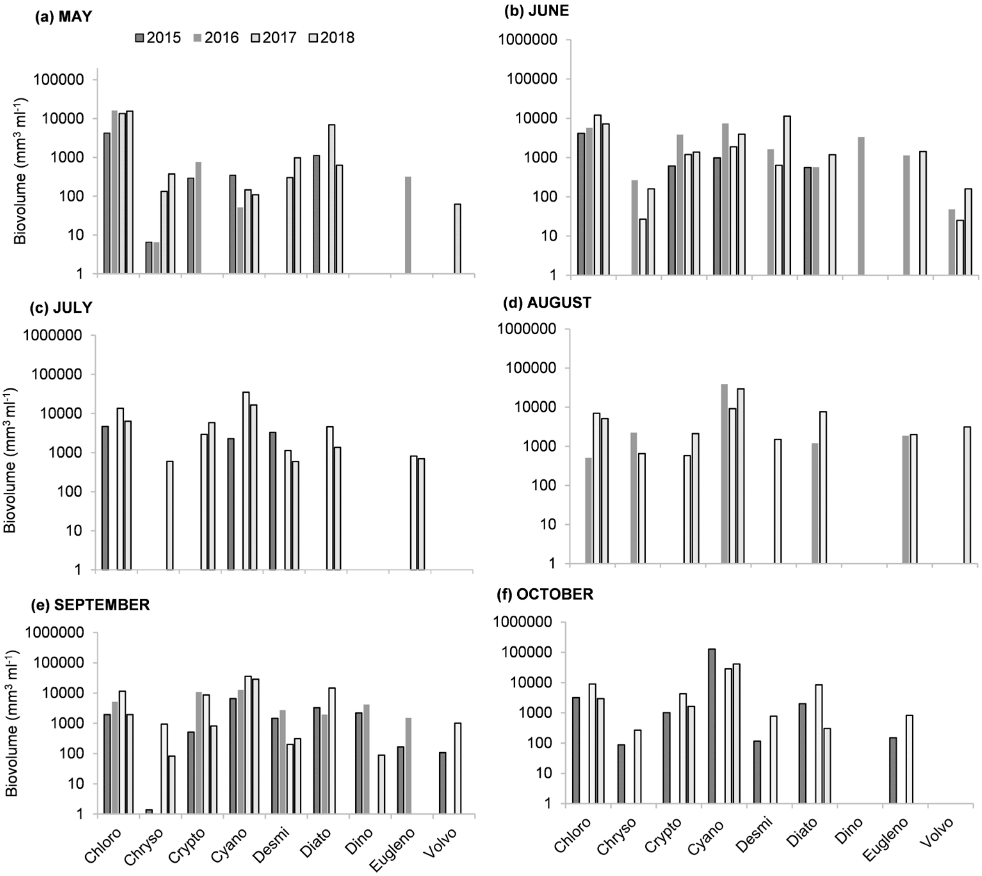

Figure 4. *Monthly values of phytoplankton biovolumes in the Dehtář pond during 2015–2018. Chloro: Chlorococcales; Chryso: Chrysophytes; Crypto: Cryptophytes, Cyano: Cyanophytes; Desmi: Desmids; Diato: Bacillariophytes; Dino: Dinoflagellates; Eugleno: Euglenophytes, Volvo: Volvocales.*

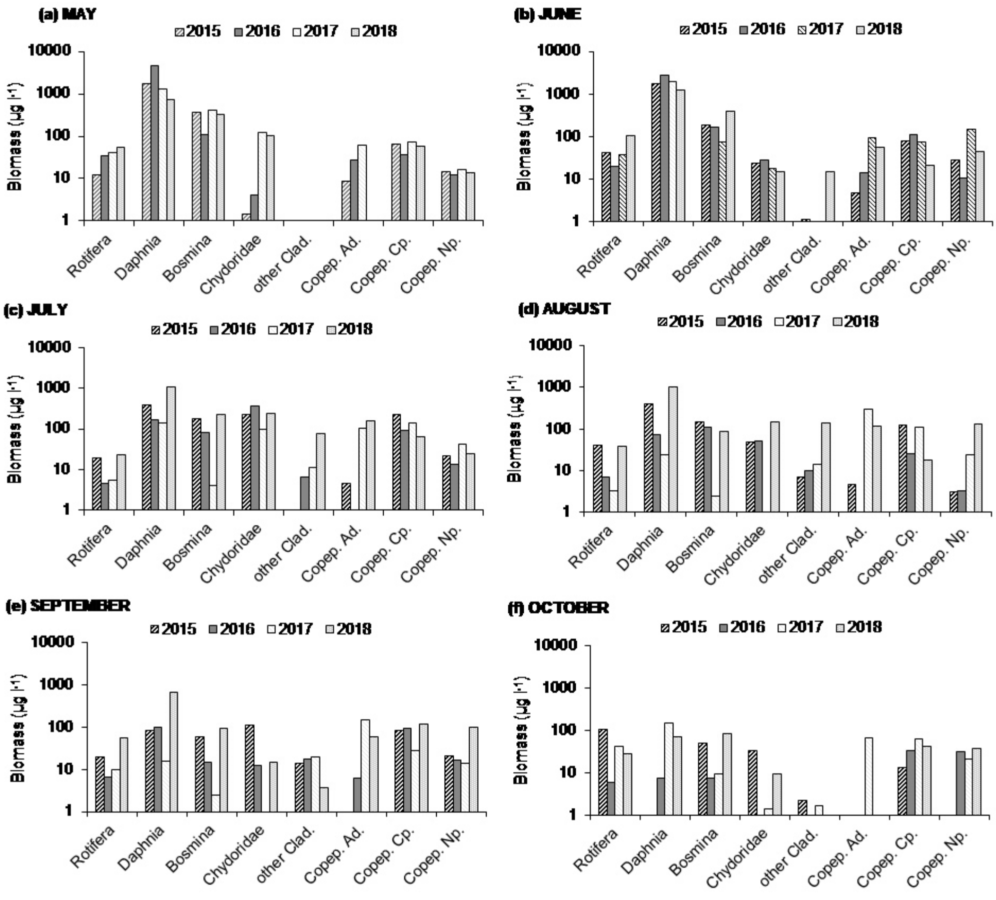

Figure 5. *Monthly zooplankton biomass values (µg l^{-1} DW). Abbreviations: other Clad: other cladocerans; Copep. Ad.: adult copepods; Copep. Cp: copepodites; Copep. Np: naupplii of copepods.*

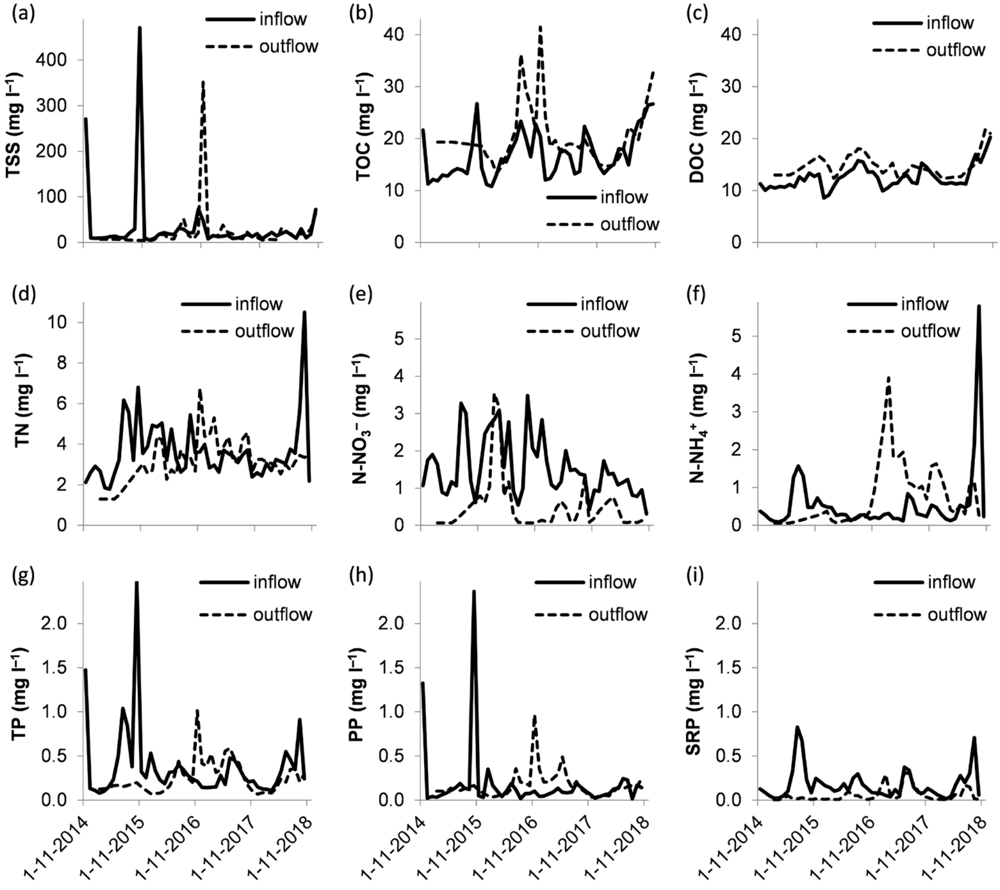

Figure 6. *Monthly average flow and time-weighted concentrations in the inflow (solid line) and outflow (dashed line) of the Dehtář pond. (a) Total suspended solids (TSS), (b) Total organic carbon (TOC), (c) Dissolved organic carbon (DOC), (d) Total nitrogen (TN), (e) Nitrate nitrogen (N-NO_3^-), (f) Ammonium nitrogen (N-NH_4^+), (g) Total phosphorus (TP), (h) Particulate phosphorus (PP), (i) Soluble reactive phosphorus (SRP).*

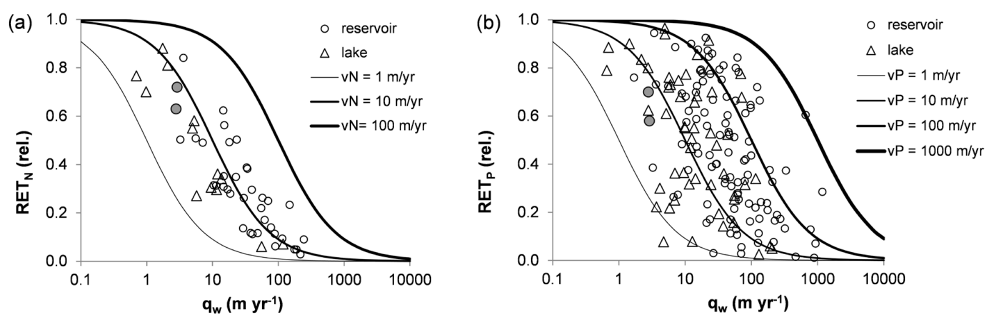

Figure 7. *The relationship between nutrient retention RET_x and water load q_w in lakes and reservoirs with curves that represent retention model (Chapra 1975, Kelly et al., 1987) for different v_x values: (a) nitrogen, (b) phosphorus retention values for the Dehtář pond in 2015–2016 and 2017–2018 are red filled circles.*

SUPPLEMENTARY INFORMATION

Table S1. *Physical and chemical parameters and methods of analysis used to characterise inflow, effluent and pond water quality in Dehtář pond from 2014 through 2018.*

Parameter	Method of analysis/instrument	Reference
Tw (°C)	Probe YSI 6600 V2-4 (Xylem Inc.)	
DO (mg.l^{-1})	Probe YSI 6600 V2-4 (Xylem Inc.)	
pH (-)	Probe YSI 6600 V2-4 (Xylem Inc.)	
Water transparency (cm)	Secchi disk	
TP (mg.l^{-1})	Inductive coupled plasma spectrometry (Agilent 8800 ICP-MSQ)	ISO (2003)
SRP (mg.l^{-1})	Spectrophotometric ammonium molybdate method (Shimadzu UV-1650 PC)	ISO (2003)
DP (mg.l^{-1})	Inductive coupled plasma spectrometry (Agilent 8800 ICP-MSQ)	ISO (2003)
TN (mg.l^{-1})	High-temperature combustion (Multi N/C 2100 analyser, Analytik Jena AG, Germany) with unfiltered water samples	DIN (2003)
N-NH_4^+ (mg.l^{-1})	Spectrophotometry (Shimadzu UV-1650 PC)	ISO (1984)
N-NO_3^- (mg.l^{-1})	Ion chromatography (Dionex ICS-1000)	ISO (2007)
Chl*a* (µg.l^{-1})	Spectrometry (Shimadzu UV-1650 PC)	ISO (1992)
TC (mg.l^{-1})	High-temperature combustion method (Multi N/C 2100 analyser, Analytik Jena AG, Germany)	ISO (1999)
TIC (mg.l^{-1})	Low-temperature acidification method (Multi N/C 2100 analyser, Analytik Jena AG, Germany)	ISO (1999)
TOC (mg.l^{-1})	TOC = TC - TIC	ISO (1999)
DC (mg.l^{-1})	High-temperature combustion method (Multi N/C 2100 analyser, Analytik Jena AG, Germany)	ISO (1999)
DIC (mg.l^{-1})	Low-temperature acidification method (Multi N/C 2100 analyser, Analytik Jena AG, Germany)	ISO (1999)
DOC (mg.l^{-1})	DOC = DC – DIC	ISO (1999)

Table S2. *Retention coefficients (R_N) and apparent settling velocity of nitrogen (v_N) in selected lakes and reservoirs. Z-mean: mean depth (m); WRT: water retention time in years (yr); [TN]: concentration of N in lake/reservoir water. The country of lake/reservoir location are given using the International country codes based on ISO3166 standard published by the International Organisation for Standardisation (www.iso.org/iso-3166-country-codes.html).*

Water Body	Location	Z-mean (m)	WRT (yr)	[TN] (mg l^{-1})	R_N	v_N (m yr^{-1})	Reference
Lakes							
Čertovo	CZE	18.3	1.58	1.07	0.29	4.9	Kopáček et al. (2001a)
Plešné	CZE	15.6	1.63	1.18	0.30	4.2	Kopáček et al. (2001c)
Černé	CZE	10	0.73	0.83	0.34	7.0	Kopáček et al. (2001b)
Findley	USA	7.8	0.14	0.13	0.06	3.6	Likens and Loucks (1978)
Mirror	USA	5.7	1.0	0.19	0.27	2.1	
Wingra	USA	2.4	0.48	2.14	0.55	6.1	
Vättern	SWE	39	56	0.57	0.76	2.3	Wilander and Persson (2001)
Dart's	USA	7.1	0.06	0.74	0.07	8.9	Kelly et al. (1987)
Langtjern	NOR	2.4	0.2	0.52	0.36	6.8	
Harp	CAN	12.4	2.35	0.58	0.58	6.8	
Plastic	CAN	8.0	3.83	0.52	0.81	10.7	
302N	USA	5.7	5.8	0.73	0.7	2.3	
239	USA	10.9	6.2	0.54	0.88	12.9	
Reservoirs							
DeGijster	NLD	13.1	0.21	4.22	0.17	13	Oskam (1982)
Hondert	NLD	15.7	0.17	3.96	0.06	6	
Petrusplaat	NLD	13	0.06	3.77	0.04	10	
Sulejow	POL	3.4	0.08	2.18	0.11	8	Galicka (1992)
Fort Supply	USA	2.3	0.7	0.89	0.5	3	Walker (1985)
Carlyle	USA	3.6	0.12	3.63	0.13	5	
John H Kerr	USA	9.3	0.24	1.23	0.11	5	
Honroe	USA	5.2	0.45	0.71	0.31	5	
Rend	USA	3.2	0.57	1.41	0.5	6	
Charles Mill	USA	1.7	0.03	2.95	0.11	6	
Barkley	USA	5.0	0.02	1.15	0.02	6	
Pomona	USA	5.5	0.37	2.29	0.3	7	
Milford	USA	7.8	1.09	1.48	0.49	7	
Sidney Lanier	USA	15.1	0.89	0.79	0.29	7	
Beaver	USA	17.8	0.95	0.78	0.27	7	
Somerville	USA	4.6	0.3	1.23	0.35	8	
Seminole	USA	3.0	0.01	1.35	0.04	9	
Shelbyville	USA	6.0	0.2	6.17	0.26	11	
Deer Creek	USA	3.1	0.03	3.98	0.11	11	
Beach City	USA	1.5	0.01	3.80	0.09	12	

Water Body	Location	Z-mean (m)	WRT (yr)	[TN] (mg l^{-1})	R_N	v_N (m yr^{-1})	Reference
Berlin	USA	5.1	0.22	2.09	0.34	12	Walker (1985)
Cumber-land	USA	22.4	0.28	0.91	0.14	13	
Mendocino	USA	13.5	0.24	0.76	0.22	16	
J Percy Priest	USA	8.3	0.2	0.89	0.29	17	
Enid	USA	5.6	0.3	0.87	0.49	18	
Harlan County	USA	6.9	1.9	1.23	0.84	19	
Lewisville	USA	6.6	0.43	0.96	0.56	19	
Allatoona	USA	9.1	0.15	0.56	0.26	20	
Table rock	USA	19.5	0.58	1.41	0.38	21	
Pleasant Hill	USA	5.8	0.08	1.55	0.24	23	
Canyon	USA	13.5	0.57	0.72	0.5	24	
Atwood	USA	4.4	0.3	0.96	0.62	24	
Bankhead	USA	9.3	0.038	1.55	0.09	24	
Rzesow Res.	POL	0.8	0.005	6.67	0.23	45	Tomaszek and Koszel-nik (2003)
Solina Res.	POL	20	0.58	2.26	0.38	21	
Hidvégi Pond	HUN	1	0.1	3.3	0.31	4.8	Pomogyi (1993)
Dehtář	CZE	1.8	0.65	2.04	0.63	4.87	This study
Dehtář	CZE	2.0	0.7	1.29	0.72	7.42	This study

