



HAL
open science

The balance of carbon emissions versus burial in fish ponds: The role of primary producers and management practices

Léo Girard, Thomas A Davidson, Vincent Tolon, Tuba Bucak, Soraya Rouifed, Alexander Wezel, Joël Robin

► To cite this version:

Léo Girard, Thomas A Davidson, Vincent Tolon, Tuba Bucak, Soraya Rouifed, et al.. The balance of carbon emissions versus burial in fish ponds: The role of primary producers and management practices. *Aquaculture Reports*, 2024, 39, pp.102456. 10.1016/j.aqrep.2024.102456 . hal-04756067

HAL Id: hal-04756067

<https://isara.hal.science/hal-04756067v1>

Submitted on 28 Oct 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License



The balance of carbon emissions versus burial in fish ponds: The role of primary producers and management practices

Léo GIRARD^{a,*}, Thomas A. DAVIDSON^b, Vincent TOLON^a, Tuba BUCAK^b, Soraya ROUIFIED^a, Alexander WEZEL^a, Joël ROBIN^a

^a Agroecology and Environment Research Unit, ISARA, Lyon, France

^b Freshwater Ecology, Department of Ecoscience, Aarhus University, Aarhus, Denmark

ARTICLE INFO

Keywords:

Sedimentation
Greenhouse gas emissions
Extensive fish farming
Climate change
Carbon storage
Fishpond

ABSTRACT

In the global carbon cycle, ponds can play a dual role: they have the capacity to store carbon through sedimentation, but also to be important greenhouse gas emitters. Of all the pond landscapes in Europe, many are managed by Humans for fish production and little is known today about their role as carbon sinks or sources. We monitored 20 fish ponds from the Dombes region (France) during a production season in 2022. We measured both sedimentation rates, the diffusion of CO₂, CH₄ and N₂O and ebullition of CH₄ over three different seasons (spring, summer and autumn) in order to provide an estimate of the carbon balance for each pond. Five were dried-out in 2023 as part of the management cycle, and were monitored for dry flux emissions during this period. On average, our measurements suggest that fish ponds were carbon sinks (6 fish ponds as sources and 14 as sinks). There was on average a net sequestration of 4.16 (+/- 10.00) tonnes of CO₂e per hectare over 6 months. Measurements from the dry year, indicate that the ponds were carbon sources (mean value of 23.89 tonnes of CO₂e emitted). However, whilst the drying out phase directly increases emissions, it also encourages the development of macrophytes in the subsequent years which improves carbon storage through sedimentation, and appears to be an important driver of the observed balances. These data are consistent with the fact that fish ponds have the capacity to be either sources or sinks of carbon for the atmosphere. Moreover, by promoting good levels of primary productivity, the presence of aquatic plants and by improving carbon storage, management practices appear to have the capacity to turn fish ponds into carbon sinks. These agroecosystems could thus play an important role in the context of climate change mitigation.

1. Introduction

Carbon is distributed in three major compartments: terrestrial, oceanic and atmospheric (Archer, 2011). Human activities have played a major role in destocking terrestrial carbon, which is then transferred in gaseous form to the atmosphere (IPCC, 2023; Archer, 2011). Greenhouse gas emissions have risen sharply in recent decades (IPCC, 2023; Yue and Gao, 2018) and atmospheric concentrations of carbon dioxide (CO₂) and methane (CH₄) are reaching record levels in the last few years (IPCC, 2023). Methane concentrations, for example, have risen from 650 to over 1810 ppb since the pre-industrial era (Saunois et al., 2016). As for CO₂, the average concentration today is over 412 ppm. The 400 ppm threshold had not been exceeded since the *Pliocene*, more than 3 million years ago (Willeit et al., 2019). In 150 years, this concentration has risen by 40 % due to anthropogenic activities. This leads to a greater retention

of the heat emitted by the Earth, resulting in global warming (IPCC, 2023). This rapid climate change has numerous consequences for all ecosystems, their biodiversity and the services they provide to humanity (IPCC, 2023).

Lakes and ponds are hot spots for biogeochemical processes and play an important role in the carbon cycle (Peacock et al., 2021; Cole et al., 2007; Battin et al., 2008). Primary producers, aquatic plants and algae in ponds, capture CO₂ from the atmosphere (Oertli and Frossard, 2013) and transform it into carbohydrates (gross primary production). Then they become the food base for primary consumers, who thus integrate the carbon into their own biomass. In this way, carbon is transferred to all organisms in the trophic chain (Oertli and Frossard, 2013). In the absence of sunlight, at night, this process is reversed. This is also the case with the constant respiration in the sediments. Primary producers respire and consume the oxygen dissolved in the water. In return, they

* Corresponding author.

E-mail address: legirard@isara.fr (L. GIRARD).

<https://doi.org/10.1016/j.aqrep.2024.102456>

Received 3 May 2024; Received in revised form 23 October 2024; Accepted 23 October 2024

2352-5134/© 2024 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

release CO₂. Lakes and ponds can therefore act alternately as sinks or sources of atmospheric CO₂, in conjunction with photosynthesis and respiration. The carbon contained in the organisms is then deposited in the sediments after their death (Oertli and Frossard, 2013). This sedimentation turns ponds into more or less long-term carbon reservoirs (Gregg *et al.*, 2021; Sun *et al.*, 2020; Boyd *et al.*, 2010). Artificial ponds (including fish ponds) can store as much or more carbon than other aquatic ecosystems. Holgerson *et al.* (2023) have shown that carbon burial rates in artificial ponds are double those in lakes and similar as for wetlands.

The decomposition of organic matter in sediments then plays a key role in carbon processes and cycling. Under anoxic conditions, among other things, by oxygen-consuming bacterial activity, this decomposition will be carried out by a variety of microbial communities, producing three gases (Chen *et al.*, 2020; Praetzel *et al.*, 2019; Davidson *et al.*, 2015): CO₂, CH₄ and nitrous oxide (N₂O). These gases produced and sometimes dissolved in water can return to the atmosphere in two ways. On the one hand, there are gas exchanges between water and the atmosphere, known as diffusive fluxes. All three gases are involved in these exchanges. For methane, ebullition is a second type of emission with methane bubbles rising up from the sediment through the water column, without the gas totally dissolving in the water. These emissions often result from decomposition and fermentation under anaerobic conditions. This flux can account for the majority (40–60 %) of CH₄ emissions in certain types of aquatic environments, particularly those of small size (Dong *et al.*, 2023; Audet *et al.*, 2017; Deemer *et al.*, 2016) and can even reach 99 % in some experiments (Davidson *et al.*, 2018). However, the spatiotemporal variability of processes can make difficult to measure methane ebullition (Deemer *et al.*, 2016). Due to these different emissions, small water bodies and shallow ponds can be significant sources of CO₂ and CH₄, particularly in tropical areas (Cole *et al.*, 2007; Battin *et al.*, 2009; Bastviken *et al.*, 2011; Raymond *et al.*, 2013; Regnier *et al.*, 2013; Borges *et al.*, 2015; DelSontro *et al.*, 2018, Finlay *et al.*, 2019). Aquatic ecosystems are estimated to contribute on average more than 50 % of anthropogenic CH₄ emissions, and higher in disturbed ecosystems with more pronounced anthropogenic impacts (Rosentreter *et al.*, 2021).

Aquatic ecosystems therefore have a dual role. They can simultaneously act as a source of carbon for the atmosphere, while accumulating and storing carbon in their sediments (Prairie *et al.*, 2018). Lakes, for example, have generally been shown to be sources of CO₂ to the atmosphere while storing organic carbon in their sediments (Dillon and Molot, 1997; Kortelainen *et al.*, 2004; Duarte and Prairie, 2005; Rantakari and Kortelainen, 2005; Sobek *et al.*, 2005).

Among the lakes and ponds on the Earth's surface, there are many that are used for fish farming. These ecosystems are often created by human activity and maintained by fish farming practices. Water is managed by humans, controlling both emptying and filling of the ponds. The management practices applied (liming, fertilization, feeding, water management and dry periods) can vary greatly from one region to another (Horvath *et al.*, 2002). These ponds are generally eutrophic to hyper-eutrophic, as primary productivity is essential to produce the energy needed by fish (Aubin *et al.*, 2017). Notwithstanding this elevated production they may still contain significant biodiversity with endemic or endangered species (Cereghino *et al.*, 2007; Robin *et al.*, 2014; Wezel *et al.*, 2013; Cereghino *et al.*, 2007; Oertli *et al.*, 2005; Williams *et al.*, 2004, Biggs *et al.*, 1994).

High primary productivity can result in greater capture of atmospheric CO₂ and therefore greater carbon storage in pond sediments. At the same time, however, it can increase and modify greenhouse gas emission patterns (Zhang *et al.*, 2022; Sun *et al.*, 2021; Audet *et al.*, 2017; Fuse *et al.*, 2016; Davidson *et al.*, 2015). The decomposition of a high biomass (algae or plants) generally leads to anoxic conditions and is favourable to methane emissions (Zhang *et al.*, 2022; Sun *et al.*, 2021; Audet *et al.*, 2017; Fuse *et al.*, 2016; Davidson *et al.*, 2015). When primary production exceeds the amount of CO₂ produced in sediments,

fishponds can act as carbon sinks (Flickinger *et al.*, 2020; Zhang *et al.*, 2020). Fish ponds are generally shallow and their water heats up faster, accelerating all biogeochemical processes (Peacock *et al.*, 2021; Rosentreter *et al.*, 2021). As an example, a shallow depth limits the potential oxidation of methane in the water column (Peacock *et al.*, 2021) but this oxidation can happen on roots and plant surfaces (Esposito *et al.*, 2023). Fertilization with organic matter or nitrogen stimulates primary productivity and thus photosynthesis (Schlumberger and Girard, 2020). However, excessive nutrient concentrations in water and eutrophic conditions can also lead to higher emissions of greenhouse gases, particularly methane (Peacock *et al.*, 2021; Gregg *et al.*, 2021, Sun *et al.*, 2021). Fish density in ponds can also increase emission levels (Oliveira Junior *et al.*, 2019). By stirring and oxygenating sediments, benthic fish reduce methane emissions but increase CO₂ emissions at the same time (Oliveira Junior *et al.*, 2019).

In the Dombes region (France), fish ponds are let dry for an entire production season on average every 4–5 years. The aim of this practice is to mineralize the organic matter that has accumulated in the sediments and thus have mineral nutrients available in the water the following year. It has been shown that this practice favours the recolonization of the environment by macrophytes during the first year rewetted after terrestrial production (Girard *et al.*, 2023; Fontanilles *et al.*, 2023). During the second year, both primary producers (macrophytes and phytoplankton) are present in the ecosystem, with an unstable equilibrium favourable to fish production (Girard *et al.*, 2023). These macrophytes appear to be an important driver of CO₂ and CH₄ emissions (Davidson *et al.*, 2018; Audet *et al.*, 2017; Davidson *et al.*, 2015). In subsequent years (3rd to 5th year with water), the ecosystem is generally dominated by phytoplankton. Partial or total dewatering of ponds, as drying-out fish ponds, by promoting decomposition of the organic matter that has accumulated (Ayub *et al.*, 1993), will lead to an increase in greenhouse gas emissions and therefore in the release of carbon into the atmosphere (Gregg *et al.*, 2021). It has been shown, for example, that tidal zones (with fluctuating water levels) favour emissions (Prairie *et al.*, 2018). Permanent ponds are said to have more carbon stored in their sediments than temporary ponds (Gregg *et al.*, 2021).

Finally, it is not clear whether the net carbon balance resulting from sedimentation and emissions is negative or positive, and how much management practices linked to fertilization and drying-out impact this balance. Few studies have focused on carbon storage and greenhouse gas emissions in these environments, despite the fact that they can play an important role in carbon cycles (Rutegwa *et al.*, 2019b,a; Downing, 2010; Abnizova *et al.*, 2012).

It is in an attempt to fill this knowledge gap that we will study the carbon balance variability observed in Dombes fish ponds over the different years of production but also during the dry phase. We will also analyse how the fish ponds management practices can influence these balances.

We hypothesize that (i) because of their high sedimentation rate, fish ponds tend to act as carbon sinks during years in water. This stored carbon is (ii) re-emitted during the dry season, but to a lesser extent, turning fishponds also into carbon sinks over the entire production cycle. Moreover (iii), by promoting primary production, management practices as fertilisation and drying-out can influence this carbon balance and help to turn fish ponds into carbon sinks.

2. Material and methods

2.1. Study area and study sites

The study focused on 20 fish ponds in the Dombes region of France (Fig. 1), monitored in 2022, with 5 of them also monitored in 2023 during their dry year. The Dombes fish ponds represent over 11,000 ha of water for more than 1100 ponds (Bernard and Lebreton, 2007). They were built by monastic communities during the Middle age (mainly in the in the XIII century, Avocat, 1975; Guichenon, 1650 cited in Sceau,

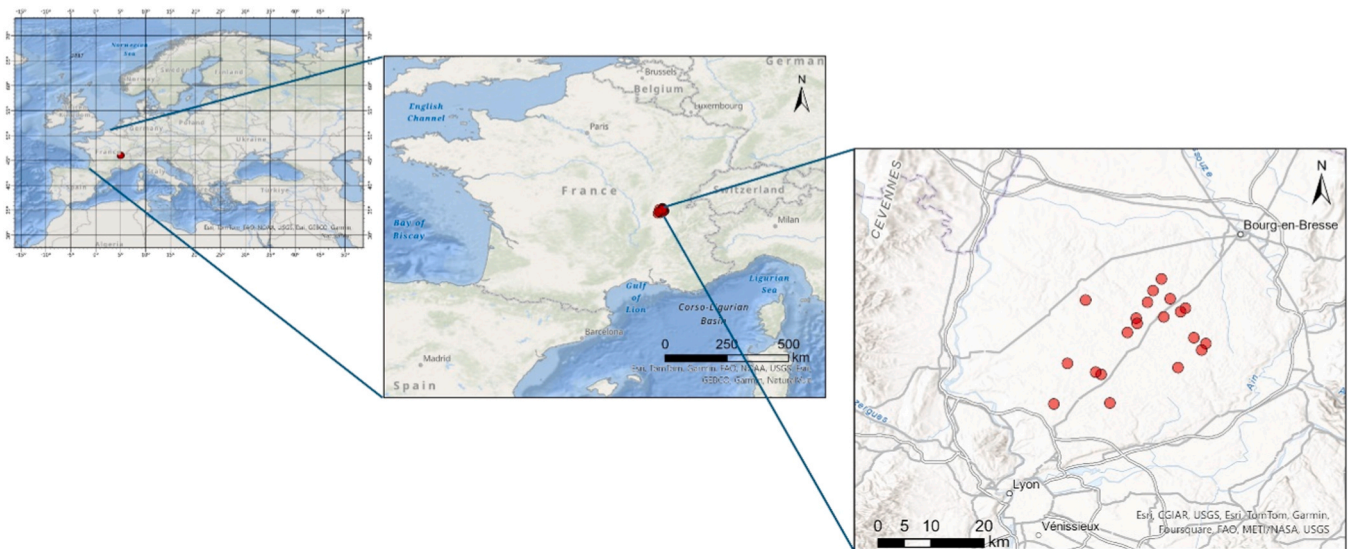


Fig. 1. Map of fishponds monitored for sedimentation and greenhouse gas emissions in 2022 and 2023, Dombes region, France.

1980). They had multiple objectives: to drain a swampy area in order to obtain arable land, but also to produce fish. This also helped reduce wetland-related diseases (Guichenon, 1650 cited in Sceau, 1980). Since then, extensive fish farming has continued, with historic management practices to maintain these ecosystems. As in many fish ponds in Europe, carp (*Cyprinus carpio*) is the main fish produced. It is generally accompanied by white fish such as roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*), tench (*Tinca tinca*), and carnivorous fish such as pike (*Esox lucius*) and pikeperch (*Sander lucioperca*). The classic polyculture consists of 70–80 % carp, accompanied by 10–20 % white fish and tench and 5–10 % carnivorous fish. To harvest fish and sell them for processing or river repopulation, the ponds are emptied every winter and then immediately refilled. In addition, every 4–5 years on average, they are drained and left empty for an entire full growth season. The main aim of this practice, known as "drying-out", is to allow the mineralization of organic matter that has accumulated in the sediment. This allows for greater primary productivity when the water returns, thanks to nutrient recycling (Fontanilles et al., 2023; Girard et al., 2023).