Table S3. *Retention coefficients (R_P) and apparent settling velocity of phosphorus (v_P) in selected lakes and reservoirs. Z-mean: mean depth (m); WRT: water retention time in years (yr); [TP]: concentration of P in lake/reservoir water. The country of lake/reservoir location are given using the International country codes based on ISO3166 standard published by the International Organisation for Standardisation (www.iso.org/iso-3166-country-codes.html).*

Water Body	Location	Z-mean	WRT	[TP]	R_P	v_P	Reference
Lakes							
Beech	CAN	9.8	0.05	7	0.06	11	Dillon and Rigler (1974)
Bob	CAN	18	2.99	7	0.73	14	
Cameron	CAN	7.1	0.06	11	0.34	54	
Cranberry	CAN	3.5	0.01	6	0.05	7	
Eagle Moose	CAN	12.8	0.51	6	0.31	10	
Four Mile	CAN	9.3	4.25	8	0.83	7	
Maple	CAN	11.6	0.14	7	0.31	28	
Oblong Hal	CAN	17.7	3.12	6	0.72	17	
Pine	CAN	7.4	0.05	8	0.02	3	
Raven Hal	CAN	0.73	0.07	9	0.55	14	
Twelve Mile	CAN	18.1	0.47	6	0.36	20	

Water Body	Location	Z-mean	WRT	[TP]	R_P	v_P	Reference
ELA 227	CAN	4.4	2.8	26	0.92	18	Fee (1979)
ELA 239 Rawso	CAN	10.5	5.35	9	0.71	5	
Annone	ITA	4	0.81	24	0.96	126	Fricker (1980)
Atter	AUT	84.2	7	11	0.46	21	
D'Alserio	ITA	5.34	0.35	105	0.85	66	
Feldsee	DEU	15.7	0.48	4	0.19	7	
Greifen	CHE	17.7	1.38	192	0.07	1	
Hallwiler	CHE	28.6	4.1	219	0.25	2	
Lunzer Unter	CHE	20	0.36	7	0.25	17	
Montorfano	ITA	4.15	1.51	15	0.8	10	
Sempacher	CHE	46	16.5	104	0.62	6	
Vierwaldst	CHE	75	1.38	21	0.15	8	
Walen	CHE	100	1.4	18	0.67	95	
Čertovo	CZE	18.3	1.58	3.5	0.31	5	Kopáček et al. (2001a)
Černé	CZE	15.6	1.63	3.5	0.36	5	Kopáček et al. (2001c)
Plešné	CZE	10	0.73	11	0.55	17	Kopáček et al. (2001b)
Findley	USA	7.8	0.14	3	0.27	21	Likens and Loucks (1978)
Mirror	USA	5.7	1.0	6	0.76	18	
Wingra	USA	2.4	0.48	12	0.94	78	
Washington	USA	32.9	3.3	21	0.55	12	Reckhow (1977)
Sammamish	USA	17.7	2.08	21	0.68	15	
Okanagan	CAN	76	52.8	16	0.9	7	
Boren	USA	6	0.2	20	0.47	24	Ryding (1980)
Malaren Ekol	SW	17.1	1.23	83	0.65	32	
Mjosa	NOR	153	6	9	0.7	64	
Mosso	DNK	8.5	2.3	189	0.22	1	
Tuusulan	FIN	3.1	0.6	126	0.61	9	
Bodensee Ober-see	DEU	100.2	4.4	7	0.79	58	Sas (1989)
Bodensee Ober-see	DEU	100.4	4.4	13	0.91	51	
Fuschlsee	AUT	37.6	3.0	17	0.5	15	
Lac Léman	CHE	172.0	11.47	48	0.68	21	
Gjersjøen	NOR	23.0	2.9	24	0.74	20	
Glumsø	DNK	1.6	0.38	886	0.3	1	
Hylke Sø	DNK	7.1	1.5	253	0.07	0.5	
LoughNeagh	GBR	8.9	1.27	115	0.36	4	
Maggiore	ITA	176.5	4.0	27	0.53	52	
Ossiachersee	AUT	19.6	1.9	16	0.77	47	
Søbygard	DNK	1.0	0.07	1421	0.33	13	
Veluwemeer	NLD	1.3	0.22	197	0.21	1	

Water Body	Location	Z-mean	WRT	[TP]	R_P	v_P	Reference
Walensee	CHE	100	1.44	13	0.77	112	Sas (1989)
Zürichsee-Untersee	CHE	51.0	1.35	56	0.14	5	
Halls	CAN	27.2	1.11	4	0.53	25	Tzaras and Pick (1994)
Vännem	SWE	25.0	38	6	0.78	2	Wilander and Persson (2001)
Vättern	SWE	39.0	56	6	0.88	5	
Reservoirs							
Labo-Broa	BRA	3.2	0.05	37	0.13	9	Chalar and Tundis (2001)
Lipno	CZE	5.6	0.35	23	0.44	14	Brandl (1973)
Ceske Udoli	CZE	2.5	0.03	214	0.42	55	Duras and Hejzlar (2001)
Ceske Udoli	CZE	2.5	0.03	352	0.17	14	
Aube	FRA	5.5	0.49	26	0.37	14	Garnier et al. (1999)
Marne	FRA	4.6	0.45	29	0.68	21	
Seine	FRA	7.6	0.3	24	0.38	22	
Bavigne	LUX	7.1	0.12	36	0.79	231	Salvia-Castellvi et al. (2001)
Misere	LUX	2.5	0.004	92	0.94	1008	
Driss I	MAR	6.1	2.09	31	0.94	49	Alaoui-Mhamdi et al. (1996)
Al Massira	MAR	18.7	1.51	32	0.89	125	Alaoui-Mhamdi and Aleya (1995)
DeGjster	NLD	13.1	0.21	240	0.27	23	Oskam Oskam (1982)
Petrusplaat	NLD	13.0	0.06	150	0.37	114	Oskam Oskam (1982)
Sulejow	POL	3.4	0.08	251	0.33	21	Galicka (1992)
Anarbe	ESP	25.7	0.41	9	0.32	30	Casas and Martínez (1984)
Azután	ESP	9.0	0.04	1766	0.16	45	
Castrejón	ESP	5.5	0.02	2077	0.17	57	
El Atazar	ESP	39.0	1.84	21	0.15	2	
El Burguillo	ESP	23.4	0.36	60	0.25	22	
Guajaraz	ESP	10.1	1.02	59	0.48	15	
Ribarroja	ESP	11.8	0.01	97	0.28	471	
Riosequillo	ESP	15.8	0.12	55	0.07	28	
San Pons	ESP	18.8	0.3	68	0.1	6	
Sau	ESP	29.4	0.29	351	0.43	72	
Valmayor	ESP	10.7	6.45	284	0.75	9	
Douglas	USA	10.7	0.11	33	0.49	33	Higgins and Kim (1981)
Fontana	USA	37.8	0.28	15	0.66	269	
Guntersville	USA	4.2	0.02	29	0.23	53	
Hiwassee	USA	20.2	0.15	17	0.17	31	
Chatuge	USA	9.5	0.43	16	0.23	7	
Cherokee	USA	13.9	0.21	33	0.78	237	
Nickjack	USA	6.7	0.008	35	0.01	25	
Norris	USA	16.3	0.37	14	0.6	75	

Water Body	Location	Z-mean	WRT	[TP]	R_P	v_P	Reference
South Holton	USA	23.4	0.55	11	0.67	89	Higgins and Kim (1981)
Tims Ford	USA	14.9	0.56	22	0.02	2	
Watauga	USA	24.5	0.68	12	0.75	116	
Watts Bar	USA	7.3	0.03	27	0.32	100	
Wilson	USA	12.3	0.01	52	0.07	72	
Callahan	USA	2.0	0.29	96	0.26	2	Schreiber and Rausch (1979)
Talquin	USA	4.1	0.12	96	0.44	34	Turner et al. (1983)
Allatoona	USA	9.1	0.15	26	0.66	114	Walker (1985)
Allegheny	USA	13.2	0.16	31	0.32	39	
Ashtabula	USA	3.8	0.49	224	0.27	39	
Atwood	USA	4.4	0.3	28	0.69	34	
Bankhead	USA	9.3	0.03	53	0.18	57	
Barkley	USA	5.0	0.02	123	0.07	18	
Barren River	USA	7.9	0.15	47	0.3	22	
Beach City	USA	1.5	0.01	209	0.21	32	
Beaver	USA	17.8	0.95	16	0.74	54	
Beltzville	USA	15.5	0.24	11	0.21	15	
Berlin	USA	5.1	0.22	58	0.84	126	
Blues Tone	USA	9.8	0.02	46	0.01	7	
Bull Shoals	USA	20.9	0.43	12	0.34	25	
Canyon	USA	13.5	0.57	11	0.43	18	
Carlyle	USA	3.6	0.12	120	0.4	20	
Clark Hill	USA	10.7	0.26	25	0.56	54	
Cumberland	USA	22.4	0.28	34	0.41	55	
Dale Hollow	USA	14.5	0.67	8	0.55	27	
Deer Creek	USA	3.1	0.03	174	0.35	49	
Delaware	USA	3.5	0.02	129	0.24	45	
Dworshak	USA	57.5	0.6	17	0.16	18	
Enid	USA	5.6	0.3	65	0.77	63	
F J Savers	USA	4.6	0.04	83	0.63	169	
Fort Supply	USA	2.3	0.7	51	0.38	2	
Harlan County	USA	6.9	1.9	123	0.73	10	
Hartwell	USA	13.8	0.53	9	0.85	156	
Hills Creek	USA	37.2	0.28	36	0.11	16	
Holt	USA	11	0.01	34	0.12	116	
Honroe	USA	5.2	0.45	13	0.62	19	
Charles Mill	USA	1.7	0.03	155	0.11	6	
J Percy Priest	USA	8.3	0.2	102	0.32	19	
John H Kerr	USA	9.3	0.24	26	0.8	162	
John Redmond	USA	2.5	0.05	178	0.53	52	

Water Body	Location	Z-mean	WRT	[TP]	R_P	v_P	Reference
John W Flannagan	USA	19.5	0.31	12	0.84	330	Walker (1985)
Keystone	USA	8.1	0.06	110	0.71	315	
Lavon	USA	5.0	0.28	49	0.79	67	
Lewisville	USA	6.6	0.43	78	0.72	40	
Mendocino	USA	13.5	0.24	63	0.51	58	
Milford	USA	7.8	1.09	60	0.88	56	
Millwood	USA	2.3	0.02	48	0.23	28	
Mississinewa	USA	7.4	0.09	132	0.61	128	
Old Hickory	USA	5.8	0.01	93	0.13	49	
Pleasant Hill	USA	5.8	0.08	55	0.02	2	
Pomona	USA	5.5	0.37	59	0.58	21	
Red Rock	USA	3.5	0.03	219	0.64	177	
Rend	USA	3.2	0.57	87	0.72	15	
Sakakawea	USA	18.2	0.89	27	0.92	250	
Seminole	USA	3.0	0.01	76	0.2	47	
Shelbyville	USA	6.0	0.2	105	0.4	20	
Shenango River	USA	3.2	0.05	71	0.27	24	
Sidney Lanier	USA	15.1	0.89	19	0.78	63	
Somerville	USA	4.6	0.3	66	0.47	13	
Stillhouse Hollow	USA	12.0	0.45	17	0.66	53	
Summersville	USA	20.0	0.06	15	0.37	199	
Table Rock	USA	19.5	0.58	18	0.79	127	
Tenkiller Ferry	USA	15.8	0.33	48	0.52	51	
Texona	USA	9.8	0.4	91	0.77	83	
Tuttle Creek	USA	7.8	0.35	135	0.87	150	
Walter F George	USA	5.9	0.08	91	0.05	4	
Hartbeespoot Dam	ZAF	9.0	0.91	621	0.69	22	Thornton and Ashton (1989)
Bort-Les-Orgues	FRA	33	0.25	50	0.52	143	Brigault and Ruban (2000)
Hidvédi-Pond	HUN	1	0.10	232	0.57	14	Pomogyi (1993)
Wahnbach Talspere	DEU	16	1.02	15	0.87	102	Sas (1989)
Wahnabach Talspere	DEU	16	0.81	11	0.61	38	
Williams Fork Reservoir	USA	18	0.76	23	0.17	5	LaBaugh (1985)
Dehtář	CZE	1.81	0.76	253	0.7	6.56	This study
Dehtář	CZE	2.02	0.65	252	0.58	3.93	This study

References

Alaoui-Mhamdi, M., Aleya, L., 1995. Assessment of the eutrophication of Al Massira reservoir (Morocco) by means of a survey of the biogeochemical balance of phosphate. Hydrobiologia 297: 75–82.

Alaoui-Mhamdi, M., Aleya, L., Bahhou, J., 1996. Nitrogen compounds and phosphate of the Driss I reservoir (Morocco): input, output and sedimentation. Hydrobiologia 335: 75–82.

Brandl, Z., 1973. Horizontal distribution of some chemical and physical characteristics in Lipno Reservoir. In: Hrbáček, J., Straškraba, M. (Eds), Hydrobiological Studies. Academia, Prague, pp. 53–90.

Brigault, S., Ruban, V., 2000. External phosphorus load estimates and P-budget for the hydroelectric reservoir of Bort-Les-Orgues, France. Water Air and Soil Pollution 119: 91–103.

Casas, J.O., Martínez, R.P., 1984. Applicability of the OECD eutrophication models to Spanish reservoirs. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 22: 1521–1535.

Chalar, G., Tundisi, J.G., 2001. Phosphorus fractions and fluxes in the water column and sediments of a tropical reservoir (Lobo-Broa–SP). International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology 86: 183–194.

Dillon, P.J., Rigler, F.H., 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. Journal of the Fisheries Board of Canada 31: 1771–1778.

DIN, 2003. Water quality. Determination of nitrogen. Determination of bound nitrogen (TNb), following oxidation to nitrogen oxides (DIN EN 12260: 2003). Deutches Institut fur Normung E.V. (DIN), Berlin.

Duras, J., Hejzlar, J., 2001. The effect of outflow depth on phosphorus retention in a small, hypertrophic temperate reservoir with short hydraulic residence time. International Review of Hydrobiology 86: 585–601

Fee, E.J., 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnology and Oceanography 24: 401–416.

Fricker, H.J., 1980. Eutrophication programme, regional project alpine lakes. Organisation for Economic Cmpration and Development Rep., Swiss Federal Board for Environmental Protection, Bern.

Galicka, W., 1992. Total nitrogen and phosphorus budgets in the lowland Sulejow Reservoir for the hydrological years 1985–1988. Arch. Hydrobiol. Suppl. 2: 159–169.

Garnier, J., Leporcq, B., Sanchez, N., Philippon, X., 1999. Biogeochemical mass-balances (C, N, P, Si) in three large reservoirs of the Seine Basin (France). Biogeochemistry 47: 119–146.

Higgins, J.M., Kim, B.R., 1981. Phosphorus retention models for Tennessee Valley Authority reservoirs. Water Resources Research 17: 571–576.

ISO, 1984. Water quality-determination of ammonium. Part 1: manual spectrometric method (ISO 7150-1: 1984). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 1992. Water quality, measurement of biochemical parameters; spectrometric determination of chlorophyll-a concentration (ISO 10260: 1992). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 1999. Water quality-Guidelines for the determination of total organic carbon (TOC) and dissolved organic carbon (DOC) (ISO 8245: 1999). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 2003. Water quality-application of inductively coupled plasma mass spectrometry (ICP-MS)-Part 2: determination of 62 elements (ISO 17294-2: 2003). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 2007. Water quality-determination of dissolved anions by liquid chromatography of ions-Part 1: determination of bromide, chloride, fluoride, nitrate, nitrite, phosphate and sulfate (ISO 10304-1:2007). Int. Organ. for Standardisation (ISO), Geneva.

Kelly, C., Rudd, J., Hesslein, R., Schindler, D., Dillon, P., Driscoll, C.T., Gherini, S., Hecky, R., 1987. Prediction of biological acid neutralization in acid-sensitive lakes. Biogeochemistry 3: 129–140.

Kopáček, J., Hejzlar, J., Kaňa, J., Porcal, P., 2001a. Element budgets in three Bohemian Forest lakes and their watersheds in the 2000 hydrological year: I. Čertovo Lake. Silva Gabreta 7: 35–52.

Kopáček, J., Hejzlar, J., Kaňa, J., Porcal, P., 2001b. Element budgets in three Bohemian Forest lakes and their watersheds in the 2000 hydrological year: III. Plešné Lake. Silva Gabreta 7: 73–86.

Kopáček, J., Hejzlar, J., Kaňa, J., Porcal, P., Pšenáková, P., 2001c. Element budgets in three Bohemian Forest lakes and their watersheds in the 2000 hydrological year: II. Černé Lake. Silva Gabreta 7: 53–72.

LaBaugh, J.W., 1985. Uncertainty in phosphorus retention, Williams Fork Reservoir, Colorado. Water Resources Research 21: 1684–1692.

Likens, G.E., O.L. Loucks, 1978. Analysis of five North American lake ecosystems. III. Sources, loading and fate of nitrogen and phosphorus. Verb. Internat. Verein. Limnol. 20: 568–573

Oskam, G., 1982. Quality aspects of the Biesbosch reservoirs. J. Water Supply Res. Technol-Aqua 6: 497–504.

Pomogyi, P., 1993. Nutrient retention by the Kis-Balaton water protection system. Hydrobiologia 251: 309–320.

Reckhow, K.H., 1977. Phosphorus models for lake management. Harvard University, Harvard.