The 20 fish ponds were selected according to the time since the last dry year, so as to be able to analyse carbon storage and greenhouse gas

emissions over the different years of the cycle. The 5 fish ponds monitored during the dry period in 2023 were selected from those already monitored in 2022. In addition, depending on the fish farmer, different practices are applied: fertilization with manure, mineral nitrogen fertilization or no fertilization, different fish stocking densities, and presence or absence of liming.

These fish ponds and their characteristics are presented in Table 1.

2.2. Sedimentation and carbon storage

In order to measure sedimentation in the ponds monitored, "sediment traps" were used. These were PVC cups 10 cm in diameter and 4 cm high (surface area 78.5 cm²). They were placed at the bottom the sediment surface for 3 months. Each pond was equipped with 3 traps, one close to the edge, a second in the middle of the pond and the last in an intermediate position, avoiding fish feeding areas. The traps remained in place during the months of June, July and August, when primary production is the highest (Rabaey et al., 2024).

At the end of this period, the accumulated sediment was collected and oven-dried for 48 hours at 105°C. Weighing the dry mass revealed

Table 1

Description of fish pond monitored with their surface area, the years after the last dry-out, net fish yields, fertilisation managements, macrophytes cover, median concentration of chlorophyll a and median concentration of cyanobacteria.

| | Surface area (ha) | Years after last dry-out | Net fish yield (kg.ha ⁻¹ .year ⁻¹) | Fertilisation management | Macrophytes cover (%) | Chlorophyll a (µg.l ⁻¹) | Cyanobacteria (µg.l ⁻¹) |
|--------|-------------------|--------------------------|---|--------------------------|-----------------------|-------------------------------------|-------------------------------------|
| FR001 | 10 | 2 | 240 | Mineral | 65 | 59.7 | 11.4 |
| FR002 | 14 | 3 | 532 | Organic | 100 | 24.4 | 5.1 |
| FR003 | 24 | 2 | - | No | 5 | 193.4 | 46.5 |
| FR004 | 6 | 4 | 474 | Mineral | 45 | 64.9 | 4.5 |
| FR005 | 5 | 3 | - | Organic | 80 | 72.7 | 40.9 |
| FR006 | 12 | 1 | 147 | No | 60 | 71.9 | 34.1 |
| FR007 | 34 | 5 | 332 | Mineral | 0 | 63.2 | 18.2 |
| FR008 | 23 | 3 | 182 | No | 5 | 194.3 | 58.1 |
| FR009 | 60 | 5 | 401 | Mineral | 10 | 118.5 | 13.7 |
| FR0010 | 49 | 5 | 211 | Mineral | 70 | 16 | 1.4 |
| FR0011 | 4 | 4 | 354 | Mineral | 75 | 114.2 | 25.3 |
| FR0012 | 4 | 5 | 87 | No | 1 | 49 | 4.6 |
| FR0013 | 24 | 1 | 481 | Organic | 30 | 55.8 | 8.4 |
| FR0014 | 7 | 3 | 514 | No | 20 | 48.9 | 6.4 |
| FR0015 | 15 | 2 | 293 | Mineral | 10 | 119.8 | 18.4 |
| FR0016 | 13 | 2 | 496 | Mineral | 30 | 22.4 | 3.8 |
| FR0017 | 5 | 3 | 262 | Mineral | 90 | 15.8 | 4.6 |
| FR0018 | 11 | 2 | 167 | No | 100 | 37.3 | 12.4 |
| FR0019 | 40 | 1 | 31 | No | 15 | 187 | 12 |
| FR0020 | 9 | 2 | -111 | Organic | 40 | 87 | 23.7 |

the quantity of sediment that had accumulated over 3 months on a given surface. The median value of the three traps was used in the analyses.

In addition, sediment samples (maximum average profile between 10 and 15 cm) were taken at the end of March using an Eckman-Birge grab sampler. Three samples were collected at three different points in the pond, at a depth of less than 120 cm and each separated by 20 m. They were then homogenized to form a single sample. This sample was analysed in the laboratory to determine the concentration of organic carbon in the sediment (in g.kg^{-1}) with the method ISO 10694 (AFNOR, 1995). This sediment sample was also used to determine pH and the concentration of exchangeable phosphorus (P_2O_5) expressed in g.kg^{-1} , using the NF X31-160 method (AFNOR, 1999).

The quantity of sediment associated with the organic carbon concentration was used to calculate the quantities of organic carbon stored in the sediment over a given period and surface area. Values are expressed in tonnes of CO_2 equivalent per hectare over 6 months. The value obtained over the 3-month period was extrapolated to obtain an estimate of sedimentation over 6 months.

2.3. Emissions during years in water

The two types of emission - diffusion and ebullition - were measured on the 20 ponds over three seasons: spring (May), summer (July) and autumn (September-October). The average of the various values was used for the overall analyses. All flows were converted into CO_2 equivalents (tonnes of) per hectare over 6 months, taking a global warming potential (GWP) of 28 for CH_4 and 265 for N_2O (IPCC, 2023). These 6-month estimates were obtained by multiplying average daily fluxes measured by 183 days.

2.3.1. Diffusion

To quantify diffusion fluxes, we measured the concentration of dissolved gases in pond surface water using head space equilibrium (Raymond et al., 1997; Cole et al., 1994). For each season, a 40-mL sample of water was taken using a 50-mL syringe. 10 mL of air was then added. The sample was shaken for one minute to allow gas exchange. The 10 mL of air in the syringe was then injected into 5.6 mL vacuum Exetainer® vials. At the same time, air samples were taken to determine the atmospheric concentrations of these gases. These were also stored in 5 mL Exetainer® vials.

These samples were then analysed in the laboratory using gas chromatography to measure CO_2 , CH_4 and N_2O concentrations. Gas concentrations were determined on an Agilent 8890 GC system (USA) interfaced with a PAL RSI 120 autosampler (CTC Analytics, Switzerland; Petersen et al., 2012). Aqueous concentrations of CH_4 and CO_2 were calculated from the headspace gas concentrations according to Henry's law and using Henry's constant corrected for temperature (Weiss R.F., 1974; Wiesenburg and Guinasso, 1979; Weiss and Price, 1980).

From here, we were able to calculate fluxes (in mg C , for CO_2 and CH_4 or $\text{N.m}^{-2}.\text{day}^{-1}$ for N_2O). Fluxes of CO_2 , CH_4 and N_2O between water and the overlying atmosphere were estimated as follows:

$$f_g = k_g \beta_g (C_{\text{water},g} - C_{\text{eq},g})$$

f_g corresponds to the gas g flux, k_g is the gas piston velocity, β_g is the chemical enhancement factor, and $C_{\text{water},g} - C_{\text{eq},g}$ is the concentration gradient between the gas concentration dissolved in the water ($C_{\text{wat},g}$) and the gas concentration that the water would have at equilibrium with the atmosphere ($C_{\text{eq},g}$), using concentrations measured in ambient air samples.

K_g is calculated as follows:

$$k_g = k_{600} \left(\frac{Sc_g}{600} \right)^x$$

Sc_g is the Schmidt number (Wanninkhof, 1992). We assigned a gas transfer velocity k_{600} of 0.36 m.d^{-1} to estimate CO_2 , CH_4 and N_2O

emissions from small ponds as described in Audet et al. (2020) and Holgerson and Raymond (2016). We have chosen $x = -2/3$ as this factor is used for smooth liquid surfaces (Deacon, 1981). This protocol is presented in more detail in Davidson et al. (2015).

2.3.2. Ebullition

For ebullition, methane bubbles rising in the water column were trapped using floating chambers (with an area of 0.075 m^2 and a total volume of 8 liters), as described in Bastviken et al. (2015). Over three seasons: spring (May), summer (July) and autumn (September-October), 6–8 chambers were placed on the ponds for one week, depending on their surface. These chambers are covered with a silver film to reflect the sun and prevent the interior from overheating. They are evenly distributed over the surface of the pond to cover a gradient of depths. Ebullition is highly variable in space and time. It's important to cover different areas of the pond with depth and sediment substrate being key factors in determining CH_4 ebullition. After one week, a 10 mL sample of the gas accumulated in the chamber was taken with a syringe and injected into a 5 mL vacuum Exetainer®. As with diffusion, the methane concentration in this sample was then analysed in the laboratory using a gas chromatograph (Agilent 8890 GC system with a PAL RSI 120 autosampler; CTC Analytics, Switzerland; Petersen et al., 2012).

Ebullitive flux of CH_4 was estimated as:

$$\frac{p_{\text{gas}} \times \text{Vol}_{\text{bub}}}{t \times A}$$

p_{gas} represents the methane concentration in the sample, Vol_{bub} the chamber volume (8 liters), t the time the chamber is placed on the pond (7 days) and A the surface area (0.075 m^2).

This method of estimating ebullition is an underestimate as it does not take into account the potential diffusion back of CH_4 in the water. However, Davidson et al. (2024) demonstrated that it provides a more reliable estimate of ebullition than a shorter period of measurement (e.g. 1–2 days) of continuous measurement.

2.4. Emissions during the dry year

CO_2 and CH_4 emissions were also monitored on five fish ponds during 2023, in the week following emptying (between April and July, depending on the ponds and their management). The same chambers used to measure methane ebullition during the in-water phase were used. The chambers were fitted with a collar to seal them at ground level, and with sensors to measure the concentrations of the two gases in the chamber directly.

For the measurement of CH_4 , Figaro TGS2611 sensor was used and for CO_2 , humidity, and temperature measurements, Sensirion SCD30 sensor module was used. These sensors were connected to electronic circuitry Arduino Mega250 board, with data is stored to an SD card every 2–4 seconds. These equipment are presented in detail in Bastviken et al. (2015), (2020).

To capture spatial variation across each pond, nine measurement points were set up. For 8 of these points, measurements were conducted for 5 minutes and for one of them, a 1-hour measurement was carried out. From 1-hour measurement, manual gas samples (using a syringe and vacuum Exetainer® vials) were also taken every fifteen minutes. These samples are then processed by gas chromatography (Agilent 8890 GC system with a PAL RSI 120 autosampler; CTC Analytics, Switzerland; Petersen et al., 2012) which served as a reference values to calibrate the methane sensors.

CO_2 sensor does not require calibration and the sensor output is in ppm. To calculate fluxes, firstly 3-point rolling average was applied to raw data to reduce the noise. Then, the last 2–3 minutes of each 5 minutes period was used for calculate flux using this formula:

$$F_{\text{dif}} = \frac{\Delta C_i}{\Delta t} * \frac{P * M}{R * T} * \frac{V_i}{A_i} * 1000$$

Where F_{diff} represents the diffusive flux ($\text{mg C m}^{-2}\cdot\text{h}^{-1}$), $\Delta C_i/\Delta t$ is the change in concentrations ($\text{ppm} \cdot 10^{-6}$), P is the atmospheric pressure (atm), R is the gas constant ($\text{L}\cdot\text{atm}/\text{mol}\cdot\text{K}$), T is the temperature (K), M is the molar mass of carbon (g mol^{-1}), V_i is the volume of the chamber (L), A_i is the area of the chamber. The value 1000 is for unit conversion from grams to milligrams.

For methane, since the sensor output is mV and highly affected by humidity, calibration is required before estimating fluxes. To calibrate methane sensor, it was exposed to different CH_4 concentrations in the lab (as an additional data to the field reference samples) at varied humidity levels and mV values were converted to ppm, following the methodology of Bastviken et al., (2020). Then for flux estimates, the same formula above used for methane diffusive flux estimation.

As with other emissions, fluxes are expressed in tonnes of CO_2 equivalent per hectare over 6 months. The values used for each pond correspond to the averages of the various measurements.

2.5. Primary producers

On six dates between April and July, 2-liter samples of water were taken. A sub-sample of the sampled water is also used to determine the chlorophyll a concentration in the water. A known volume is filtered through a Whatman GF/C filter, which is then incubated in a 90 % acetone solution for 24 hours. After centrifugation, absorbance values are taken at wavelengths of 630, 645, 663 and 750 nm with a Shimadzu UV/VIS spectrophotometer UV-2101 (Shimadzu Corporation, Kyoto, Japan). The concentration is then calculated using the formula of Parsons and Strickland (1963). It is used as a proxy for phytoplankton biomass within the pond. In parallel, the concentration of cyanobacteria was measured using a BBE AlgaeTorch directly in-situ on the same six dates. For both, it is the median value of the concentrations obtained or measured on the six dates and is expressed in $\mu\text{g}\cdot\text{l}^{-1}$.

Macrophyte coverage of ponds (expressed in %) was estimated visually once in summer, after having explored the entire surface of the pond with an inflatable boat. The most dominant species are *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Najas marina* and *N. minor* but also *Potamogeton nodosus*.

2.6. Management practices

All information concerning the various practices applied was gathered from the fish registers kept by the fish pond managers and collected by the local fish farming association. Fertilization is broken down into three categories: mineral nitrogen, organic manure, and no fertilization applied, respectively coded as 2, 1 and 0 in the analyses. All these data and the date of the last dry-out are available in Table 1. Nitrogen fertilization is applied at a rate of 40 liters of 39 % ammonia solution per hectare. Manure is applied at a rate of around 5–6 tonnes per hectare. Feed intake varies even more between managers, and can rise to over 250 kg/ha/year.

2.7. Statistical analysis

All sedimentation and emissions calculations, followed by the carbon balance and conversions into the various units, were carried out using R and R Studio software (R Development Core Team, 2024). All the figures were drawn using the ggplot2 package (Wickham, 2016) and its various graphical options. The comparison of emissions over the different seasons was carried out using a non-parametric Kruskal-Wallis test and pairwise comparisons.

In order to analyse the effects of primary producers and fish farming management practices (predictors X: macrophytes cover, chlorophyll a concentration, cyanobacteria concentration, fertilization, and time since the last dry-out) on the carbon balance variables (response Y: sedimentation/diffusion of CO_2 , CH_4 and N_2O , CH_4 ebullition), we first

carried out a Principal Component Analysis (PCA) with respect to Instrumental Variable (PCAiv using the ade4 package; Thioulouse et al., 2018). This method first applied multiple linear regressions of each carbon balance variable (each Y column) by the full explanatory variables dataset (X), and analysed the Y predictions table with a classical principal component analysis. This procedure exhibit how and how much primary producers and fish farming management practices (X) explained linearly the carbon balance variables (Y), accounting for all variables covariations. We reported the percentage of Y explained by X and computed a permutation test (Monte-Carlo) to evaluate the significance of this link. As with the first hypotheses, the results are presented visually using the ggplot2 package (Wickham, 2016).

All these statistical analyses were conducted with R and R Studio software (R Development Core Team, 2024).

3. Results

3.1. Carbon storage and emissions

Sediment traps (78 cm^2) yielded highly contrasting values from one pond to another, ranging from 3 to over 120 g of sediment collected over 3 months. The concentration of organic carbon in the sediment ranged from 10 to $32 \text{ g}\cdot\text{kg}^{-1}$. These two measurements give a carbon storage in sediments ranging from 450 kg (FR003) to over 24 tonnes of CO_2 equivalent per hectare for 6 months (FR011; Fig. 2, part 1). On average, this carbon storage amounts to around 12 tonnes per hectare over 6 months. It is therefore mainly linked to the quantity of sediment produced, rather than to its carbon concentration.

Emissions also vary widely, from pond to pond (Fig. 2, part 2), but also over seasons (Fig. 3). Overall, they range from 2.73 tonnes (FR008) to over 20 tonnes of CO_2 equivalent (FR004; Fig. 2, part 2). The average is 8.08 tonnes of CO_2 equivalent emitted into the atmosphere by the fish ponds in the form of CO_2 , CH_4 and N_2O . Methane ebullition account for the majority of these emissions for most of the fish ponds monitored (Fig. 2, part 2). On average, 5.59 tonnes (+/- 4.00) of CO_2 equivalent are emitted by ebullition, compared with 2.49 tonnes (+/- 2.42) by diffusion.