Ryding, S., 1980. Monitoring of inland waters: OECD eutrophication programme-the Nordic project publication. Nordic Co-operative Organisation of Applied Research (NORDFORSK), Helsinki, Finland.

Salvia-Castellvi, M., Dohet, A., Vander Borght, P., Hoffmann, L., 2001. Control of the eutrophication of the reservoir of Esch-sur-Sûre (Luxembourg): Evaluation of the phosphorus removal by predams. Hydrobiologia 459: 61–71.

Sas, H., 1989. Lake restoration by reduction of nutrient loading: expectations, experiences, extrapolations. Richarz, Academia Verlag, 497 pp.

Schreiber, J. Rausch, D., 1979. Suspended sediment-phosphorus relationships for the inflow and outflow of a flood detention reservoir 1. Journal of Environmental Quality 8: 510–514.

Thornton, J., Ashton, P., 1989. Aspects of the phosphorus cycle in Hartbeespoort Dam (South Africa) Phosphorus loading and seasonal distribution of phosphorus in the reservoir. Hydrobiologia 183: 73–85.

Tomaszek, J.A., Koszelnik, P., 2003. A simple model of nitrogen retention in reservoirs. Hydrobiologia 504: 51–58.

Turner, R.R., Laws, E.A., Harris ,R.C., 1983. Nutrient retention and transformation in relation to hydraulic flushing rate in a small impoundment. Freshwater Biology 13: 113–127.

Tzaras, A., Pick, F.R., 1994. The relationship between bacterial and heterotrophic flagellate abundance in oligotrophic to mesotrophic temperate lakes. Marine mICROBIAL FOOD Webs 8: 347–355.

Walker, W.W., 1985. Empirical Methods for Predicting Eutrophication in Impoundments. Report 1. Phase III. Model Refinements. US Army Engineering Waterways Experiment Station, Vicksburg, MS.

Wilander, A., Persson, G., 2001. Recovery from eutrophication: experiences of reduced phosphorus input to the four largest lakes of Sweden. AMBIO: A Journal of the Human Environment 30: 475–485.

CHAPTER 4

DIFFUSIVE METHANE EMISSIONS FROM TEMPERATE SEMI-INTENSIVE CARP PONDS

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FEATURE ARTICLE

Diffusive methane emissions from temperate semi-intensive carp ponds

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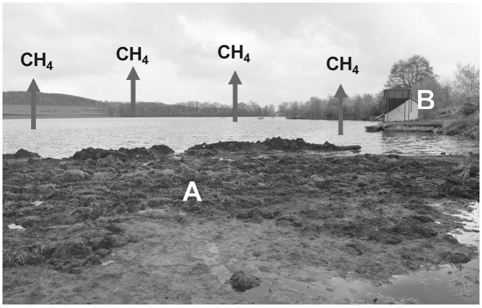
ABSTRACT: Manuring and supplementary feeding are common practices used to sustain high fish production in temperate semi-intensive carp ponds. However, the low use efficiency of added nutrients and organic matter may cause carp ponds to be 'hot spots' of methane (CH_4) production and emission. Surface CH_4 concentrations were measured and diffusive CH_4 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 CH_4 were 1.3 ± 0.9 µM and 0.8 ± 0.8 µM in nursery and main ponds, respectively. All ponds were sources of CH_4, with diffusive CH_4 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 CH_4 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 CH_4 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



Emission of diffusive methane from a temperate fishpond and inputs inducing CH_4 production in carp ponds: (A) manuring and (B) feeding.

Photo credit: *Dr. Bořek Drozd*
(Faculty of Fisheries, University of South Bohemia)

1. INTRODUCTION

Globally averaged atmospheric methane (CH_4) concentration has increased from approximately 650 to 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 CH_4 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 CH_4 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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CH_4 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). CH_4 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 CH_4 production in aquatic ecosystems (Huttunen et al. 2003). Oxygen is an important factor in CH_4 production and consumption (Huttunen et al. 2006, Juutinen et al. 2009); lack of oxygen enhances CH_4 production in sediment, while its presence promotes its microbial oxidation (Bastviken et al. 2002, Attermeyer 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 CH_4 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 km^2 in France, 410 km^2 in the Czech Republic, 420 km^2 in Germany, 25 669 km^2 in China, and 87 500 km^2 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 resources 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 CH_4 and its subsequent evasion to the atmosphere (Gelesh et al. 2016). Indeed, Juutinen et al. (2009) found that CH_4 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 CH_4 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 CH_4 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 CH_4 and CO_2 *in situ* emissions from fishponds to confirm a positive net carbon sequestration. Studies of CH_4 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, Všetičková et al. 2012, Všetičková & Adámek 2013, Hlaváč et al. 2014, Four et al. 2017). CH_4 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 CH_4 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 CH_4 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 15^{th} and 16^{th} 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 multiparameter 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 (NO_3-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 CO_2 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 CO_2, bicarbonate, and carbonate to gaseous CO_2, 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 (NH_4-N) was determined by the spectrophotometric method with bis-pyrazolon according to Kopáček & Procházková (1993). NO_3-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. C_0: common carp *Cyprinus carpio* fingerlings; C_2–C_4: 2–4 yr old common carp; P_0: northern pike *Esox lucius* fingerlings; P_1 = 1 yr old northern pike

Fishpond	Type	GPS coordinates °N	GPS coordinates °E	Area (ha)	Depth (m) Max	Depth (m) Mean	Fish
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 × 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 10 000 ppm of CH_4. The detection limit for CH_4 analysis was 0.1 ppm, and the precision of measurements was ±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 µmol l^{-1}, C_{eq} is the gas concentration in surface water in equilibrium with the atmosphere in µmol 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: $Sc_{CH4} = 1897.8 - 114.28t + 3.2902t^2 - 0.039061t^3$, where t (°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 CH_4 in pond surface water, CH_4 saturation levels, and diffusive CH_4 flux. This analysis was followed by Tukey's post hoc tests to determine differences in CH_4 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 CH_4 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 CH_4 concentration and flux were identified based on the weight of each predictor variable and total explanatory capacity (R^2 of Y and R^2 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 concentration 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). NH_4-N (Fig. 1l), NO_3-N (Fig. 1m), DN (Fig. 1n), and TN (Fig. 1o) showed a slight decreasing trend during the study period. Only NH_4-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; NH_4-N: ammonium nitrogen; NO_3-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 *a* (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

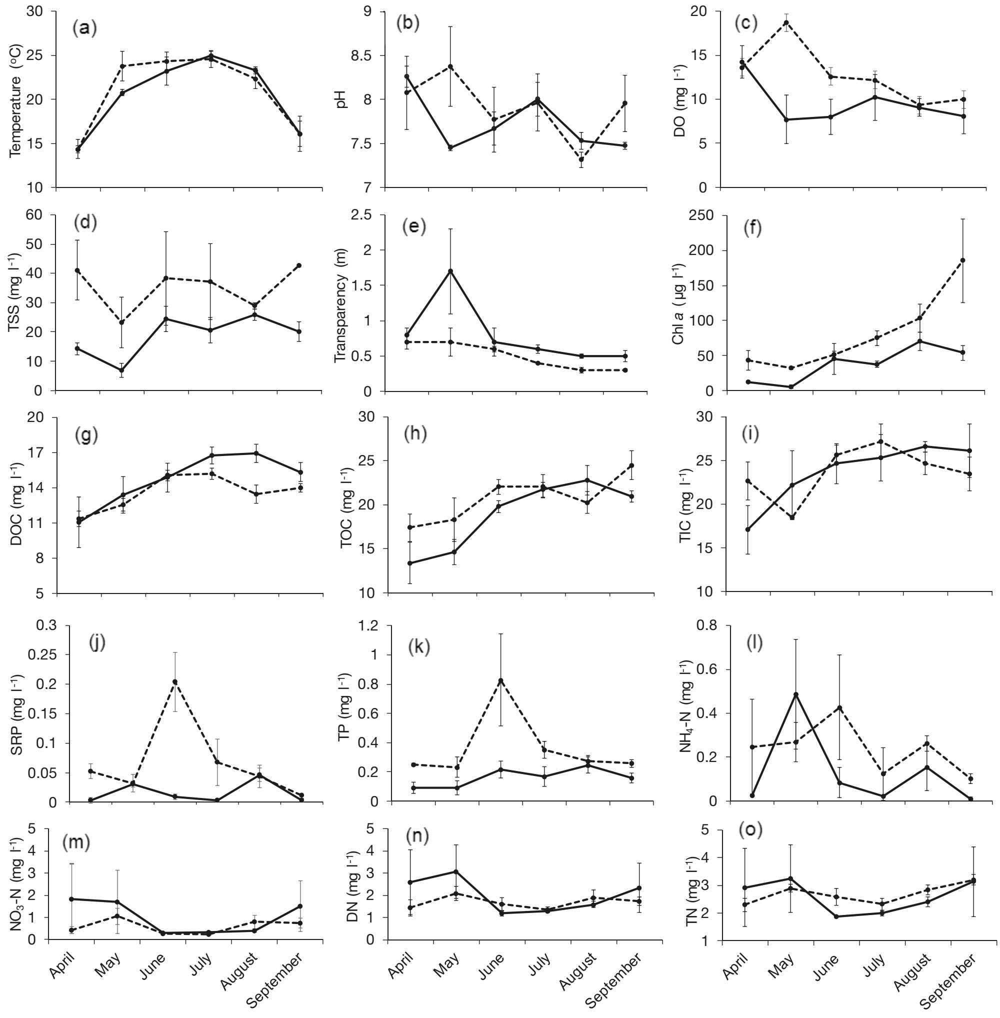

Fig. 1. Temporal dynamics of physico-chemical characteristics of water in main (dotted line) and nursery (continuous line) ponds. Variable abbreviations as in Table 2. Values are means ± SE

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

3.2. CH_4 concentrations and diffusive emissions

The mean (±SD) surface concentrations of dissolved CH_4 were 0.8 ± 0.8 and 1.3 ± 0.9 µM 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 CH_4 concentrations ranged from 0.06 to 4.8 µM 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

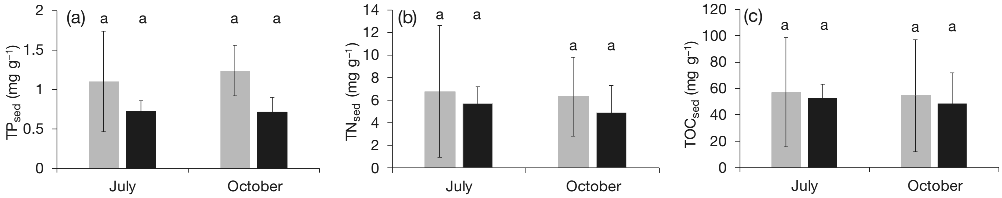

Fig. 2. Sediment composition in nursery (black bars) and main (grey bars) ponds. Variable abbreviations as in Table 2. Values are means ± SE

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 supersaturated with CH_4. The mean saturation degree was 41 824 ± 28 932 % and 20 770 ± 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 (CH_4-C) ranged from 0.19 to 32 mg m^{-2} d^{-1} in all ponds with a mean of 7.8 ± 7.0 mg m^{-2} 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 CH_4-C were slightly higher in nursery ponds (9.1 ± 6.8 mg m^{-2} d^{-1}) than in main ponds (6.4 ± 6.9 mg m^{-2} 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).

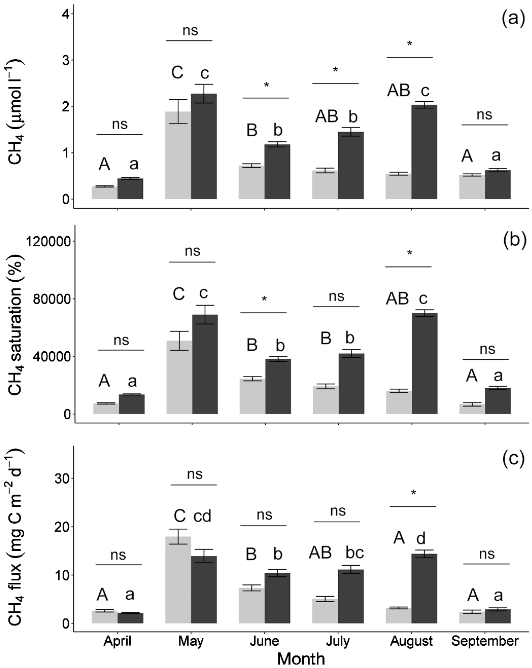

Fig. 3. Temporal variability of (a) CH_4 concentration, (b) CH_4 saturation, and (c) diffusive flux of CH_4 in nursery (black bars) and main (grey bars) ponds. Data are means ± SE. Different letters denote significant (p < 0.05) differences in the same pond type over time (uppercase letters = main ponds, 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 physicochemical 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. R^2Y: explained variability of dependent variables (CH_4 concentration or CH_4 diffusive flux); R^2X: 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 *a*	−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^2Y	0.4	0.11	0.04	0.34
R^2X	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 CH_4 flux (Table 3). This component was positively associated with water temperature, but the association was not significant.

4. DISCUSSION

The increase in CH_4 concentration and flux that occurred from April to May suggests that the increase in CH_4 concentration was primarily related to the increase in water temperature (Table 3). Water temperature influences CH_4 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, CH_4 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 CH_4 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 CH_4 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 ± 0.5 m s^{-1}) than above nursery ponds (1.0 ± 0.5 m s^{-1}).

CH_4 concentration and flux in the main ponds decreased in summer and became lower than in nursery ponds. Other studies have shown CH_4 emissions to be highly correlated with temperature throughout the growing season (Natchimuthu et al. 2014, Wik et al. 2014). The observed low CH_4 concentration and flux in the main ponds may be explained by CH_4 oxidation and the behaviour of carp over 1 kg body weight burrowing in search of food at the bottom of the ponds. CH_4 oxidation is an important pathway that reduces surface water CH_4 concentration and its emission from water bodies (Bastviken et al. 2008, Juutinen et al. 2009). Oxidation probably plays an important role in CH_4 dynamics in carp ponds as well, despite its short time exposure due to shallowness of the ponds (Table 1). In shallow lakes, CH_4 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 NO_3 (Table 2) may be a limiting factor in CH_4 oxidation occurring in deeper areas near pond outlets (Bastviken et al. 2008, Deutzmann et al. 2014, Roland et al. 2017). CH_4 oxidation rates are positively correlated to consumption of NO_3 under anoxic conditions (Roland et al. 2017). Bioturbation of the top sediment layer by carp may reduce CH_4 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).

CH_4 concentration was negatively related to DOC (Table 3), implying that DOC was not the primary source of, or a factor strongly associated with, CH_4 production. The increase in CH_4 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). CH_4 production in lakes of temperate and boreal regions might differ substantially depending on the chemical composition of sediments (Emilson et al. 2018). Sediments containing organic matter from macrophytes and aquatic plants produce more CH_4 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 CH_4 concentration and flux than those without, or with low abundance, of macrophytes (Selvam et al. 2014). Similarly, Ma et al. (2018) reported higher CH_4 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 influence 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 ± 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 (mg l^{-1}d^{-1})	Ebul CH_4 (mg l^{-1}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 CH_4 production and release by disturbing sediment and maintaining the upper layer in oxic conditions. The CH_4 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 CH_4 release into the atmosphere in order to define the local and global role of carp ponds in CH_4 emissions.