Diffusive fluxes are mainly composed of CO_2 fluxes: an average of 1.76 tonnes (+/- 2.13) per hectare over 6 months, compared with 0.81 tonnes (+/- 0.64) for methane emissions. For N_2O , it is mostly absorbed by fish ponds over the monitoring periods (81 kg (+/- 32) of CO_2 equivalent absorbed per hectare over 6 months, Fig. 3). Exchanges of this gas are minor compared to CO_2 and CH_4 , even taking into account its much greater greenhouse effect.

For all these fluxes, a significant season effect was observed (Kruskal-Wallis, $p < 0.05$, Fig. 3). CO_2 emissions are highest in spring (median value of $729 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ emitted), while in summer, fishponds become predominantly CO_2 sinks ($172 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ absorbed). Overall over the three seasons, four ponds are CO_2 sinks (diffusive fluxes of CO_2), while all the others emit more than they absorb.

Methane emissions by diffusion are higher in spring and summer (median values respectively 10.4 and $12.5 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, Fig. 3), and significantly lower in autumn ($4 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$). Ebullition processes are more pronounced in summer, with a median value of $90 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, compared with 36 mg and 40 mg respectively in spring and autumn.

Emissions measured during the dry year on 5 fish ponds ranged from 19.40 tonnes of CO_2 equivalent per hectare over 6 months to 27.20 tonnes. CO_2 emissions ranged from 8.89 to 13.07 tonnes for a mean value of 11.07 tonnes, while methane emissions varied from 7.98 to over 17 tonnes for a mean value of 12.82 tonnes. We therefore observe greater variability in methane emissions. The differences are significant between a pond emptied in early July and two others emptied in May.

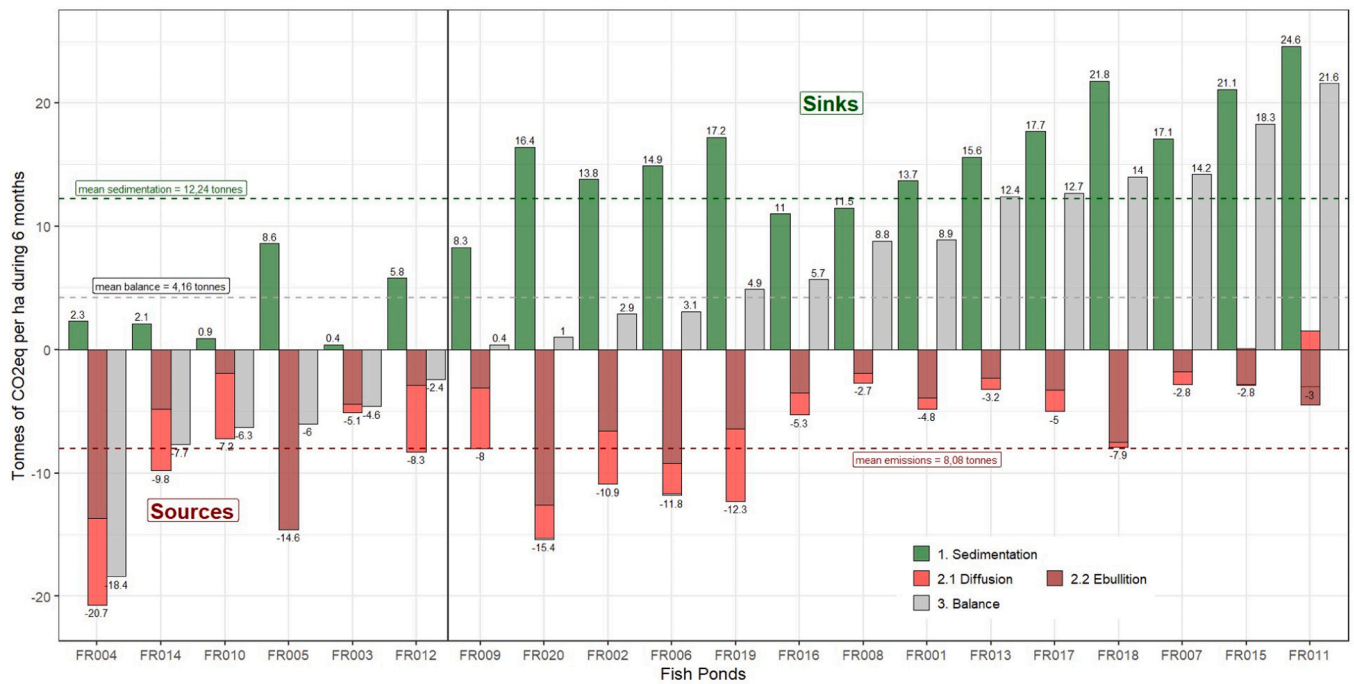


Fig. 2. Synthesis of sedimentation (green), emissions (diffusion and ebullition in red) and carbon balance (grey) for each pond monitored. Sedimentation, emissions and carbon balance are expressed in ton of CO₂ equivalent per hectare over 6 months. Ponds are classified according to their carbon balance: on the left are sources, emitting carbon into the atmosphere, and on the right are sinks, storing carbon. For emissions the indicated values correspond to the sum of the two types of fluxes (diffusion and ebullition).

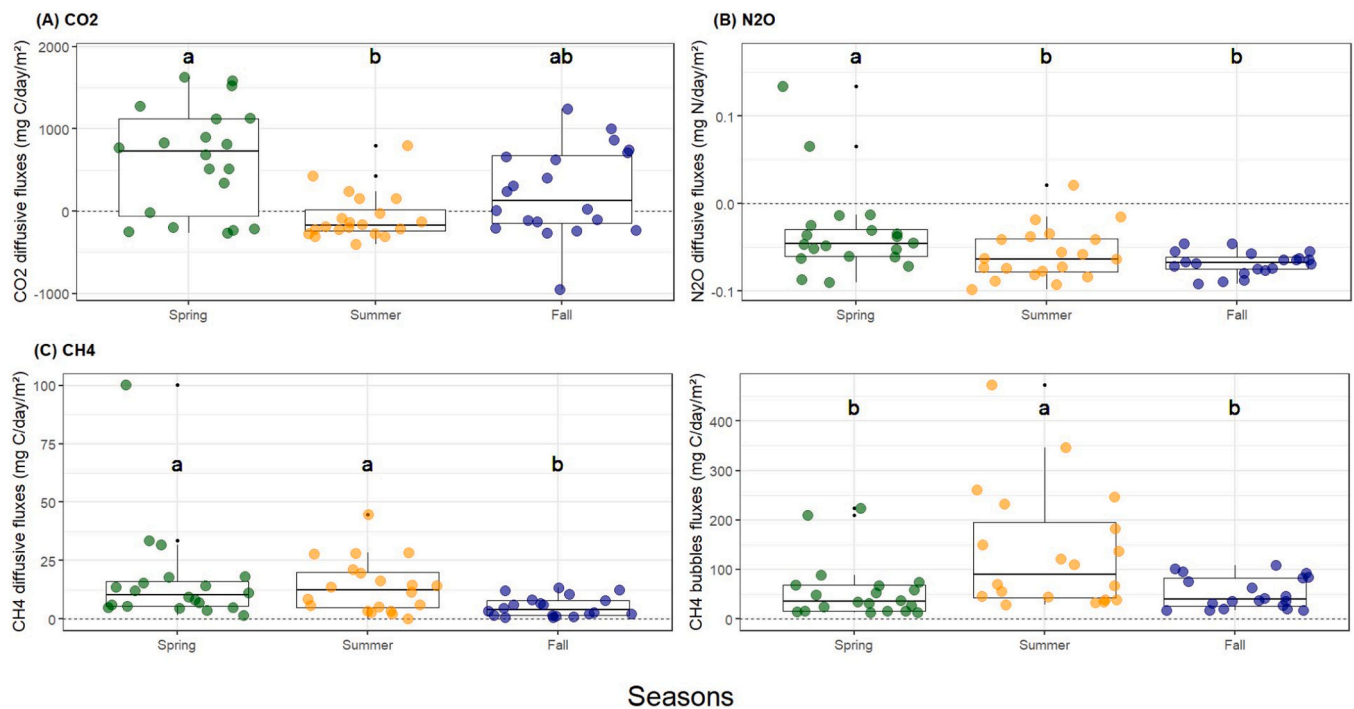


Fig. 3. Different types of emissions (CO₂, CH₄ and N₂O diffusion and CH₄ ebullition) measured on each pond over three seasons (spring, summer and autumn). Values are expressed in mg of C or N per m² per day. Groups not sharing a letter have a significantly different mean (pairwise comparisons). Positive values represent emissions.