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LITERATURE CITED

Abnizova A, Siemens J, Langer M, Boike J (2012) Small ponds with major impact: the relevance of ponds and lakes in permafrost landscapes to carbon dioxide emissions. Global Biogeochem Cycles 26:GB2041

Adámek Z (2014) Hydrobiology in fisheries. In: Adámek Z, Helešic J, Maršálek B, Rulík M (eds) Applied hydrobiology. USB, Vodňany, p 307–351

Attermeyer K, Flury S, Jayakumar R, Fiener P and others (2016) Invasive floating macrophytes reduce greenhouse gas emissions from a small tropical lake. Sci Rep 6:20424

Banas D, Masson G, Leglize L, Usseglio-Polatera P, Boyd CE (2008) Assessment of sediment concentration and nutrient loads in effluents drained from extensively managed fishponds in France. Environ Pollut 152:679–685

Bastviken D, Ejlertsson J, Tranvik L (2002) Measurement of methane oxidation in lakes: a comparison of methods. Environ Sci Technol 36:3354–3361

Bastviken D, Cole JJ, Pace ML, Tranvik L (2004) Methane emissions from lakes: dependence of lake characteristics, two regional assessments, and a global estimate. Global Biogeochem Cycles 18:GB4009

Bastviken D, Cole JJ, Pace ML, Van de Bogert MC (2008) Fates of methane from different lake habitats: connecting whole lake budgets and CH_4 emissions. J Geophys Res Biogeosci 113:G02024

Bastviken D, Santoro AL, Marotta H, Pinho LQ, Calheiros DF, Crill P, Enrich-Prast A (2010) Methane emissions from Pantanal, South America, during the low water season: toward more comprehensive sampling. Environ Sci Technol 44:5450–5455

Bastviken D, Tranvik LJ, Downing JA, Crill PM, Enrich-Prast A (2011) Freshwater methane emissions offset the continental carbon sink. Science 331:50

Battin TJ, Kaplan LA, Findlay S, Hopkinson CS and others (2008) Biophysical controls on organic carbon fluxes in fluvial networks. Nat Geosci 1:95–100

Bednařík A, Blaser M, Matoušů A, Hekera P, Rulík M (2017) Effect of weir impoundments on methane dynamics in a river. Sci Total Environ 584–585:164–174

Bhattacharyya P, Sinhababu DP, Roy KS, Dash PK and others (2013) Effect of fish species on methane and nitrous oxide emission in relation to soil C, N pools and enzymatic activities in rainfed shallow lowland rice-fish farming system. Agric Ecosyst Environ 176:53–62

Bogard MJ, Del Giorgio PA, Boutet L, Chaves MCG, Prairie YT, Merante A, Derry AM (2014) Oxic water column methanogenesis as a major component of aquatic CH_4 fluxes. Nat Commun 5:5350

Borges A, Abril G, Delille B, Descy JP, Darchambeau F (2011) Diffusive methane emissions to the atmosphere from Lake Kivu (Eastern Africa). J Geophys Res Biogeosci 116:G03032

Borges AV, Abril G, Darchambeau F, Teodoru CR and others (2015a) Divergent biophysical controls of aquatic CO_2 and CH_4 in the World's two largest rivers. Sci Rep 5: 15614

Borges AV, Darchambeau F, Teodoru CR, Marwick TR and others (2015b) Globally significant greenhouse-gas emissions from African inland waters. Nat Geosci 8:637–642

Borges AV, Darchambeau F, Lambert T, Bouillon S and others (2018) Effects of agricultural land use on fluvial carbon dioxide, methane and nitrous oxide concentrations in a large European river, the Meuse (Belgium). Sci Total Environ 610–611:342–355

Boyd CE, Wood CW, Chaney PL, Queiroz JF (2010) Role of aquaculture pond sediments in sequestration of annual global carbon emissions. Environ Pollut 158:2537–2540

Breslow NE, Clayton DG (1993) Approximate inference in generalized linear mixed models. J Am Stat Assoc 88: 9–25

Carvalho A, Meireles L, Malcata F (1998) Rapid spectrophotometric determination of nitrates and nitrites in marine aqueous culture media. Analusis 26:347–351

Casper P, Maberly SC, Hall GH, Finlay BJ (2000) Fluxes of methane and carbon dioxide from a small productive lake to the atmosphere. Biogeochemistry 49:1–19

Cole JJ, Prairie YT, Caraco NF, McDowell WH and others (2007) Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10:172–185

Crusius J, Wanninkhof R (2003) Gas transfer velocities measured at low wind speed over a lake. Limnol Oceanogr 48:1010–1017

Descloux S, Chanudet V, Serça D, Guérin F (2017) Methane and nitrous oxide annual emissions from an old eutrophic temperate reservoir. Sci Total Environ 598:959–972

Deutzmann JS, Stief P, Brandes J, Schink B (2014) Anaerobic methane oxidation coupled to denitrification is the dominant methane sink in a deep lake. Proc Natl Acad Sci USA 111:18273–18278

Downing JA (2010) Emerging global role of small lakes and ponds. Limnetica 29:9–24

Emilson EJ, Carson MA, Yakimovich KM, Osterholz H and others (2018) Climate-driven shifts in sediment chemistry enhance methane production in northern lakes. Nat Commun 9:1801

Four B, Arce E, Danger M, Gaillard J, Thomas M, Banas D (2017) Catchment land use-dependent effects of barrage fishponds on the functioning of headwater streams. Environ Sci Pollut Res Int 24:5452–5468

Gaillard J, Thomas M, Lazartigues A, Bonnefille B and others (2016) Potential of barrage fish ponds for the mitigation of pesticide pollution in streams. Environ Sci Pollut Res Int 23:23–35

Gál D, Pekár F, Kerepeczki É (2016) A survey on the environmental impact of pond aquaculture in Hungary. Aquacult Int 24:1543–1554

Gelesh L, Marshall K, Boicourt W, Lapham L (2016) Methane concentrations increase in bottom waters during summertime anoxia in the highly eutrophic estuary, Chesapeake Bay, USA. Limnol Oceanogr 61:S253–S266

Grossart HP, Frindte K, Dziallas C, Eckert W, Tang KW (2011) Microbial methane production in oxygenated water column of an oligotrophic lake. Proc Natl Acad Sci USA 108:19657–19661

Hlaváč D, Adámek Z, Hartman P, Másílko J (2014) Effects of supplementary feeding in carp ponds on discharge water quality: a review. Aquacult Int 22:299–320

Hofmann H, Federwisch L, Peeters F (2010) Wave induced release of methane: littoral zones as source of methane in lakes. Limnol Oceanogr 55:1990–2000

Huttunen JT, Alm J, Liikanen A, Juutinen S and others (2003) Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. Chemosphere 52:609–621

Huttunen JT, Väisänen TS, Hellsten SK, Martikainen PJ (2006) Methane fluxes at the sediment-water interface in some boreal lakes and reservoirs. Boreal Environ Res 11: 27–34

Juutinen S, Rantakari M, Kortelainen P, Huttunen J and others (2009) Methane dynamics in different boreal lake types. Biogeosciences 6:209–223

Kalinichenko I, Demutskaya L (2004) Determination of nitrates in drinking water by three-wavelength ultraviolet photometry. J Anal Chem 59:211–214

Kelly C, Rudd J, Bodaly R, Roulet N and others (1997) Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. Environ Sci Technol 31:1334–1344

Kopáček J, Hejzlar J (1993) Semi-micro determination of total phosphorus in fresh waters with perchloric acid digestion. Int J Environ Anal Chem 53:173–183

Kopáček J, Procházková L (1993) Semi-micro determination of ammonia in water by the rubazoic acid method. Int J Environ Anal Chem 53:243–248

Kopáček J, Borovec J, Hejzlar J, Porcal P (2001) Spectrophotometric determination of iron, aluminum, and phosphorus in soil and sediment extracts after their nitric and perchloric acid digestion. Commun Soil Sci Plant Anal 32:1431–1443

Liu S, Hu Z, Wu S, Li S, Li Z, Zou J (2016) Methane and nitrous oxide emissions reduced following conversion of rice paddies to inland crab–fish aquaculture in Southeast China. Environ Sci Technol 50:633–642

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol Oceanogr 12:343–346

Ma Y, Sun L, Liu C, Yang X and others (2018) A comparison of methane and nitrous oxide emissions from inland mixed-fish and crab aquaculture ponds. Sci Total Environ 637-638:517–523

Maberly SC, Barker PA, Stott AW, De Ville MM (2013) Catchment productivity controls CO_2 emissions from lakes. Nat Clim Chang 3:391

Miller S, Crowl T (2006) Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. Freshw Biol 51:85–94

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:31–36

Musenze RS, Grinham A, Werner U, Gale D, Sturm K, Udy J, Yuan Z (2014) Assessing the spatial and temporal variability of diffusive methane and nitrous oxide emissions from subtropical freshwater reservoirs. Environ Sci Technol 48:14499–14507

Natchimuthu S, Selvam BP, Bastviken D (2014) Influence of weather variables on methane and carbon dioxide flux from a shallow pond. Biogeochemistry 119:403–413

Natchimuthu S, Sundgren I, Gålfalk M, Klemedtsson L, Crill P, Danielsson Å, Bastviken D (2016) Spatio temporal variability of lake CH_4 fluxes and its influence on annual whole lake emission estimates. Limnol Oceanogr 61: S13–S26

Noguchi K, Gel YR, Brunner E, Konietschke F (2012) nparLD: an R software package for the nonparametric analysis of longitudinal data in factorial experiments. J Stat Softw 50:1–23

Oertli B, Biggs J, Cereghino R, Grillas P, Joly P, Lachavanne JB (2005) Conservation and monitoring of pond biodiversity: introduction. Aquat Conserv 15:535–540

Pechar L (2000) Impacts of long-term changes in fishery management on the trophic level water quality in Czech fish ponds. Fish Manag Ecol 7:23–31

Pokorný J, Hauser V (2002) The restoration of fish ponds in agricultural landscapes. Ecol Eng 18:555–574

Pokorný J, Pechar L (2000) Development of fishpond ecosystems in the Czech Republic. Role of management and nutrient input. Sylvia (Praha) 36:8–15

Potužák J, Hůda J, Pechar L (2007) Changes in fish production effectivity in eutrophic fishponds — impact of zooplankton structure. Aquacult Int 15:201–210

Rahman M, Verdegem M, Nagelkerke L, Wahab M, Milstein A, Verreth J (2006) Growth, production and food preference of rohu *Labeo rohita* (H.) in monoculture and in polyculture with common carp *Cyprinus carpio* (L.) under fed and non-fed ponds. Aquaculture 257: 359–372

RCoreTeam (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Repo M, Huttunen J, Naumov A, Chichulin A, Lapshina E, Bleuten W, Martikainen P (2007) Release of CO_2 and CH_4 from small wetland lakes in western Siberia. Tellus B Chem Phys Meterol 59:788–796

Ritvo G, Kochba M, Avnimelech Y (2004) The effects of common carp bioturbation on fishpond bottom soil. Aquaculture 242:345–356

Roland FA, Darchambeau F, Morana C, Bouillon S, Borges AV (2017) Emission and oxidation of methane in a meromictic, eutrophic and temperate lake (Dendre, Belgium). Chemosphere 168:756–764

Saunois M, Bousquet P, Poulter B, Peregon A and others (2016) The global methane budget 2000–2012. Earth Syst Sci Data 8:697–751

Scheffer M, Carpenter S, Foley JA, Folke C, Walkerk B (2001) Catastrophic shifts in ecosystems. Nature 413: 591–596

Selvam PB, Natchimuthu S, Arunachalam L, Bastviken D (2014) Methane and carbon dioxide emissions from inland waters in India — implications for large scale greenhouse gas balances. Glob Change Biol 20:3397–3407

Tušer M, Picek T, Sajdlová Z, Jůza T, Muška M, Frouzová J (2017) Seasonal and spatial dynamics of gas ebullition in a temperate water storage reservoir. Water Resour Res 53:8266–8276

Všetičková L, Adámek Z (2013) The impact of carp pond management upon macrozoobenthos assemblages in recipient pond canals. Aquacult Int 21:897–925

Všetičková L, Adamek Z, Rozkošný M, Sedláček P (2012) Effects of semi-intensive carp pond farming on discharged water quality. Acta Ichthyol Piscat 42:223–231

Wanninkhof R (1992) Relationship between wind speed and gas exchange over the ocean. J Geophys Res Oceans 97: 7373–7382

Wiesenburg DA, Guinasso NL Jr (1979) Equilibrium solubilities of methane, carbon monoxide, and hydrogen in water and sea water. J Chem Eng Data 24:356–360

Wik M, Thornton BF, Bastviken D, MacIntyre S, Varner RK, Crill PM (2014) Energy input is primary controller of methane bubbling in subarctic lakes. Geophys Res Lett 41:555–560

Williams J, Crutzen P (2010) Nitrous oxide from aquaculture. Nat Geosci 3:143

Xiong Y, Wang F, Guo X, Liu F, Dong S (2017) Carbon dioxide and methane fluxes across the sediment-water interface in different grass carp *Ctenopharyngodon idella* polyculture models. Aquacult Environ Interact 9:45–56

Yang P, He Q, Huang J, Tong C (2015) Fluxes of greenhouse gases at two different aquaculture ponds in the coastal zone of southeastern China. Atmos Environ 115:269–277

Yang P, Lai DYF, Huang JF, Tong C (2018a) Effect of drainage on CO_2, CH_4, and N_2O fluxes from aquaculture ponds during winter in a subtropical estuary of China. J Environ Sci (China) 65:72–82

Yang P, Zhang Y, Lai DY, Tan L, Jin B, Tong C (2018b) Fluxes of carbon dioxide and methane across the water–atmosphere interface of aquaculture shrimp ponds in two subtropical estuaries: the effect of temperature, substrate, salinity and nitrate. Sci Total Environ 635:1025–1035

Zeger SL, Liang KY (1992) An overview of methods for the analysis of longitudinal data. Stat Med 11:1825–1839

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CHAPTER 5

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

General discussion

For decades, an increasing human population combined with a decline of the natural supply of fishery products caused aquaculture to become one of the fastest growing economic sector (FAO, 2018). Fish farming in ponds is considered the oldest aquaculture production system with a rich tradition worldwide (Henares et al., 2020). However, there has been a long-term debate on pond culture pollution potential. Several studies assessed the role of fishponds in water pollution (Všetičková et al., 2012; Tahar et al., 2018). In many countries, including countries in Central and Eastern Europe, fishponds are still not considered as a significant source of water pollution (Banas et al., 2008) or are not included in regular monitoring campaigns (Koschorreck et al., 2020). The use of low-input, low-level technology, the natural ability of ponds to process and utilize a large fraction of nutrients and organic matter, and the assumed utilization of natural food by cultured fish represent keystones for considering a low pollution potential of the fishponds (Pouil et al., 2019). Nevertheless, it has been noted that fish farming intensification has been associated with pond environmental deterioration (Pechar, 2000). With the rise of environmental concern of pond culture, the utilization efficiency as well as the fate of autochthonous and allochthonous nutrients in ponds already occurring or entering the pond (from supply water, atmospheric deposition and fishery management), respectively, attracted attention of researchers worldwide (Všetičková et al., 2012; Wezel et al., 2013; Zhang et al., 2016; Tahar et al., 2018). Moreover, the concern of global warming urged an inclusion of relative contributions of all sources in the inventory of the greenhouse gas emissions, including aquaculture ponds that were largely underrepresented (Liu et al., 2015; Ma et al., 2018; Oliveira Junior et al., 2019). The aims of the present Ph.D. thesis were to assess the use efficiency of inputs in temperate fishponds in Central Europe during a vegetation (growing) season and the evaluation of their greenhouse gases production potential.

In semi-intensive aquaculture systems, supplementary feeding (mainly cereals) is used in addition to natural food (phytoplankton, plants, zooplankton, benthic and phytophilous macroinvertebrates) produced in the ponds. The quality of fish feed, ecosystem structure integrity reflected by pond water quality, and fish stock management (monoculture versus polyculture production systems) significantly influence the use efficiency of both natural food and supplementary feed. Fishponds not only produce fish but also perform other ecosystem functions such as nutrients and organic matter retention, local climate and flood regulation, serving as recreation sites and habitat for endangered species (Koschorreck et al., 2020). Safeguarding production and non-production functions of fishponds are key challenges faced by fishery managers.

In our first and second study (Chapter II and Chapter III), we monitored water quality of inflow, pond water and outflow of a representative eutrophic semi-intensively managed fishpond (Dehtář) with polyculture in South Bohemia, Czech Republic. We identified sources and fates of inputs during one growing season (May – October2015) and during two subsequent two-year fish production cycles (from autumn 2014 to autumn 2018). We used the 24h-oxygen measurements based on the free water method to calculate ecosystem metabolic rates (Staehr et al., 2010) in order to estimate autochthonous organic carbon production. We also used nutrients (N and P) and organic carbon (OC) balances to assess sources and fates of N, P and OC in the system (Adhikari et al., 2012). This knowledge provides information whether there is a balance between the total amount of nutrients and organic matter added into the fishponds and the fraction used to produce fish biomass. Nutrients retention and removal rates in the pond were assessed as well.

In chapter IV, we used the transboundary layer model to determine and compare the levels of dissolved and diffusive CH_4 from two types of fishponds differing in individual fish size of cultured common carp in the Region of South Bohemia, Czech Republic. The factors influencing dissolved and diffusive CH_4 were identified as well. The study was carried out from April to September 2017. The ponds differed in the fishery management. The main ponds serve for producing the common carp in a market size ("heavy" carp). These ponds are stocked with 2-year old carp that are harvested after two years. Manure and supplementary feeding are used. The nursery ponds produce fish to stock into the main ponds. The nursery ponds are stocked with carp fingerlings ("light" fish). They are not manured and supplementary feeding is not used.

Effects of fish farming practices on water quality, inputs utilization efficiency and nutrients retention

The OECD (Organization for Economic Co-operation and Development) water quality indices, species composition of zooplankton and phytoplankton assemblages in Dehtář fishpond were characteristic of a water body under intensive eutrophic pressure. The phytoplankton trophic index (PTI) and zooplankton: phytoplankton biomass ratio further confirmed this eutrophication pressure (Jeppesen et al., 2000; Phillips et al., 2013). The average Secchi depth was 0.7±0.1 m. The average concentration of total phosphorus (TP) was 0.20±0.01 mg.l^{-1}. The average concentration of chlorophyll-*a* (Chl*a*) was 87±9 µg.l^{-1} and the seasonal Chl*a* maximal values ranged between 110 and 330 µg.l^{-1}. Representative phytoplankton species were from the genera *Aphanizomenon, Oocystis, Closterium, Dolichospermum, Coelastrum,* and *Planktothrix*. The zooplankton were mainly composed of rotifers (represented by the genera *Brachionus, Keratella, Polyarthra* and *Filinia)*, small sized cladoceran species (*Daphnia cucullata, Ceriodaphnia* spp., *Bosmina longistris* and *Bosmina coregoni*). Larger size classes of zooplankton represented by *Daphnia galeata* were present only at the beginning of the growing the relationship between bacterial and heterotrophic flagellate abundance in oligotrophic to mesotrophic temperate lakes season. Chlorophyll-*a*, total carbon (TC), and dissolved organic carbon (DOC), total nitrogen (TN) and total phosphorus (TP) showed an increase during the growing season. The reason for the TOC, TN, and TP increase was apparently caused by an increase of phytoplankton biomass as evidenced by an increase of Chl*a* concentration and reduced water transparency. Our results are in agreement with those reported by Lemmens et al. (2013) who found that the intensification of fishery management increases TP, TN, Chl*a* levels and reduces water transparency.

The degradation of water quality was partly caused by an increase in the amount of nutrients added to this historically oligotrophic pond in order to increase its ability to produce more natural food and fish (Pokorný and Pechar, 2000). In general, nitrogen loads increased in Czech semi-intensive fishponds from 0.1 kg.ha^{-1} in the 1930s to 46 kg.ha^{-1} in the 1990s, while those of P increased from 0.3 kg.ha^{-1} to 10 kg.ha^{-1} in the same period (Pechar, 1995). The source of nutrients may be partly attributed to feed addition, manure application, and sediment bioturbation by feeding common carp (Rahman et al., 2006), nutrient cycling in the water column (Kamarainen et al., 2009; Knoll et al., 2016) and probably from fish excretion and defecation (Chumchal and Drenner, 2004). The average loads of P (13 kg.ha^{-1}) and N (47 kg.ha^{-1}) originating from manure and feeds during the period of this study are comparable to those from the 1990s. A change of land use surrounding ponds also increased nutrient loads from the catchments (Pokorný and Pechar, 2000). Contrarily, concentrations of ammonium nitrogen ($N\text{-}NH_4^+$), nitrate nitrogen ($N\text{-}NO_3^-$), soluble reactive phosphorus (SRP) and dissolved phosphorus (DP) were relatively low in summer months indicating their uptake by phytoplankton. This uptake was enabled by slower water flushing rates in Dehtář pond. It has been shown that slower water flushing rates allow algae to extract nutrients from the whole water column (Salvia-Castellvi et al., 2001).

The results of ecosystem metabolic rates revealed that gross primary production (GPP) was the main source of organic carbon (OC) while ecosystem respiration (ER) was the main fate of OC. Based on comparison between GPP and ER, Dehtář pond was assessed as a slightly autotrophic system indicating that the amount of organic matter produced by primary production was higher than the amount degraded by the respiration processes. Our results of GPP and ER were comparable to those from other autotrophic lakes where ER is mainly fueled by autochthonous organic matter (Laas et al., 2012). These values were higher than those from oligotrophic lakes whose respiration processes are mainly sustained by allochthonous organic matter (Duarte and Prairie, 2005). Ecosystem metabolic rates further support that over the course of time, Dehtář pond as well as other Czech fishponds became eutrophic systems as a result of imbalance in nutrient inputs and nutrient assimilation. Indeed, feed and manure were the main inputs of N and P during the growing season (Chapter II). However, nutrient balance calculated over hydrological years revealed that inflow was the main source of N while the feed still remained the main source of P (Chapter III). An enrichment of inflow in N may be explained by its passage through a cascade of ponds located upstream to Dehtář pond. The main fate of the unused fraction of these macronutrients (N, P) was the accumulation in a water column and retention in sediments, respectively.

We found that the use efficiency of OC and nutrients inputs was low in Dehtář pond (Chapters II, III). The use efficiency rates of OC from our study are in agreement with the results of Boyd et al. (2010), yet lower than those reported by Zhang et al. (2016). The main plausible reason to explain the low use of OC was a poor transfer of carbon (C) from phytoplankton to fish via zooplankton and/or macroinvertebrates as the primary production was the main source of OC. Indeed, the common carp needs an intermediate food chain level to use the primary production as this fish does not feed directly on phytoplankton (Adámek et al., 2003). The second reason explaining the low use of OC is the low nutrients (P, N) digestibility contained in cereals that are used as a common fish supplementary feed (mainly wheat) in the Czech pond culture practice. The absence of the enzyme phytase in the carp digestive tract concomitantly with the presence of digestive-enzymes resistant compounds in cereals such as phytates do not allow the common carp to efficiently assimilate nutrients from the grains, including wheat into the body mass (Fagbenro, 1999; Degani 2006). The higher use of OC in the study by Zhang et al. (2016) resulted from a better exploitation of OC inputs by cultured fish species that used different feeding niches. This fact indicates that polyculture practiced in Dehtář pond does not maximize the use of all available feeding niches.

In Chapter III, our results showed that Dehtář pond still has an ability to retain nutrients and eventually organic matter as well. Nitrogen and phosphorus retention coefficients and removal rates were in a range of the values from other temperate shallow lakes and reservoirs. High loads of nutrients in Dehtář pond increase its potential of N and P retention through algal uptake, fish production, sedimentation of algal biomass, and denitrification. This is in agreement with the findings of previous studies, which showed that nutrient retention is proportional to the amount of nutrient loads as increased loads means that more nutrients are available in the system for uptaking (Saunders and Kalff, 2001b; Coppens et al., 2016). On the other hand, the outflow quality was affected by the high loads of nutrients that were above the assimilatory capacity of the pond. More nutrients were added through manure and fish feed, although pond sediment and water were already enriched with nutrients. Besides, inefficient use of the feed and primary production create additional wastes (Boyd et al., 2010; Adhikari et al., 2012). In addition to the high loads, nutrient retention in Dehtář pond may also be explained by a long water residence time and low depth of the pond. Both parameters allow interactions and contact of a water column with sediment, thereby enhancing nutrients uptake by the sediment and their recycling when soluble nitrogen and phosphorus fractions are released by mineralisation of organic compounds (Saunders and Kalff, 2001b). Nitrogen is permanently lost from the water bodies through denitrification which substantially contributes to N loss from lentic ecosystems (Seitzinger et al., 2006). We also noticed that the total suspended solids, nutrients and organic matter concentrations were higher in the outflow during the harvesting time. This increase was caused by the techniques and activities associated with fish harvesting. Banas et al. (2008) noticed in French fishponds that in the last phase of fish harvesting, sediments are resuspended by fish concentrated in a small area, outflowing water, seining and the movement of fishermen in the mud. Similar activities occur during fish harvesting in the Czech Republic and may also explain the degradation of outflow water quality from the Dehtář fishpond.

Methane emission from temperate carp ponds differing in individual fish size of the common carp stock

In recent years, the increased concentrations of greenhouse gases (GHGs) in the atmosphere have been stimulating researchers to determine their production and emission potentials in different ecosystems (Selvam et al., 2014). Inland waters are one of the important natural sources of GHGs (Bastviken et al., 2004). Methane (CH_4) that is among the GHGs has a higher global warming potential than carbon dioxide (CO_2) (IPCC, 2013). In aquatic ecosystems, CH_4 is produced both in anoxic sediments (Bastviken et al., 2004) and aerobic water columns (Grossart et al., 2011; Bogard et al., 2014). The produced CH_4 is released into atmosphere by diffusion, ebullition, by aquatic plants (Bastviken et al., 2004), or oxidised in the water column (Bastviken et al., 2002; Attermeyer et al., 2016). As fishponds have a low efficiency use of inputs, their organic wastes may fuel CH_4 production (Williams and Crutzen, 2010; Yang et al., 2018a).

We found that the concentrations of both dissolved CH_4 and diffusive emissions of CH_4 varied with time and showed different patterns in both types of ponds. In general, the concentrations of dissolved CH_4 were lower in the main ponds than in the nursery ponds. Methane concentrations increased from April to May in both types of ponds and decreased again in the following months. The increase of CH_4 in spring may be explained by the temperature elevation. This is in agreement with the field and experimental studies that showed that CH_4 production and concentration in water columns increase with temperature as the latter stimulates the activity of methanogenic bacteria (Hofmann et al., 2010; Natchimuthu et al., 2014; Borges et al., 2018). A decrease of CH_4, which was remarkable in the main ponds in the subsequent months, was probably due to intensive CH_4 oxidation (Bastviken et al., 2004; Juutinen et al., 2009) and sediment bioturbation by adult carp. Oliveira et al. (2019) proved in experimental trials that mesocosms with benthivorous fish produced and emitted less CH_4 than fishless mesocosms. They suggested that oxidation of sediments and an increase of CH_4 oxidation by phytoplankton caused by fish grazing pressure on zooplankton may explain this reduction. A second peak of CH_4 concentration was observed in the late summer (August) in the nursery ponds only. This peak was probably caused by a massive decomposition of senescing aquatic plants occurring in the nursery ponds but lacking in the main ponds. Emilson et al. (2018) showed that sediment containing organic matter originating from aquatic plants and phytoplankton produce more CH_4 than sediment rich in organic matter of terrestrial origin.

Both types of ponds were sources of CH_4 with a significantly higher emission from the nursery ponds in August. This emission was a consequence of increased availability of labile organic matter in the nursery ponds as discussed above. The main ponds had a higher emission of CH_4 than nursery ponds in May, but this difference was not statistically significant. This higher emission was a result of an enhanced release of CH_4 from pond sediment by the adult carp searching for food (Bhattacharyya et al., 2013; Xiong et al., 2017) and a higher wind speed above main ponds than nursery ponds. Methane in the main ponds was built up because of reduced moving activities of the common carp during previous cold months. Temperature was the main environmental factor influencing CH_4 concentrations in the investigated ponds. Diffusive CH_4 did not correlate to any measured environmental factors indicating that wind speed was probably its main driver (Musenze et al., 2014). Our findings were in a range of values obtained from other aquatic water bodies (Repo et al., 2007; Borges et al., 2011; Natchimuthu et al., 2016; Bednařík et al., 2017). Our study is in agreement with some other studies showing that aquaculture is an appreciable source of GHGs. However, our results did not deal with ebullitive CH_4, which may in some cases contribute up to 90 % of the total CH_4 amount emitted from aquatic ecosystems (Casper et al., 2000; Bastviken et al., 2004). We highly recommend undertaking more measurements of emission, including all pathways of CH_4 emissions and its spatial and temporal variability, as well as focusing on different aquaculture systems.

Impact of the maximization of fish production on other fishpond ecosystem functions

Fishponds are mostly located in lowlands formerly occupied by wetlands, floodplains or mangrove forests (Pokorný and Hauser, 2002). These natural vegetation communities play a vital role in water quality regulation (Patrick, 1994). Fishponds play a similar role too (Nhan et al., 2006; Všetičková et al., 2012; Gaillard et al., 2016; Uwimana et al., 2018). The low efficiency use of nutrients and organic matter inputs is reflected in the pond water quality and further reduce the potential of the fishpond to regulate water quality (Henares et al., 2020). However, Rahman and Verdegem (2007) showed that stocking an adequate number of phytophagous fish may lessen the side effects of the low use of carbon input from feed on water quality regulation in ponds.

Several studies reached conclusions similar to ours that fishpond management types influence local and regional species richness of macrophytes, invertebrates, mollusks and zooplankton with an exception to phytoplankton (Broyer and Curtet, 2011; Lemmens et al., 2013; Francová et al., 2019). Ponds with larger size classes of carp have a poor biodiversity contrarily to ponds with young of the year fish as a result of plant uprooting, habitat degradation for macrophytes and therefore suppressing the refuges for invertebrates (Miller and Crowl, 2006; Lemmens et al., 2013; Nieoczym and Kloskowski, 2014). These effects are enhanced .when fish farmers add supplementary feeds and manure, thus strengthening eutrophication and phytoplankton bloom (Všetičková et al., 2012). The phytoplankton bloom reduces the use of fishponds for recreational purposes.

Pond has the ability to retain nutrients but this retention is temporal as shown in chapter III of this study and other studies (Banas et al., 2008; Kufel, 2012; Henares et al., 2020). Všetičková et al. (2012) found that ponds act as sinks or source of nutrients and organic matter when they receive inflow rich or poor in nutrients and organic matter, respectively. The use of high quality feed, feeding strategy, right amount and frequency of manure application, use of settling ponds to treat pond effluents are some measures that can enhance the retention of nutrients from aquaculture ponds.

Ecological sustainable fishponds may offer a balance between production and non-production functions but such ponds are rare. There exist instead ponds with different levels of sustainability (Valenti et al., 2018). There is a room for improvement especially in the tropic regions where small scale farmers who use low input and low level technology are not ready to use new technologies to reduce the pollution potential of ponds because these technologies are complex and may incur additional costs (Bush et al., 2013). Besides there might be a tendency for policy makers in the tropics to focus more on food security than on environmental regulations (Beveridge et al., 2010). Our study was conducted under variable environmental factors and with a monthly or biweekly sampling frequency. The approach used may be appropriate for pollution studies (Waters and Webster-Brown, 2016). However, we suggest more detailed studies to determine economical and social acceptable strategies to improve non-production functions of fishponds.

Conclusion

Our studies focused on the sources and fates of inputs in semi-intensive fish culture systems in the temperate fishponds in Central Europe. Our results revealed that:

- Fish culture practices significantly affected and are still affecting the water quality of semi-intensively managed fishponds as indicated by OECD water quality indices, ecosystem metabolic rates, phytoplankton and zooplankton assemblages' structure.
- The utilisation efficiency of inputs to produce fish biomass is low.
- Fish (mainly the common carp) farming has a remarkable pollution potential to downstream water bodies as well as to the atmosphere.
- Downstream water bodies receiving effluents from the fishpond may become eutrophic due to nutrients and organic matter released from pond outflow. This is contrary to the former view that prevailed in Central and Eastern Europe that semi-intensive fishponds are not a threat to water bodies in their catchments.
- Semi-intensive fishponds have an ability to retain nutrients to the detriment of their water quality. However, high loads of nutrient inputs are above their assimilation capacity and unused inputs are released during the regulation of water level and during pond harvesting.
- Methane, an important greenhouse gas, is produced and released from fishponds. Data of greenhouse gases production in temperate fishponds are rare and are not included in the national GHGs inventories even in countries with an important aquaculture sector.

References

Adámek, Z., 2014. Hydrobiology in Fisheries. In: Adámek, Z., Helešic, J., Maršálek, B., Rulík, M. (Eds), Applied Hydrobiology. FFPW USB, Vodňany, CZE, pp. 307–351.

Adámek, Z., Sukop, I., Rendón, P.M., Kouřil, J., 2003. Food competition between 2+ tench (*Tinca tinca* L.), common carp (*Cyprinus carpio* L.) and bigmouth buffalo (*Ictiobus cyprinellus* Val.) in pond polyculture. Journal of Applied Ichthyology 19: 165–169.

Adhikari, S., Sahu, B.C., Dey, L., 2012. Nutrients budget and effluents characteristics in polyculture of scampi (*Macrobrachium rosenbergii*) and Indian major carps ponds using organic inputs. Water Science and Technology 66: 1540–1548.

Alaoui-Mhamdi, M., Aleya, L., 1995. Assessment of the eutrophication of Al Massira reservoir (Morocco) by means of a survey of the biogeochemical balance of phosphate. Hydrobiologia 297: 75–82.

Alaoui-Mhamdi, M., Aleya, L., Bahhou, J., 1996. Nitrogen compounds and phosphate of the Driss I reservoir (Morocco): input, output and sedimentation. Hydrobiologia 335: 75–82.

Anderson, N.J., Bennion, H., Lotter, A.F., 2014. Lake eutrophication and its implications for organic carbon sequestration in Europe. Global Change Biology 20: 2741–2751.

Attermeyer, K., Flury, S., Jayakumar, R., Fiener, P., Steger, K., Arya, V., Wilken, F., van Geldern, R., Premke, K., 2016. Invasive floating macrophytes reduce greenhouse gas emissions from a small tropical lake. Scientific Reports 6: 20424.

Balmer, M.B, Downing, J.A., 2011. Carbon dioxide concentrations in eutrophic lakes: undersaturation implies atmospheric uptake. Inland Waters 1: 125–132.

Banas, D., Masson, G., Leglize, L., Usseglio-Polatera, P., Boyd, C.E., 2008. Assessment of sediment concentration and nutrient loads in effluents drained from extensively managed fishponds in France. Environmental Pollution 152: 679–685.

Bastviken, D., Cole, J.J., Pace, M.L., Tranvik, L., 2004. Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. Global Biogeochemical Cycles 18: GB4009.

Bastviken, D., Ejlertsson, J., Tranvik, L., 2002. Measurement of methane oxidation in lakes: a comparison of methods. Environmental Science & Technology 36: 3354–3361.

Bednařík, A., Blaser, M., Matoušů, A., Hekera, P., Rulík, M., 2017. Effect of weir impoundments on methane dynamics in a river. Science of The Total Environment 584: 164–174.

Beveridge, M., Phillips, M., Dugan, P., Brummet, R., 2010. Barriers to aquaculture development as a pathway to poverty alleviation and food security.

Bhattacharyya, P., Sinhababu, D., Roy, K., Dash, P., Sahu, P., Dandapat, R., Neogi, S., Mohanty, S., 2013. Effect of fish species on methane and nitrous oxide emission in relation to soil C, N pools and enzymatic activities in rainfed shallow lowland rice-fish farming system. Agriculture, Ecosystems & Environment 176: 53–62.

Bielarnska-Grajner, I., Ejsmont-Karabin, J., Radwan, S., 2015. Rotifers (Rotifera). Freshwater Fauna of Poland. Jagiellonian University Press, Wyda, p. 578.

Bogard, M.J., Del Giorgio, P.A., Boutet, L., Chaves, M.C.G., Prairie, Y.T., Merante, A., Derry, A. M., 2014. Oxic water column methanogenesis as a major component of aquatic CH_4 fluxes. Nature Communications 5: 5350.

Borges, A., Abril, G., Delille, B., Descy, J.P., Darchambeau, F., 2011. Diffusive methane emissions to the atmosphere from Lake Kivu (Eastern Africa). Journal of Geophysical Research: Biogeosciences 116: G03032.

Borges, A.V., Darchambeau, F., Lambert, T., Bouillon, S., Morana, C., Brouyère, S., Hakoun, V., Jurado, A., Tseng, H.-C., Descy, J.-P., 2018. Effects of agricultural land use on fluvial carbon dioxide, methane and nitrous oxide concentrations in a large European river, the Meuse (Belgium). Science of the Total Environment 610: 342–355.

Bosma, R.H., Verdegem, M.C., 2011. Sustainable aquaculture in ponds: principles, practices and limits. Livestock Science 139: 58–68.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., Weglenska, T., 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24: 419–456.

Boyd, C.E., Tucker, C., McNevin, A., Bostick, K., Clay, J., 2007. Indicators of resource use efficiency and environmental performance in fish and crustacean aquaculture. Reviews in Fisheries Science 15: 327–360.