3.2. Carbon balance per fish pond

The combination of storage and emissions measured on each fish pond gives similarly highly variable carbon balances (Fig. 2). FR004 is a source of CO₂ to the atmosphere at 18 tonnes per hectare during six

months, while FR011 stores over 21 tonnes (Fig. 2, part 3). On average, the fish ponds monitored are carbon sinks at 4.16 tonnes (+/- 10.00) of CO₂ equivalent per hectare over 6 months (median value at 4.01 tonnes of CO₂eq.ha⁻¹ during 6 months). Of the 20 fish ponds, 6 are sources and 14 are sinks.

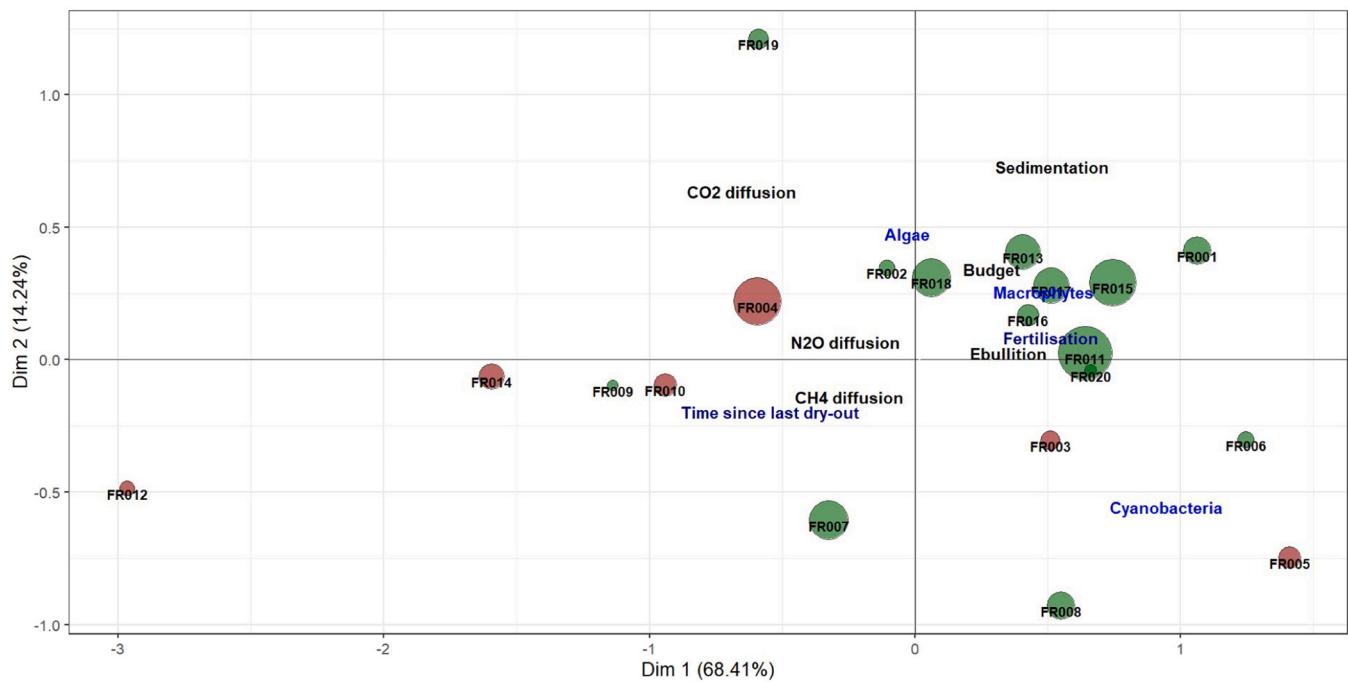


Fig. 4. PCAiv results on the first two dimensions. Each circle represents a fish pond, the size is proportional to the absolute value of the carbon balance, in red the sources ponds and in green the sinks ponds. The balance and its components are shown in black. Explanatory variables are shown in blue: macrophytes cover (%), chlorophyll a and cyanobacteria concentration ($\mu\text{g.l}^{-1}$), as well as time since the last dry-out and type of fertilization applied.

The 6 fish ponds that are sources of carbon are both those that store the least in their sediments and those that emit the most (FR004 for example; Fig. 2).

3.3. Carbon balance during a cycle of production

The results of the carbon balance by production year are presented in the table below (Table 2), according to an average 6 year management cycle with 5 years of water for fish production, followed by one year of dry-out. We note that, on average, the carbon balance is about 6.80 (+/- 4.91) tonnes of CO₂ equivalent stored for ponds in the first year of water and about 7.20 (+/- 8.40) in the second year. Negative balances, with emitting ponds, can be observed from the second year, which is not the case in the first one. In the fourth year, we observe a very high variability (SD of 21.29) in the balances, ranging from 18.40 tonnes emitted to 21.60 tonnes stored (the two extreme ponds, Fig. 2). Year 5 is characterized overall by carbon-emitting fish ponds (average of 2.80 +/- 3.35 tonnes emitted). Overall, over the five years of production, an average fish pond could store 19.24 tonnes of CO₂ equivalent per hectare.

Emissions during the dry year average 23.89 tonnes, giving an overall balance of 4.75 tonnes emitted. Over an entire production cycle,

Table 2
Carbon balances according to the different years of production and the dry year. Average 6-year production cycle: 5 years of water to produce fish, then one year of dry-out. Overall balances are based on average values for each year. Positive values correspond to carbon storage and negative ones to carbon emissions.

| Tonnes of CO ₂ eq/ha/6 months | Mean | Median | Min | Max | SD | Sum |
|--|--------|--------|--------|--------|-------|--------|
| Year 1 | 6.80 | 4.91 | 3.12 | 12.38 | 4.91 | 19.14 |
| Year 2 | 7.20 | 7.27 | -4.63 | 18.33 | 8.40 | |
| Year 3 | 2.12 | 2.86 | -7.68 | 12.66 | 8.93 | |
| Year 4 | 5.82 | 14.25 | -18.40 | 21.61 | 21.29 | |
| Year 5 | -2.79 | -2.44 | -6.30 | 0.36 | 3.35 | |
| Dry year | -23.89 | -25.35 | -19.43 | -27.19 | 3.16 | -23.89 |

fish ponds tended to be sources of carbon for the atmosphere.

3.4. Drivers: primary producers and management practices

The PCAiv analysis reveal that the total inertia of the carbon balance (100 % not showed in this study) was explained linearly at 26 % by the set of environmental pond variables (macrophytes cover, chlorophyll a and cyanobacteria concentrations) and management practices (fertilisation and years since last dry-out). This 26 % explained inertia was then decomposed on the first and second axis (68.41 % and 14.24 % of the explained inertia respectively). The first axis is mainly explained on the negative side by ponds at the end of their production cycle, which last dry-out was four to five years ago, with low macrophytes cover and chlorophyll a concentration (Fig. 3). These fish ponds are in response mainly sources of carbon for the atmosphere, with both low sedimentation rate and higher diffusion emissions. Conversely, on the positive side of this first dimension, we find fish ponds that are rather close to the last dry-out, characterized by a high presence of macrophytes and fertilized. These ponds turned into carbon sinks (except FR003 and FR005) with strong sedimentation rate and low emissions by diffusion. On the second dimension, the positive part showed fish ponds with highest algae concentration and lowest concentration of cyanobacteria. This result came from one pond (FR019) that tend to be carbon sink due to a high sedimentation rate balanced by a high CO₂ diffusion. The negative part is mostly characterized by fish ponds where cyanobacteria are well developed. This profile concerned five ponds characterized by low sedimentation and CO₂ emission rates. Their global carbon balance was highly heterogeneous, varying from sink (FR006, FR007, FR008) to source (FR005, FR003).