Boyd, C.E., Wood, C.W., Chaney, P.L., Queiroz, J.F., 2010. Role of aquaculture pond sediments in sequestration of annual global carbon emissions. Environmental Pollution 158: 2537–2540.

Brandl, Z., 1973. Horizontal distribution of some chemical and physical characteristics in Lipno Reservoir. In: Hrbáček, J., Straškraba, M. (Eds), Hydrobiological Studies. Academia, Prague, pp. 53–90.

Brigault, S., Ruban, V., 2000. External phosphorus load estimates and P-budget for the hydroelectric reservoir of Bort-Les-Orgues, France. Water Air and Soil Pollution 119: 91–103.

Broyer, J., Curtet, L., 2011. The influence of fish farming intensification on taxonomic richness and biomass density of macrophyte-dwelling invertebrates in French fishponds. Knowledge and Management of Aquatic Ecosystems: 10.

Broyer, J., Curtet, L., 2012. Biodiversity and fish farming intensification in French fishpond systems. Hydrobiologia 694: 205–218.

Burford, M.A., Costanzo, S., Dennison, W., Jackson, C., Jones, A. McKinnon, A., Preston, N., Trott, L., 2003. A synthesis of dominant ecological processes in intensive shrimp ponds and adjacent coastal environments in NE Australia. Marine Pollution Bulletin 46: 1456-1469.

Bush, S.R., Belton, B., Hall, D., Vandergeest, P., Murray, F.J,. Ponte, S., Oosterveer, P., Islam, M.S., Mol, A.P., Hatanaka M., 2013. Certify sustainable aquaculture? Science 341: 1067–1068.

Carpenter, S., Kitchell, J., Hodgson, J., 1985. Cascad~ ng trophic Interactions and lake productivity. BioScience 35: 634–639.

Casas, J.O., Martínez, R.P., 1984. Applicability of the OECD eutrophication models to Spanish reservoirs. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 22: 1521–1535.

Casper, P., Maberly, S.C. Hall, G.H., Finlay B.J., 2000. Fluxes of methane and carbon dioxide from a small productive lake to the atmosphere. Biogeochemistry 49: 1–19.

Chalar, G., Tundisi, J.G., 2001. Phosphorus fractions and fluxes in the water column and sediments of a tropical reservoir (Lobo-Broa–SP). International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology 86: 183–194.

Chapra, S.C., 1975. Comment on 'An empirical method of estimating the retention of phosphorus in lakes' by WB Kirchner and PJ Dillon. Water Resources Research 11: 1033–1034.

Cho, C., Bureau, D., 2001. A review of diet formulation strategies and feeding systems to reduce excretory and feed wastes in aquaculture. Aquaculture Research 32: 349–360.

Chumchal, M.M., Drenner, R.W., 2004. Interrelationships between phosphorus loading and common carp in the regulation of phytoplankton biomass. Archiv für Hydrobiologie 161: 147–158.

Ćirić, M., Subakov-Simić, G., Dulić, Z., Bjelanović, K., Ćičovački, S., Marković, Z., 2015. Effect of supplemental feed type on water quality, plankton and benthos availability and carp (*Cyprinus carpio* L.) growth in semi-intensive monoculture ponds. Aquaculture Research 46: 777–788.

Cole, J.J., Pace, M.L., Carpenter, S.R. Kitchell, J.F., 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnology and Oceanography 45: 1718–1730.

Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10: 171–184.

Coppens, J., Hejzlar, J., Šorf, M., Jeppesen, E., Erdoğan, Ş., Scharfenberger, U., Mahdy, A., Nõges, P., Tuvikene, A., Baho, D.L., 2016. The influence of nutrient loading, climate and water depth on nitrogen and phosphorus loss in shallow lakes: a pan-European mesocosm experiment. Hydrobiologia 778: 13–32.

Craig, S., Helfrich, L.A., Kuhn, D., Schwarz, M.H., 2017. Understanding fish nutrition, feeds, and feeding. Page 4 PublicationVirginia State University, Yorktown, Virginia. No. 420–256.

Culver, D.A., Boucherle, M.M., Bean, D.J., Fletcher, J.W., 1985. Biomass of freshwater crustacean zooplankton from length–weight regressions. Canadian Journal of Fisheries and Aquatic Sciences 42: 1380–1390.

Datta, A., Nayak, D., Sinhababu, D., Adhya, T., 2009. Methane and nitrous oxide emissions from an integrated rainfed rice-fish farming system of Eastern India. Agriculture, ecosystems & environment 129: 228–237.

Degani, G., 2006. Digestible energy in dietary sorghum, wheat bran, and rye in the common carp (*Cyprinus carpio* L.). Journal of Aquaculture – Bamidgeh 58: 71–77.

Dickman, E.M., Newell, J.M., Gonzalez, M.J., Vanni, M.J., 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proceedings of the National Academy of Sciences of the United States of America 105: 18408–18412.

Dillon, P.J., Rigler, F.H., 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. Journal of the Fisheries Board of Canada 31: 1771–1778.

DIN, 2003. Water quality. Determination of nitrogen. Determination of bound nitrogen (TNb), following oxidation to nitrogen oxides (DIN EN 12260: 2003). Deutches Institut fur Normung E.V. (DIN), Berlin.

Dodds, W.K., Whiles, M.R., 2004. Quality and quantity of suspended particles in rivers: continent-scale patterns in the United States. Environmental Management 33: 355–367.

Duarte, C.M., Prairie, Y.T., 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862–870.

Duras, J., Hejzlar, J.,2001. The effect of outflow depth on phosphorus retention in a small, hypertrophic temperate reservoir with short hydraulic residence time. International Review of Hydrobiology 86: 585–601

El Samra, M., Oláh, J., 1979. Significance of nitrogen fixation in fish ponds. Aquaculture 18: 367–372.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, S., Interlandi, A., Kilham, S.S., McCauley, E., Schulz, K.L., 2000a. Nutritional constraints in terrestrial and freshwater food webs. Nature 408: 578.

Elser, J.J., Sterner, R.W., Galford, A.E., Chrzanowski, T.H., Findlay, D.L., Mills, K.H., Paterson, M.J., Stainton, M.P., Schindler, D.W., 2000b. Pelagic C : N : P stoichiometry in a eutrophied lake: Responses to a whole-lake food-web manipulation. Ecosystems 3: 293–307.

Emilson, E.J., Carson, M.A. Yakimovich, K.M., Osterholz, H., Dittmar, T., Gunn, J., Mykytczuk, N., Basiliko, N., Tanentzap, A., 2018. Climate-driven shifts in sediment chemistry enhance methane production in northern lakes. Nature Communications 9: 1801.

Fagbenro, O., 1999. Apparent digestibility of various cereal grain by-products in common carp diets. Aquaculture International 7: 277–281.

FAO, 2018. The state of World fisheries and aquaculture. FAO, Rome, Italy.

Fee, E.J., 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnology and Oceanography 24: 401–416.

Four, B., Arce, E., Danger, M., Gaillard, J., Thomas, M., Banas, D., 2017. Catchment land use-dependent effects of barrage fishponds on the functioning of headwater streams. Environmental Science and Pollution Research 24: 5452–5468.

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

Frei, M., Razzak, M., Hossain, M., Oehme, M., Dewan, S., Becker, K., 2007. Methane emissions and related physicochemical soil and water parameters in rice-fish systems in Bangladesh. Agriculture, Ecosystems & Environment 120: 391–398.

Fricker, H.J., 1980. Eutrophication programme, regional project alpine lakes. Organisation for Economic Cmpration and Development Rep., Swiss Federal Board for Environmental Protection, Bern.

Fry, J. P., Mailloux, N.A., Love, D. C., Milli, M. C., Cao, L., 2018. Feed conversion efficiency in aquaculture: do we measure it correctly? Environmental Research Letters 13: 024017.

Gaillard, J., Thomas, M., Lazartigues, A., Bonnefille, B., Pallez, C., Dauchy, X., Feidt, C., Banas, D., 2016. Potential of barrage fish ponds for the mitigation of pesticide pollution in streams. Environmental Science and Pollution Research 23: 23–35.

Galicka, W., 1992. Total nitrogen and phosphorus budgets in the lowland Sulejow Reservoir for the hydrological years 1985–1988. Arch. Hydrobiol. Suppl. 2: 159–169.

Garg, S., Bhatnagar, A., 2000. Effect of fertilization frequency on pond productivity and fish biomass in still water ponds stocked with *Cirrhinus mrigala* (Ham.). Aquaculture Research 31: 409–414.

Garnier, J., Leporcq, B., Sanchez, N., Philippon, X., 1999. Biogeochemical mass-balances (C, N, P, Si) in three large reservoirs of the Seine Basin (France). Biogeochemistry 47: 119–146.

Gross, A., Boyd, C.E., Wood, C., 2000. Nitrogen transformations and balance in channel catfish ponds. Aquacultural Engineering 24: 1–14.

Grossart, H.-P., Frindte, K., Dziallas, C., Eckert, W., Tang, K.W., 2011. Microbial methane production in oxygenated water column of an oligotrophic lake. Proceedings of the National Academy of Sciences 108: 19657–19661.

Haberman, J., Laugaste, R., 2003. On characteristics reflecting the trophic state of large and shallow Estonian lakes (L. Peipsi, L. Võrtsjärv). Hydrobiologia 506: 737–744.

Hargreaves, J.A., 1998. Nitrogen biogeochemistry of aquaculture ponds. Aquaculture 166: 181–212.

Havens, K.E., Phlips, E.J., Cichra, M.F., Li, B.L., 1998. Light availability as a possible regulator of cyanobacteria species composition in a shallow subtropical lake. Freshwater Biology 39: 547–556.

Henares, M.N., Medeiros, M.V., Camargo, A.F., 2020. Overview of strategies that contribute to the environmental sustainability of pond aquaculture: rearing systems, residue treatment, and environmental assessment tools. Reviews in Aquaculture 12: 453–470.

Hendzel, L., Hecky, R., Findlay, D., 1994. Recent changes of N2-fixation in Lake 227 in response to reduction of the N: P loading ratio. Canadian Journal of Fisheries and Aquatic Sciences 51: 2247–2253.

Higgins, J.M., Kim, B.R., 1981. Phosphorus retention models for Tennessee Valley Authority reservoirs. Water Resources Research 17: 571–576.

Hofmann, H., Federwisch, L., Peeters, F., 2010. Wave induced release of methane: Littoral zones as source of methane in lakes. Limnology and Oceanography 55: 1990–2000.

Holdren, C., Jones, B., Taggart, J., 2001. Managing lakes and reservoirs. North American Lake Management Society; Terrene Insitute, Madison.

Houser, J.N., 2006. Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. Canadian Journal of Fisheries and Aquatic Sciences 63: 2447–2455.

Hu, Z., Lee, J.W., Chandran, K., Kim, S., Khanal, S.K., 2012. Nitrous oxide (N_2O) emission from aquaculture: a review. Environmental Science & Technology 46: 6470–6480.

Hu, Z., Lee, J.W., Chandran, K., Kim, S., Sharma, K., Brotto, A.C., Khanal, S.K., 2013. Nitrogen transformations in intensive aquaculture system and its implication to climate change through nitrous oxide emission. Bioresource technology 130: 314–320.

Huotari, J., Ojala, A., Peltomaa, E., Nordbo, A., Launiainen, S., Pumpanen, J., Rasilo, T., Hari, P., Vesala, T., 2011. Long-term direct CO_2 flux measurements over a boreal lake: Five years of eddy covariance data. Geophysical Research Letters 38: L18401.

Huttunen, J.T., Alm, J., Liikanen, A., Juutinen, S., Larmola, T., Hammar, T., Silvola, J. Martikainen, P.J., 2003. Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. Chemosphere 52: 609–621.

IPCC, 2013. The Physical Science Basis, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

ISO, 1984. Water quality-determination of ammonium. Part 1: manual spectrometric method (ISO 7150-1: 1984). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 1992. Water quality, measurement of biochemical parameters; spectrometric determination of chlorophyll-a concentration (ISO 10260: 1992). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 1999. Water quality-Guidelines for the determination of total organic carbon (TOC) and dissolved organic carbon (DOC) (ISO 8245: 1999). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 2003. Water quality-application of inductively coupled plasma mass spectrometry (ICP-MS)-Part 2: determination of 62 elements (ISO 17294-2: 2003). Int. Organ. for Standardisation (ISO), Geneva.

ISO, 2007. Water quality-determination of dissolved anions by liquid chromatography of ions-Part 1: determination of bromide, chloride, fluoride, nitrate, nitrite, phosphate and sulfate (ISO 10304-1:2007). Int. Organ. for Standardisation (ISO), Geneva.

Jeppesen, E., Jensen, J.P., Jensen, C., Faafeng, B., Hessen, D.O., Søndergaard, M., Lauridsen, T., Brettum, P. , Christoffersen, K., 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the arctic. Ecosystems 6: 313–325.

Jeppesen, E., Søndergaard, M., Sortkjær, O., Mortensen, E., Kristensen, P., 1990. Interactions between phytoplankton, zooplankton and fish in a shallow, hypertrophic lake: a study of phytoplankton collapses in Lake Søbygård, Denmark. In: Trophic Relationships in Inland Waters, Springer, pp. 149–164.

Jeppesen, E., Peder Jensen, J., SØndergaard, M., Lauridsen, T., Landkildehus, F., 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology 45: 201–218.

Juutinen, S., Rantakari, M., Kortelainen, P., Huttunen, J., Larmola, T., Alm, J., Silvola, J., Martikainen, P., 2009. Methane dynamics in different boreal lake types. Biogeosciences 6: 209–223.

Kalff, J., 2002. Limnology: Inland Water Ecosystems. Prentice Hall, Upper Saddle River, N.J.

Kamarainen, A.M., Penczykowski, R.M., Van de Bogert, M.C., Hanson, P.C., Carpenter, S.R., 2009. Phosphorus sources and demand during summer in a eutrophic lake. Aquatic Sciences 71: 214–227.

Kelly, C., Rudd, J., Hesslein, R., Schindler, D., Dillon, P., Driscoll, C.T., Gherini, S., Hecky, R., 1987. Prediction of biological acid neutralization in acid-sensitive lakes. Biogeochemistry 3: 129–140.

Kestemont, P., 1995. Different systems of carp production and their impacts on the environment. Aquaculture 129: 347–372.

Knoll, L.B., Morgan, A., Vanni, M.J., Leach, T.H., Williamson, T.J., Brentrup, J.A., 2016. Quantifying pelagic phosphorus regeneration using three methods in lakes of varying productivity. Inland Waters 6: 509–522.

Knud-Hansen, C.F., Batterson, T.R., McNabb, C.D., Harahat, I.S., Sumantadinata, K., Eidman, H.M., 1991. Nitrogen input, primary productivity and fish yield in fertilized freshwater ponds in Indonesia. Aquaculture 94: 49–63.

Knud-Hansen, C.F., Hopkins, K.D., Guttman, H., 2003. A comparative analysis of the fixed-input, computer modeling, and algal bioassay approaches for identifying pond fertilization requirements for semi-intensive aquaculture. Aquaculture 228: 189–214.

Kopáček, J., Prochazkova, L., Hejzlar, J., Blažka, P., 1997. Trends and seasonal patterns of bulk deposition of nutrients in the Czech Republic. Atmospheric Environment 31: 797–808.

Kopáček, J., Hejzlar, J., Kaňa, J., Porcal, P., 2001a. Element budgets in three Bohemian Forest lakes and their watersheds in the 2000 hydrological year: I. Čertovo Lake. Silva Gabreta 7: 35–52.

Kopáček, J., Hejzlar, J., Kaňa, J., Porcal, P., 2001b. Element budgets in three Bohemian Forest lakes and their watersheds in the 2000 hydrological year: III. Plešné Lake. Silva Gabreta 7: 73–86.

Kopáček, J., Hejzlar, J., Kaňa, J., Porcal, P., Pšenáková, P., 2001c. Element budgets in three Bohemian Forest lakes and their watersheds in the 2000 hydrological year: II. Černé Lake. Silva Gabreta 7: 53–72.

Koschorreck, M., Downing, A.S., Hejzlar, J., Marcé, R., Laas, A., Arndt, W.G., Keller, P.S., Smolders, A.J., van Dijk, G., Kosten, S., 2020. Hidden treasures: Human-made aquatic ecosystems harbour unexplored opportunities. Ambio 49: 531–540.

Kufel, L. 2012. Are fishponds really a trap for nutrients? – a critical comment on some papers presenting such a view/Czy stawy rybne są rzeczywiście pułapką dla pierwiastków biogennych? – krytyczny komentarz do pewnych prac prezentujących taki pogląd. Journal of water and land development 17: 39–44.

Laas, A., Noges, P., Koiv, T., Noges, T., 2012. High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694: 57–74.

LaBaugh, J.W., 1985. Uncertainty in phosphorus retention, Williams Fork Reservoir, Colorado. Water Resources Research 21: 1684–1692.

Leal, J.J.F., dos Santos Furtado, A. L., de Assis Esteves, F., Bozelli, R.L., Figueiredo-Barros, M. P., 2007. The role of *Campsurus notatus* (Ephemeroptera: Polymitarcytidae) bioturbation and sediment quality on potential gas fluxes in a tropical lake. Hydrobiologia 586: 143–154.

Lemmens, P., Mergeay, J., De Bie, T., Van Wichelen, J., De Meester, L., Declerck, S.A.J., 2013. How to maximally support local and regional biodiversity in applied conservation? Insights from Pond Management. Plos One 8.

Likens, G.E., O.L. Loucks, 1978. Analysis of five North American lake ecosystems. III. Sources, loading and fate of nitrogen and phosphorus. Verb. Internat. Verein. Limnol. 20: 568–573

Lin, , C.K., Shrestha, M.K., Yi, Y., Diana, J.S., 2001. Management to minimize the environmental impacts of pond effluent: harvest draining techniques and effluent quality. Aquacultural Engineering 25: 125–135.