We did not detect a global significant link between explanatory and response variables (Monte-Carlo permutation test, p>0.45). The value of explained inertia in the PCAiv was therefore not higher than the randomised values after permutations between carbon balance data and environmental and management practices pond variables. These results probably came from our small sample size that strongly limit the statistical power, despite the congruent observed patterns.

The ebullition, a major driver of the global carbon balance, was not clearly explained by biotic and management variables. This link could be absent but also more complex.

4. Discussion

4.1. Sedimentation and carbon storage

Our results confirmed that fish ponds can store significant amounts of carbon through sedimentation, but with high inter-site variability and depending on the fish pond. These environments are therefore similar to lakes and ponds (Gregg et al., 2021; Sun et al., 2020; Boyd et al., 2010) with their variable capacity to store carbon through sedimentation. On average, sampled fish ponds store 12 tonnes of CO₂ equivalent per hectare over 6 months. On a shallow, eutrophic lake, Lin et al. (2022) measured storage of between 17.4 and 43.5 g of organic carbon per m² per year, equivalent to 640 kg - 1.6 tonnes of CO₂ equivalent stored per hectare. Sun et al. (2020) found values ranging from 1.1 to 25.6 g.m⁻².year⁻¹, with an average of 9.8 g.m⁻².year⁻¹ (360 kg CO₂ equivalent per hectare) for a large, shallow lake in the Yangtze River basin. Holgerson et al. (2023) measured this storage on temperate ponds, with results ranging from 38.3 g.m⁻².year⁻¹ to 113.6 g.m⁻².year⁻¹, with an average of 67 g.m⁻².year⁻¹ (2.5 tonnes of CO₂ equivalent per ha). Taylor et al. (2019) have measured carbon burial rates of 5.2 tonnes of CO₂ equivalent per ha (min-max 2.9 - 9.1 tonnes) in small ponds from UK. All these values remain well below the average observed in fish ponds. The results obtained on ponds (Taylor et al., 2019; Holgerson et al., 2023) and the high values of some eutrophic lakes (Lin et al., 2022) are close to the values obtained on some fish ponds. In another type of aquatic ecosystem, Villa and Bernal (2018) have measured, for example, carbon storage in wetlands ranging from one tonne to over 6 tonnes of CO₂ equivalent per hectare per year.

In this study, we chose to express storage (and emissions) in terms of a 6-month period, rather than a year, as has been done in other articles (Holgerson et al., 2023; Lin et al., 2022; Sun et al., 2020). This choice is based on the fact that primary producers and therefore primary production are present in ponds mainly during spring and summer (April to September). The related processes are therefore mainly effective during this period. Our measurements were carried out mainly during the summer, when primary production is at its highest, and therefore sedimentation is also most likely. It may therefore be slightly overestimated over 6 months. Furthermore, the fish ponds are emptied every year in order to harvest the fish. Fish ponds are dry for a few days to a few weeks, and in the absence of water, sedimentation cannot logically take place. The sedimentation value obtained over 6 months therefore are comparable across the different ponds. Nevertheless, sedimentation is not completely nil in the other months of the year (October to March) but in the absence of washing in of allochthonous materials are likely to be much lower than in the summer, which might in part explain the higher sediment rates recorded here.

These higher rates of C burial might be explained by several parameters. Generally, fish ponds are eutrophic or even hyper-eutrophic environments with high levels of primary productivity. These levels of primary production are deliberately kept high by management practices to encourage fish production. The addition of organic matter, such as manure, or the use of nitrogen fertilization helps stimulate primary production and thus increase sedimentation rates. In addition, the presence of fish increases the amount of organic matter deposited on the sediment surface (Vanni, 2002). Sedimentation dynamics therefore appear to be stronger in fish ponds than in natural environments, even eutrophic ones. Primary production (Rutegwa et al., 2019b,a), inputs of allochthonous matter and land use in the area around ponds are parameters that can influence sedimentation and hence carbon storage (Lin et al., 2022), but still few studies have analysed the effects of primary producers and how they enhance carbon fixation and storage in ponds (Brothers et al., 2013; Zimmer et al., 2016; Hilt et al., 2017).

Conversely, some of the organic matter present in the traps may have been decomposed or even mineralized over the 3-month period.

The results obtained from the sediment traps set up in each pond also showed considerable intra-site variability. They are consistent with the spatial heterogeneity of sedimentation already mentioned in Lin et al. (2022). Sediment accumulation is generally greater in areas where macrophytes are well developed (Barko and James, 1998). This variability justifies the use of a median value in our calculations and analyses. The presence of benthivorous fish such as carp and tench in fish ponds can also contribute to sediment resuspension and this might influence the results obtained in the traps. Nevertheless, our analyses showed no effect of benthic fish density on the results obtained.

4.2. Emissions from fish ponds

Our results showed that ponds have emissions with an average around 8 tonnes of CO₂ equivalent per hectare over 6 months. However, there was considerable variability, inter and intra sites. This variability was also very different according to the season and is already well known in the literature on small lakes and ponds (Ray and Holgerson, 2023). CO₂ emissions by diffusion were highest in spring, while ponds tended to be sinks in summer. These significant differences are undoubtedly due to the activities of primary producers, with photosynthesis, capturing CO₂ from the water and the atmosphere to a greater extent in spring than in other seasons (Sun et al., 2021). Finley et al. (2019) and Trolle et al. (2012) showed that most CO₂ emissions in lakes take place in spring, and the dynamics are likely similar for fish ponds. Most of the water in the fish ponds comes from rainfall, so the CO₂ concentration of the water arriving in the ponds is not influenced by the local geology or soils. The CO₂ concentrations and fluxes observed are therefore linked to the pond's own functioning. Methane diffusion was highest in spring and summer, and lowest in autumn. Emissions by ebullition were very high in summer, in line with the generally warmer, more productive period which may lead to anoxic conditions during this period. Warmer water temperatures, combined with a lack of oxygen, favour these emissions as already been observed by Peacock et al. (2021).

In this study, greenhouse gas emissions by diffusion were measured only during the day, unlike those by ebullition, which were measured over a 7-day period (including days and nights). The respiration of primary producers during the night results in the production of CO₂ (Oertli and Frossard, 2013), which can boost emissions. These nocturnal processes would be interesting to integrate to complete the carbon balances obtained. Other studies (David et al., 2021; Flickinger et al., 2020) have shown that, by integrating night-time measurements, ponds dedicated to fish production can nevertheless absorb more CO₂ than they emit. Moreover, CO₂ emissions from diffusion represent a small percentage of overall emissions compared with CH₄ emissions. We can therefore assume that the overall results obtained will be little affected by these night-time measurements.

For N₂O, apart from three measurements, fish ponds were under saturated and therefore captured more of this gas than they emit. Webb et al. (2019) have also shown that ponds could be sinks of N₂O. Among the three points that were sources, two were measured in spring, most certainly after fertilization. The addition of mineral nitrogen as fertilization directly into the fish pond may contribute to these N₂O emissions. It's also important to point out here that diffusion emissions were only measured on three dates. Higher frequency measurements would be required to integrate variability and obtain a better estimate of fluxes as there may be 'hot moments' of emissions.

Overall, methane emissions by ebullition account for an average of 5.6 tonnes of CO₂ equivalent, compared with only 2.5 tonnes for emissions by diffusion (1.7 tonnes for CO₂, 0.8 tonnes for CH₄ and 0.08 tonnes for N₂O). We can therefore see that methane emissions are in the majority compared with the other greenhouse gases produced by ponds.

These results are consistent with other studies already showing the

predominant role of this gas (Dong et al., 2023; Waldemer and Koschorreck, 2023; Zhang et al., 2022; DelSontro et al., 2018; Deemer et al., 2016). Despite the wide variability observed between different fish ponds, methane still accounts for the majority of emissions. Despite its strong greenhouse effect, N₂O plays a relatively minor role in the overall emissions measured on fish ponds. This type of emission (N₂O diffusion) can be very diffuse and short-lived, making it difficult to estimate. Measurements following fertilization processes could be relevant to a better understanding of the effects and impacts of this practice on nitrogen losses in the form of N₂O.