Liu, S., Hu, Z., Wu, S., Li, S., Li, Z., Zou, J., 2015. Methane and nitrous oxide emissions reduced following conversion of Rice paddies to inland crab-fish aquaculture in Southeast China. Environmental Science & Technology 50: 633–642.

Ma, Y., Sun, L., Liu, C., Yang, X., Zhou, W., Yang, B., Schwenke, G., Li Liu, D., 2018. A comparison of methane and nitrous oxide emissions from inland mixed-fish and crab aquaculture ponds. Science of the Total Environment 637: 517–523.

Malzahn, A.M., Aberle, N., Clemmesen, C., Boersma, M., 2007. Nutrient limitation of primary producers affects planktivorous fish condition. Limnology and Oceanography 52: 2062–2071.

Martin-Creuzburg, D., von Elert, E., Hoffmann, K.H., 2008. Nutritional constraints at the cyanobacteria – *Daphnia magna* interface: the role of sterols. Limnology and Oceanography 53: 456–468.

Miller, S., Crowl, T., 2006. Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. Freshwater Biology 51: 85–94.

Milstein, A., 1992. Ecological aspects of fish species interactions in polyculture ponds. Hydrobiologia 231: 177–186.

Musenze, R.S., Grinham, A., Werner, U., Gale, D., Sturm, K., Udy, J., Yuan Z., 2014. Assessing the spatial and temporal variability of diffusive methane and nitrous oxide emissions from subtropical freshwater reservoirs. Environmental Science & Technology 48: 14499–14507.

Natchimuthu, S., Selvam, B.P., Bastviken, D., 2014. Influence of weather variables on methane and carbon dioxide flux from a shallow pond. Biogeochemistry 119: 403–413.

Natchimuthu, S., Sundgren, I., Gålfalk, M., Klemedtsson, L., Crill, P., Danielsson, Å., Bastviken, D., 2016. Spatio-temporal variability of lake CH_4 fluxes and its influence on annual whole lake emission estimates. Limnology and Oceanography 61: S13–S26.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C., Clay, J., Folke, C., Lubchenco, J., Mooney, H., Troell, M., 2000. Effect of aquaculture on world fish supplies. Nature 405: 1017.

Nhan, D. K., A. Milstein, M. C. Verdegem, and J. A. Verreth. 2006. Food inputs, water quality and nutrient accumulation in integrated pond systems: a multivariate approach. Aquaculture 261: 160–173.

Nieoczym, M., Kloskowski, J., 2014. Responses of epibenthic and nektonic macroinvertebrate communities to a gradient of fish size in ponds. Journal of Limnology 74.

Nixdorf, B., Mischke, U., Rücker, J., 2003. Phytoplankton assemblages and steady state in deep and shallow eutrophic lakes—an approach to differentiate the habitat properties of *Oscillatoriales*. In: Phytoplankton and Equilibrium Concept: The Ecology of Steady-State Assemblages. Springer, pp. 111–121.

OECD, 1982. Eutrophication of Waters, Monitoring, Assessment and Control. Final Report. OECD, Paris.

Olah, J., Sinha, V., Ayyappan, S., Purushothaman, C., Radheyshyam, S., 1986. Primary production and fish yields in fish ponds under different management practices. Aquaculture 58: 111–122.

Oliveira Jr., E.S., Temmink, R.J., Buhler, B.F., Souza, R.M., Resende, N., Spanings, T., Muniz, C.C., Lamers, L.P., Kosten, S., 2019. Benthivorous fish bioturbation reduces methane emissions, but increases total greenhouse gas emissions. Freshwater Biology 64: 197–207.

Oltra, R., Alfonso, M. T., Sahuquillo, M., Miracle, M.R., 2001. Increase of rotifer diversity after sewage diversion in the hypertrophic lagoon, Albufera of Valencia, Spain. In: Rotifera IX. Springer, pp. 213–220

Oskam, G., 1982. Quality aspects of the Biesbosch reservoirs. J. Water Supply Res. Technol-Aqua 6: 497–504.

Pacheco, F.S., Roland, F., Downing, J.A., 2014. Eutrophication reverses whole-lake carbon budgets. Inland Waters 4: 41–48.

Pálffy, K., Présing, M., Vörös, L., 2013. Diversity patterns of trait-based phytoplankton functional groups in two basins of a large, shallow lake (Lake Balaton, Hungary) with different trophic state. Aquatic Ecology 47: 195–210.

Patrick , J.W.H., 1994. From wastelands to wetlands. Journal of Environmental Quality 23: 892–896.

Pechar, L., 1995. Long-term changes in fish pond management as' an unplanned ecosystem experiment': Importance of zooplankton structure, nutrients and light for species composition of cyanobacterial blooms. Water Science and Technology 32: 187–196.

Pechar, L., 2000. Impacts of long-term changes in fishery management on the trophic level water quality in Czech fish ponds. Fisheries Management and Ecology 7: 23–31.

Phillips, G., Lyche-Solheim, A., Skjelbred, B., Mischke, U., Drakare, S., Free, G., Järvinen, M., de Hoyos, C., Morabito, G., Poikane, S., 2013. A phytoplankton trophic index to assess the status of lakes for the Water Framework Directive. Hydrobiologia 704: 75–95.

Pokorný, J., Hauser, V., 2002. The restoration of fish ponds in agricultural landscapes. Ecological Engineering 18: 555–574.

Pokorný, J., Pechar, L., 2000. Development of fishpond ecosystems in the Czech Republic. Role of management and nutrient input (Limnological review). Sylvia 36: 8–15.

Pokorný, J., Prikryl, I., Faina, R., Kansiime, F., Kaggwa, R.C., Kipkemboi, J., Kitaka, N., Denny, P., Bailey, R., Lamtane, H., 2005. Will fish pond management principles from the temperate zone work in tropical fish ponds. Natural and constructed Wetlands: Nutrients, Metals and Management: 382–399.

Pomogyi, P., 1993. Nutrient retention by the Kis-Balaton water protection system. Hydrobiologia 251: 309–320.

Potužák, J., Hůda, J., Pechar, L., 2007. Changes in fish production effectivity in eutrophic fishponds-impact of zooplankton structure. Aquaculture International 15: 201–210.

Pouil, S., Samsudin, R., Slembrouck, J., Sihabuddin, A., Sundari, G., Khazaidan, K., Kristanto, A. H., Pantjara, B., Caruso, D., 2019. Nutrient budgets in a small-scale freshwater fish pond system in Indonesia. Aquaculture 504: 267–274.

Přikryl, I., 1996. Development of fishery management in ponds and its reflection in zooplankton structure as a possible criterion of pond's biological value in the Czech Republic. In: Flajšhans, M. (Ed.), Collection of scientific work to 75th anniversary of establishment of Research Institute of Fish Culture and Hydrobiology. USB, Vodňany, CZ, pp. 153–166.

Rahman, M.M., Verdegem, M.C.J., 2007. Multi-species fishpond and nutrient balance. In: van der Zijpp, A.J., Verreth, J.A.J., Tri, L.Q., van Mensvoort, M.E.F., Bosma, R.H., Beveridge, M.C.M. (Eds), Fishponds in farming systems. Wageningen Academic Publishers, Wageningen, The Netherlands, p. 311

Rahman, M., Verdegem, M., Nagelkerke, L., Wahab, M., Milstein, A., Verreth, J., 2006. Growth, production and food preference of rohu *Labeo rohita* (H.) in monoculture and in polyculture with common carp *Cyprinus carpio* (L.) under fed and non-fed ponds. Aquaculture 257: 359–372.

Rahman, M., Jo, Q., Gong, Y., Miller, S., Hossain, M., 2008a. A comparative study of common carp (*Cyprinus carpio* L.) and calbasu (*Labeo calbasu* Hamilton) on bottom soil resuspension, water quality, nutrient accumulations, food intake and growth of fish in simulated rohu (*Labeo rohita* Hamilton) ponds. Aquaculture 285: 78–83.

Rahman, M.M., Nagelkerke, L.A., Verdegem, M.C., Wahab, M.A., Verreth, J.A., 2008b. Relationships among water quality, food resources, fish diet and fish growth in polyculture ponds: A multivariate approach. Aquaculture 275: 108–115.

Reckhow, K.H., 1977. Phosphorus models for lake management. Harvard University, Harvard.

Repo, M., Huttunen, J., Naumov, A., Chichulin, A., Lapshina, E., Bleuten, W., Martikainen, P., 2007. Release of CO_2 and CH_4 from small wetland lakes in western Siberia. Tellus B 59: 788–796.

Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L., Melo, S., 2002. Towards a functional classification of the freshwater phytoplankton. Journal of Plankton Research 24: 417–428.

Robin, J., Wezel, A., Bornette, G., Arthaud, F., Angelibert, S., Rosset, V., Oertli, B., 2014. Biodiversity in eutrophicated shallow lakes: determination of tipping points and tools for monitoring. Hydrobiologia 723: 63–75.

Rutegwa, M., Potužák, J., Hejzlar, J., Drozd, B., 2019. Carbon metabolism and nutrient balance in a hypereutrophic semi-intensive fishpond. Knowledge & Management of Aquatic Ecosystems: 49.

Ryding, S., 1980. Monitoring of inland waters: OECD eutrophication programme-the Nordic project publication. Nordic Co-operative Organisation of Applied Research (NORDFORSK), Helsinki, Finland.

Ságová-Marecková, M., 2002. Distribution of benthic macroinvertebrates in relationship to plant roots, sediment type and spatial scale in fishponds and slow streams. Archiv für Hydrobiologie 156: 63–81.

Sahu, B.C., Adhikari, S., Mahapatra, A. S., Dey, L., 2013. Carbon, nitrogen, and phosphorus budget in scampi (*Macrobrachium rosenbergii*) culture ponds. Environmental Monitoring and Assessment 185: 10157–10166.

Salvia-Castellvi, M., Dohet, A., Vander Borght, P., Hoffmann, L., 2001. Control of the eutrophication of the reservoir of Esch-sur-Sûre (Luxembourg): Evaluation of the phosphorus removal by predams. Hydrobiologia 459: 61–71.

Sas, H., 1989. Lake restoration by reduction of nutrient loading: expectations, experiences, extrapolations. Richarz. Academia Verlag, 497 pp.

Saunders, D., Kalff, J., 2001a. Denitrification rates in the sediments of Lake Memphremagog, Canada – USA. Water Research 35: 1897–1904.

Saunders, D., Kalff, J., 2001b. Nitrogen retention in wetlands, lakes and rivers. Hydrobiologia 443: 205–212.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walkerk, B., 2001. Catastrophic shifts in ecosystems. Nature 431: 591–596.

Schindler, D., 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnology and Oceanography 23: 478–486.

Schreiber, J. Rausch, D., 1979. Suspended Sediment-Phosphorus Relationships for the Inflow and Outflow of a Flood Detention Reservoir 1. Journal of environmental quality 8: 510–514.

Seitzinger, S., Harrison, J. A., Böhlke, J., Bouwman, A., Lowrance, R., Peterson, B., Tobias, C., Drecht, G.V., 2006. Denitrification across landscapes and waterscapes: a synthesis. Ecological applications 16: 2064–2090.

Selvam, P.B., Natchimuthu, S., Arunachalam, L., Bastviken, D., 2014. Methane and carbon dioxide emissions from inland waters in India–implications for large scale greenhouse gas balances. Global Change Biology 20: 3397–3407.

Šimek, K., Grujčić, V., Nedoma, J., Jezberová, J., Šorf, M., Matoušů, A., Pechar, L., Posch, T., Bruni, E.P., Vrba, J., 2019. Microbial food webs in hypertrophic fishponds: Omnivorous ciliate taxa are major protistan bacterivores. Limnology and Oceanography 64: 2295–2309.

Sondergaard, M., Jensen, P.J., Jeppesen, E., 2001. Retention and internal loading of phosphorus in shallow, eutrophic lakes. The Scientific World Journal 1: 427–442.

Staehr, P.A., Bade, D., Van de Bogert, M.C., Koch, G.R., Williamson, C., Hanson, P., Cole, J.J., Kratz, T., 2010. Lake metabolism and the diel oxygen technique: State of the science. Limnology and Oceanography-Methods 8: 628–644.

Šusta, J., 1898. Fünf Jahrhunderte der Teichwirtschaft zu Wittingau. Herrke und Lebeling, Stettin.

Sychra, J., Adámek, Z., 2011. The impact of sediment removal on the aquatic macroinvertebrate assemblage in a fishpond littoral zone. Journal of Limnology 70: 129–138.

Tahar, A., Kennedy, A.M., Fitzgerald, R.D., Clifford, E., Rowan, N., 2018. Longitudinal evaluation of the impact of traditional rainbow trout farming on receiving water quality in Ireland. PeerJ 6: e5281.

Thornton, J., Ashton, P., 1989. Aspects of the phosphorus cycle in Hartbeespoort Dam (South Africa) Phosphorus loading and seasonal distribution of phosphorus in the reservoir. Hydrobiologia 183: 73–85.

Tomaszek, J.A., Koszelnik, P., 2003. A simple model of nitrogen retention in reservoirs. Hydrobiologia 504: 51–58.

Troell, M., Naylor, R.L., Metian, M., Beveridge, M., Tyedmers, P.H., Folke, C., Arrow, K.J., Barrett, S., Crépin, A.-S., Ehrlich, P.R., 2014. Does aquaculture add resilience to the global food system? Proceedings of the National Academy of Sciences 111: 13257–13263.

Tsai, J.-W., Kratz, T.K., Hanson, P.C., Wu, J.-T., Chang, W.Y.B., Arzberger, P.W., Lin, B.-S., Lin, F.-P., Chou, H.-M., Chiu, C.-Y., 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. Freshwater Biology 53: 1929–1941.

Turner, R.R., Laws, E.A., Harris, R.C., 1983. Nutrient retention and transformation in relation to hydraulic flushing rate in a small impoundment. Freshwater Biology 13: 113–127.

Tzaras, A., Pick, F.R., 1994. The relationship between bacterial and heterotrophic flagellate abundance in oligotrophic to mesotrophic temperate lakes. Marine mICROBIAL FOOD Webs 8: 347–355.

Utermöhl, H., 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik: mit 1 Tabelle und 15 abbildungen im Text und auf 1 Tafel. Internationale Vereinigung für theoretische und angewandte Limnologie: Mitteilungen 9: 1–38.

Uwimana, A., van Dam, A., Irvine, K. 2018. Effects of conversion of wetlands to rice and fish farming on water quality in valley bottoms of the Migina catchment, southern Rwanda. Ecological Engineering 125: 76–86.

Valenti, W.C., Kimpara, J.M. Preto, B.d.L., Moraes-Valenti, P., 2018. Indicators of sustainability to assess aquaculture systems. Ecological Indicators 88: 402–413.

van Dam, A.A., Beveridge, M.C.M., Azim, M.E., Verdegem, M.C.J., 2002. The potential of fish production based on periphyton. Reviews in Fish Biology and Fisheries 12: 1–31.

Vanacker, M., Wezel, A., Payet, V., Robin, J., 2015. Determining tipping points in aquatic ecosystems: The case of biodiversity and chlorophyll alpha relations in fish pond systems. Ecological Indicators 52: 184–193.

Všetičková, L., Adámek, Z., Rozkošný, M., Sedláček P., 2012. Effects of semi-intensive carp pond farming on discharged water quality. Acta Ichthyologica et Piscatoria 42: 223–231.

Vuille, T., 1991. Abundance, standing crop and production of microcrustacean populations (Cladocera, Copepoda) in the littoral zone of Lake Biel, Switzerland. Archiv für Hydrobiologie 123: 165–185.

Walker, W.W., 1985. Empirical Methods for Predicting Eutrophication in Impoundments. Report 1. Phase III. Model Refinements. US Army Engineering Waterways Experiment Station, Vicksburg, MS.

Waters, S., Webster-Brown, J., 2016. The use of a mass balance phosphorus budget for informing nutrient management in shallow coastal lakes. Journal of Hydro-environment Research 10: 32–49.

Wetzel, R.G. 2001. Limnology: lake and river ecosytems. 3rd edition. Academic Press, San Diego.

Wetzel, R.G., Likens, G.E., 2000. Limnological Analyses. Springer-Verlag, New York.

Wezel, A., Robin, J., Guerin, M., Arthaud, F., Vallod, D., 2013. Management effects on water quality, sediments and fish production in extensive fish ponds in the Dombes region, France. Limnologica 43: 210–218.

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

Wilander, A., Persson, G., 2001. Recovery from eutrophication: experiences of reduced phosphorus input to the four largest lakes of Sweden. AMBIO: A Journal of the Human Environment 30: 475–485.

Williams, J., Crutzen, P., 2010. Nitrous oxide from aquaculture. Nature Geoscience 3: 143.

Woynarovich, A., Bueno, P. B., Altan, O., Jeney, Z., Reantaso, M., Xinhua, Y., Van Anrooy, R., 2011. Better management practices for carp production in Central and Eastern Europe, the Caucasus and Central Asia. FAO Fisheries and Aquaculture Technical Paper 566. FAO, Ankara.

Xiong, Y., Wang, F., Guo, X., Liu, F., Dong, S., 2017. Carbon dioxide and methane fluxes across the sediment-water interface in different grass carp *Ctenopharyngodon idella* polyculture models. Aquaculture Environment Interactions 9: 45–56.

Yang, P., Lai, D.Y.F., Huang, J.F., Tong, C., 2018a. Effect of drainage on CO_2, CH_4, and N_2O fluxes from aquaculture ponds during winter in a subtropical estuary of China. Journal of Environmental Sciences 65: 72–82.

Yang, P., Zhang, Y., Lai, D.Y., Tan, L., Jin, B., Tong C., 2018. Fluxes of carbon dioxide and methane across the water–atmosphere interface of aquaculture shrimp ponds in two subtropical estuaries: The effect of temperature, substrate, salinity and nitrate. Science of The Total Environment 635: 1025–1035.

Zhang, K., Tian, X.-l., Dong, S.-l., Feng, J., He, R.-p., 2016. An experimental study on the budget of organic carbon in polyculture systems of swimming crab with white shrimp and short-necked clam. Aquaculture 451: 58–64.

English summary

Pond ecosystem dynamics in terms of production ecology

Marcellin Rutegwa

Aquaculture emerged as an alternative enterprise to replace declining capture fisheries. This was in order to meet the increasing market demand for fish and fishery products. Pond aquaculture is responsible for 80% of the fish produced in aquaculture.

The majority of pond aquaculture in the Czech Republic is semi-intensively managed. Semi-intensive fishponds have been considered as a minor source of pollution. This opinion was based on their ability to retain a large level of nutrients and organic matter inputs having simultaneously no significant effect upon quality of outflowing water. Further studies showed later that the intensification of pond culture management (massive fertilisation, supplementary feeding and high density of fish stock) altered the structure and therefore the functioning of fishpond ecosystems. The main consequence was the eutrophication of fishponds. Eutrophication of fishponds resulted in turn in a reduced biodiversity, a high primary production of phytoplankton and its low utilisation efficiency by both zooplankton and fish. It is likely that fishpond eutrophication may have a severe environmental impact not only on other water bodies in areas where fishponds are widespread but also on the atmosphere. With the rise of environmental concerns, fishpond managers are urged to improve pond water quality and pond effluent in order to achieve an ecological sustainable aquaculture. Consequently, there is a need to assess the pollution potential of semi-intensive fishponds.

We monitored pond water and effluent quality in Dehtář pond, a representative Czech semi-intensive polyculture fishpond (Chapters II, III). Plankton and OECD water quality parameters i.e. total phosphorus (TP), chlorophyll a (Chl*a*) and Secchi depth were used to determine the trophic status of the pond. We used the nutrient balance and ecosystem metabolic rates in order to assess the input use efficiency and nutrient retention. Phytoplankton and zooplankton structure and biomass were also analysed in order to assess the grazing food web efficiency. The transboundary layer model was used to quantify methane concentration and emission from two types of carp ponds in order to identify the effect of fishpond management on greenhouse gas production and emission (Chapter IV).

Dehtář pond can be classified as hypereutrophic water body according to OECD. Phytoplankton and zooplankton community were dominated by eutrophic-tolerant species. The phytoplankton trophic index and the zooplankton: phytoplankton biomass ratio further confirmed that the pond is under strong eutrophication pressure. The gross primary production was the main source of organic carbon in Dehtář pond during the growing seasons. Ecosystem respiration was the main output of organic carbon. However, the comparison between the gross primary production and respiration showed that Dehtář was slightly autotrophic, meaning that the system produce more organic matter than the amount used in respiration. The manure and fish feed were the main source of nitrogen and phosphorus during the growing seasons. Nevertheless, inflow was the main source of nitrogen and feed remained the main source of phosphorus if the nutrient balance is calculated over hydrological years. Accumulation in sediments was the main fate of phosphorus whereas accumulation in water was the main fate of nitrogen indicating that it was incorporated into the phytoplankton.

The utilisation efficiency of organic carbon, nitrogen and phosphorus to produce fish biomass was low. The utilisation efficiency of organic carbon was lower compared to results from other studies. The species composition of phytoplankton (large colonies, large filaments),

zooplankton (small sized), eutrophication and a high density of fish stock may explain this low efficiency. This induced a poor transfer of carbon from phytoplankton via zooplankton and/or macroinvertebrates to fish. The analysis of fatty acid content in meat (poor in n-3 and n-6 PUFA) of common carp produced in Czech semi-intensive fishponds further supports our argument. Nonetheless, Dehtář pond still can in these conditions retain nutrients (N and P) but to the detriment of its water quality. High external nutrient loads, algal uptake, fish production, long water residence time, sedimentation, denitrification and shallowness of the pond favoured the retention of nutrients. However, this retention is crucial only during the years the pond is not drained. During the years with fish harvest, sediments, nutrients and organic matter are extensively released and this has increases the pollution potential of the pond.

Temperature, availability of labile organic matter, bioturbation and concentration levels of dissolved oxygen are important factors influencing methane production and emission in aquatic ecosystems. Methane was produced both in nursery ponds (stocked with fingerlings) and in main ponds (stocked with 2 year old common carp). Methane concentration was higher in nursery ponds and was significantly different between the two types of ponds in June, July and August. Low concentration of methane in main ponds was probably due to methane oxidation as a result of fish bioturbation. According to other studies, fish bioturbation reduces methane concentration but may increase emission of carbon dioxide. Methane concentration increased in both types of ponds from April to May following an increase of temperature. Main ponds had a higher concentration of methane only in May and this peak may be additionally explained by the bioturbation of sediment by fish searching for food. A second peak of methane concentration was observed in August in nursery ponds following probably the decay of submerged and floating plants that were present in nursery ponds only. Both types of ponds were a source of diffusive methane to atmosphere. The diffusive methane flux was significantly different between the two types of ponds only in August reflecting a high production of methane and low methane oxidation rate in ponds stocked with small fish. Diffusive methane flux was not significantly related to any environmental variables we measured, indicating that wind speed was its main driving factor.

In conclusion, we observed a low utilisation efficiency of inputs in Dehtář pond, a representative eutrophic semi-intensive carp pond. This low efficiency was caused by eutrophication, high fish stock density and the quality of supplementary feed. Eutrophication and high fish stock density favour the development of phytoplankton and zooplankton community structure that do not allow a maximisation of the utilisation of the primary production. Dehtář pond can still retain nutrients even though the nutrient loads was above its assimilatory capacity. A large fraction of unused autochthonous organic matter and fish harvesting techniques have led to its effluent being of poor quality. The availability of labile organic matter supplies substrate for methanogens (mainly methanogenic bacteria) in carp ponds, ie. producers of methane to the atmosphere. It follows from the above that current pond management practices need to be thoroughly revised in order to find trade-offs between fish production in ponds and other pond ecosystem functions. These measures will help increase the ecological sustainability of fish farming in ponds and introduce further topics for pond research as well.

Czech summary

Dynamika rybničního ekosystému z hlediska produkční ekologie

Marcellin Rutegwa

Akvakultura vznikla jako náhrada klesajícího výlovku z volných vod z důvodu uspokojení rostoucí poptávky na trhu po rybách a produktech rybolovu. Rybniční akvakultura dnes zodpovídá za produkci zhruba 80 % ryb celkově vyprodukovaných v akvakultuře.

Většina rybníků v České republice je obhospodařována polo-intenzivním způsobem. Takto obhospodařované rybníky byly tradičně považovány za nevýznamný zdroj znečištění vod. Tento názor byl založen na schopnosti rybníků zachovat si velkou úroveň vstupů živin a organických látek neprojevující se zhoršením kvality odtékající vody. Pozdější studie však ukázaly, že intenzifikace rybničního chovu (masivní hnojení, přikrmování a vysoké rybí obsádky) kompletně změnila strukturu a tím i fungování rybničního ekosystému. Hlavním důsledkem byla eutrofizace projevující se sníženou biologickou rozmanitostí, vysokou primární produkcí fytoplanktonu a jeho nízkou efektivitou využití jak zooplanktonem, tak i rybami. Eutrofizace rybníků má však vážný environmentální dopad nejen na jiné vodní útvary v oblastech, kde se rybníky nachází, ale také na atmosféru. Se vzrůstajícími obavami o životní prostředí jsou subjekty hospodařící na rybnících naléhavě nabádány, aby přijaly opatření vedoucí ke zlepšení kvality vody nejen v rybnících, ale také ve vodách z rybníků vytékajících, s cílem dosáhnout ekologické a udržitelné akvakultury. V důsledku toho je nezbytné posoudit znečišťující potenciál těchto polo-intenzivně obhospodařovaných rybníků.

V rámci doktorské práce jsme monitorovali kvalitu vody v rybníku Dehtář a na jeho odtoku. Dehtář je typický zástupce českých polo-intenzivně obhospodařovaných rybníků s polykulturní obsádkou ryb (Kapitoly II, III). Pro určení trofického stavu rybníka byla použita data o planktonu a parametry kvality vody dle OECD metodiky – koncentrace celkového fosforu (TP), chlorofylu a (Chla) a průhlednost měřená Secchi deskou. Bilance živin a metabolická rychlost ekosystému byly použity pro posouzení účinnosti využití vstupů a zadržování živin. Dále byla také analyzována struktura a biomasa fytoplanktonu a zooplanktonu z důvodu vyhodnocení účinnosti fungování pastevní trofické sítě. Pro kvantifikaci koncentrace a emise metanu ze dvou typů rybníků byl použit model přeshraniční vrstvy, aby byl identifikován vliv obhospodařování rybníků na produkci a emise skleníkových plynů (Kapitola IV).

Rybník Dehtář lze podle OECD metodiky klasifikovat jako hypereutrofní vodní útvar. Ve společenstvech fytoplanktonu a zooplanktonu dominovaly vysokou trofii (eutrofii) tolerující druhy. Poměr biomasy fytoplanktonu vůči struktuře a biomase zooplanktonu také potvrdil silný eutrofizační tlak. Hrubá primární produkce byla během sledovaných vegetačních období hlavním zdrojem organického uhlíku. Respirace ekosystému byla hlavním výstupem organického uhlíku. Porovnání mezi hrubou primární produkcí a respirací však ukázalo, že Dehtář byl mírně autotrofní systém, tzn., že produkoval více organické hmoty, než bylo množství energie použité na respiraci. Hnojení (chlévská mrva) a krmivo pro ryby (obilí) byly hlavním zdrojem dusíku a fosforu během sledovaných vegetačních období. Nicméně přítok lze považovat za hlavní zdroj dusíku a krmivo pak zase fosforu, pokud se bilance živin počítá v hydrologických letech. Akumulace v sedimentech byla hlavním osudem fosforu, akumulace ve vodě pak dusíku. To naznačuje, že byl dusík začleněn do masy fytoplanktonu.

Jak účinnost využití organického uhlíku, tak i dusíku a fosforu k produkci rybí biomasy v Dehtáři byla během sledovaného období nízká. Účinnost využití organického uhlíku byla ve srovnání s výsledky z jiných studií nižší. Tato nízká transformační účinnost uhlíku může být vysvětlena jak pozorovaným druhovým složením fytoplanktonu (velké kolonie, vláknité druhy) a zooplanktonu (druhy s malou velikostí), tak i přeživinováním (eutrofizací) či vysokou hustotou rybích obsádek. Došlo tak ke špatnému přenosu uhlíku z fytoplanktonu přes biomasu zooplanktonu a / nebo dalších (velkých) bezobratlých (především bentosu) do biomasy ryb. Naše argumentace je také podpořena analýzou obsahu mastných kyselin v mase (nízký obsah n-3 a n-6 polynenasycených mastných kyselin) kaprů produkovaných v českých polo-intenzivně obhospodařovaných rybnících. Nicméně rybník Dehtář dokáže i v těchto podmínkách stále zadržovat živiny (N a P), avšak na úkor kvality vody. Vysoký vnos živin z vnějšku, řasový nárůst, produkce ryb, dlouhá doba zdržení vody, sedimentace, denitrifikace a velký podíl mělkých částí na celkové ploše rybníka podporovaly zadržování živin. Tato retence živin je však rozhodující pouze v letech, kdy rybník není vypouštěn. V letech, kdy je rybník loven za účelem získání produkované rybí obsádky, se naopak sedimenty, živiny a organické látky masivně uvolňují. To významně zvyšuje znečišťující potenciál rybníka pro povodí.

Teplota, dostupnost reaktivní organické hmoty, bioturbace a koncentrace rozpuštěného kyslíku jsou důležité faktory ovlivňující produkci a emise metanu ve vodních ekosystémech. Metan byl produkován jak v plůdkových rybnících (nasazených tohoročním plůdkem kapra pro produkci násady), tak v hlavních rybnících (nasazených dvou letou násadou pro produkci tržních kaprů). Koncentrace metanu byla vyšší v plůdkových rybnících a významně se lišila mezi oběma typy rybníků v červnu až srpnu. Nízká koncentrace metanu v hlavních rybnících byla pravděpodobně způsobena oxidací metanu v důsledku bioturbační aktivity ryb. Koncentrace metanu se v obou typech rybníků zvýšila od dubna do května po nástupu zvýšení teploty vzduchu a následně vody. Hlavní rybníky měly vyšší koncentraci metanu jen v květnu. Tento vrchol může být vysvětlen bioturbací sedimentu rybami hledajícími potravu. Druhý vrchol koncentrace metanu byl pozorován v srpnu, a to pouze v plůdkových rybnících, a to pravděpodobně jako důsledek rozpadu ponořených a plovoucích rostlin. Ty byly přítomny pouze v tomto typu rybníků. Oba typy rybníků byly zdrojem difúzního metanu pro atmosféru. Difuzní tok metanu se mezi oběma typy rybníků významně lišil jen v srpnu. To odráželo vysokou produkci metanu a nízkou rychlost oxidace metanu v rybnících nasazených malými rybami (plůdkem). Difuzní tok metanu nesouvisel významně s žádnými proměnnými prostředí, které jsme měřili. To naznačuje, že rychlost větru byla jeho hlavním hnacím faktorem.

V souhrnu, v Dehtáři, eutrofním polo-intenzivně obhospodařovaném kaprovém rybníku, jsme během sledovaného období pozorovali nízkou efektivitu využití vstupů (živin), která byla pravděpodobně způsobena eutrofizací (vysokou živinovou bohatostí), vysokou hustotou populace ryb a kvalitou doplňkového krmiva ryb. Eutrofizace a vysoká hustota rybích populací podporují rozvoj takové struktury společenstev fytoplanktonu a zooplanktonu, která neumožňuje maximalizaci využití primární produkce. Rybník Dehtář stále může živiny zadržovat, i když obsah živin byl nad jeho asimilační kapacitou. Velký podíl nepoužité autochtonní organické hmoty a používané techniky výlovu ryb vedly ke špatné kvalitě vody na výtoku z rybníka. Dostupná (nadbytečná) reaktivní organická hmota představuje substrát pro metanogenní organizmy (hlavně bakterie) v rybnících, producenty metanu uvolňujícího se z rybníku do atmosféry. Z výše uvedeného tak vyplývá, že je nezbytné současné postupy obhospodařování rybníků podrobit důkladné revizi, aby mohly být nalezeny kompromisy mezi produkcí ryb v rybnících a dalšími ekosystémovými funkcemi rybníka. Tato opatření pomohou zvýšit ekologickou udržitelnost chovu ryb v rybnících a navodí další témata rybničního výzkumu.

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List of publications

Peer-reviewed journals with IF

Rutegwa, M., Gebauer, R., Veselý, L., Regenda, J., Strunecký, O., Hejzlar, J., Drozd, B., 2019. Diffusive methane emissions from temperate semi-intensive carp ponds. Aquaculture Environment Interactions 11: 19–30. (IF 2018 = 2.380)

Rutegwa, M., Potužák, J., Hejzlar, J., Drozd, B., 2019. Carbon metabolism and nutrient balance in a hypereutrophic semi-intensive fishpond. Knowledge and Management of Aquatic Ecosystems 420: 49. (IF 2018 = 1.265)

Vanina, T., Gebauer, R., Toomey, L., Stejskal, V., **Rutegwa, M**., Kouřil, J., Bláha, M., Lecocq, T., 2019. Genetic and aquaculture performance differentiation among wild allopatric populations of European perch (Percidae, *Perca fluviatilis*). Aquaculture 503: 139–145. (IF 2017 = 3.022)

Peer-reviewed journals without IF

Manirafasha, E., Vajhuabmuas Vangh, A., Murwanashyaka, T., Rugabirwa, B., Ndikubwimana, T., Mukagatare, G., Damascene Ndayambaje, J., Guo, L., Shen, L., Zeng, X., Jing, K., **Rutegwa**, **M.**, Lu, Y., 2019. Algal resources exploitation for green economy and sustainable development: A review. Adv Biochem Biotechnol 7: 1089. DOI: 10.29011/2574-7258.001089.

Abstracts and conference proceedings

Rutegwa, M., Hejzlar, J., Drozd, B., 2018. Diffusive methane emissions from carp ponds (South Bohemia, Czech Republic). Aquaculture Europe 2018 Abstracts. Montpellier, France, August 25–29, 2018, p. 664. (Poster presentation)

Traning and supervision plan during study

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Dr. Gabriel Singer, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany (1 month, learning techniques of measuring greenhouse gases from aquatic ecosystems)	2017
Dr. Gabriel Singer, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany (2 months, data analysis and paper writing: Diffusive methane emissions from temperate semi-intensive carp ponds. Aquacult Environ Interact 11: 19-30 DOI: 10.3354/aei00296 (IF 2018 = 2.380)	2017

Pedagogical activities	**Year**
Lecturing students of the International Summer school (Ecology of fishponds & Sustainable aquaculture: the forgotten accountability), discipline Fishery at USB FFPW in range of 5 hours	2017
Leading an international summer school project entitled Effect of fish size on methane emissions from carp ponds at Summer school	2018
Lecturing talented students from South Bohemia region (Ecology of fishponds), discipline Fishery at USB FFPW in range of 10 hours	2018
Lecturing Yspertal students (Ecology of fishponds), discipline Fishery at USB FFPW in range of 20 hours	2017–2018
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