Combining methane emissions from diffusion and ebullition, fish ponds emit an average of around 6.4 tonnes of CO₂ equivalent per hectare over 6 months. These emissions are lower than the 8.2 tonnes measured in ponds for agriculture in Sweden (Stadmark and Leonardson, 2005), the 9 tonnes recorded in wet stormwater basins in the United States (McPhillips and Walter, 2015) and well below what has been measured in tropical ponds: 29 tonnes in ponds from India (Panneer Selvam et al., 2014) and from 11 to over 46 tonnes in Australia (Grinham et al., 2018; Ollivier et al., 2019; Ollivier et al., 2019). Nevertheless, these emissions are higher than those reported by Peacock et al. (2019) on urban ponds in Sweden (around 3.1 tonnes of CO₂ equivalent per hectare per year). Methane emissions on nine ponds and seven ditches ranged from 28 kg to over 12 tonnes of CO₂ equivalent (Peacock et al., 2021). Rutegwa et al. (2019a) measured diffusive methane emissions of between 0.4 and 0.6 tonnes of CO₂ equivalent per hectare for 6 months on extensive carp ponds in the Czech Republic. These values are quite similar to those measured in the Dombes fish ponds. These methane diffusion emissions can vary significantly, from day to day, from week to week and from one year to the next (Yang et al., 2024). Monitoring at high frequency over several years would therefore be relevant to obtain a better estimate of emissions from fish ponds.

For CO₂ emissions, Peacock et al. (2019) measured 2.7 tonnes, corresponding to higher values than those we observed. And this is also the case compared to the 10.9 tonnes emitted by tropical ponds in India (Panneer Selvam et al., 2014) and the 4 tonnes emitted by Australian ponds (Ollivier et al., 2019). Conversely, CO₂ emissions from fish ponds in the Dombes region are higher than the 180 kg of CO₂ equivalent emitted by Swedish urban ponds (Natchimuthu et al., 2014).

For these two gases, the emissions measured on the twenty Dombes fish ponds seem consistent with the great variability of emissions measured on other types of ponds or aquatic environments.

With regard to emissions measured during the dry year, variations between fish ponds are less marked. With the exception of one pond, methane accounts for more than half of total emissions. This emission profile seems logical in view of the period during which the measurements were taken, that being just after drainage, and the sediments were still wet. These anoxic conditions are conducive to methane emissions. This hypothesis seems to be confirmed by the measurement points near the fishery and residual water (as the wettest part of the pond), which showed higher fluxes than in other areas of the pond. These trends have also been observed in other environments, such as rice paddies. Dewatering, by promoting aerobic conditions, limits these methane emissions (Hwang et al., 2020). In this study, we estimated emissions during the dry-out based on a single measurement date. We can assume that the emissions profile varies as the pond gradually dries out. It is therefore very likely that methane emissions, which have a greater greenhouse effect, and also CO₂ are overestimated with this single date measurement.

4.3. Carbon balance

The high variability in storage and emissions also leads to very high variability in the carbon balances of individual fish ponds. Nevertheless, on average, they appear to be carbon sinks, at the 6 month scale, thus validating the first hypothesis. The processes at work in the winter might change the balance and need further investigation. In comparison, in

France, forests store an average of 5.3 tonnes of CO₂eq per hectare per year (EFESE, 2019). Fish ponds therefore have the capacity to store almost as much as a forest. In mainland France, a meadow would store between 0.18 and 2 tonnes of CO₂eq per hectare per year (Sousanna et al., 2010). In terms of agricultural landscapes, fish ponds can therefore play an important role in carbon storage. In the Dombes region, ponds represent around 8000 ha of water, which could correspond to a storage potential of almost 100,000 tonnes of CO₂ equivalent per year.

However, these trends need to be qualified by the effects of the dry year, during which the ponds seem to release at least as much as they were able to store during the wet years. As already mentioned above, this requires more detailed monitoring of emissions over the dry year, in order to gain a better understanding of its role in the overall balance of the production cycle. Here we find the dual role that ponds can have, with the potential to be both carbon sources and sinks (Prairie et al., 2018).

4.4. Fish management practices as levers for action?

Drying out therefore appears to be a practice that promotes carbon emissions into the atmosphere, tending to make ponds sources during this period. However, multivariate analyses show that it also plays a role in turning ponds into sinks during the first production years. In fact, it has been shown that drying out promotes the recolonization of macrophytes when the ponds are re-watered (Fontanilles et al., 2023; Girard et al., 2023). In the subsequent years, the ecosystem generally becomes dominated by phytoplankton, then the abundance of primary producers and therefore primary production drops off at the end of the cycle (Girard et al., 2023). The second year is the one with the best balance between the two, which is favourable for biodiversity and production (Girard et al., 2023). Our results show that this second year includes the fish ponds with the highest carbon storage and carbon balance values. The models tested also show these elements. Macrophytes cover decreases with time since the last dry-out, as does chlorophyll a concentration. This reduction in the quantity of algae seems less pronounced, but this may be due to the fact that the relationship is not linear. We also note the key role played by macrophytes, which promote sedimentation and hence storage, reduce CO₂ diffusion and, conversely, appear to promote methane ebullition. With regard to the latter, we can hypothesize that the decomposition of these organisms favours anoxic conditions, conducive to this type of emission. This result runs counter to those highlighted by Davidson et al. (2018). The key role of macrophytes in controlling CO₂ and CH₄ emissions had already been demonstrated by Audet et al. (2017). Phytoplankton show the same results, but to a lesser extent. Lapiere et al. (2017) had shown that the variability of CO₂ emissions during the summer was partly explained by chlorophyll a concentration. Eutrophication and algal blooms generally reduce CO₂ emissions but increase methane emissions (Bartosiewicz et al., 2015, 2016; Davidson et al., 2015; Huttunen et al., 2003; Tranvik et al., 2009; Zhang et al., 2022). Overall, our results are in line with those of Rutegwa et al. (2019a,b), who mentioned primary production as a major source of organic carbon in extensive or semi-extensive fish ponds.

We were unable to identify any significant role for primary producers in methane diffusion. These results do not concur with those of Davidson et al. (2015), who showed that higher macrophytes abundance was associated with lower methane emissions by diffusion.

In addition to drying-out, fertilization is the second practice that seems to have the greatest impact on observed carbon balances. Its aim is to stimulate primary production, but also to limit the risk of cyanobacteria development by rebalancing the N/P ratio. This stimulation of primary production promotes carbon storage. Our results show that when fertilization is applied in the form of mineral nitrogen, the absolute value of the carbon balance is on average significantly higher than for the other modalities (median value of 12.5 tonnes of CO₂ equivalent against around 5 tonnes for organic manure or no fertilization). Fertilization can therefore both contribute to a better storage and at the same

time promote emissions, depending on the conditions at the time of application.

Contrary to our expectations, our results showed no significant effect of fish density in the pond on either storage or emissions. Waldemer and Koschorreck (2023) showed that feeding areas are hotspots for methane and carbon dioxide emissions. They also hypothesized that ebullition was higher in the morning due to benthic fish activity. Furthermore, Zhang et al. (2022) showed that CO₂ and CH₄ emissions per diffusion were influenced by the amount of feed not consumed. Rutegwa et al. (2019a) hypothesized a decrease in methane production in ponds producing benthic fish. Sediment disturbance by carp maintains aerobic conditions, limiting methane production. Generally speaking, the effect of fish and stocking composition on GHG emissions remains little studied and need to be more investigated in the future, with high frequency measurements.

Despite the relatively clear trends in the effect of management practices, the PCAiv is based on 20 fish ponds only. This small statistical size is a limitation. However, PCAiv results seem in line with previous knowledge on pond ecology and carbon sequestration and emissions. Our results of PCAiv may therefore be more considered as an encouraging exploration than a true validation of process driving pond carbon balance. Nevertheless, the results obtained using macrophytes cover as a proxy for biomass are interesting. Even by approximating the primary production of the ponds, we can see the key role played by macrophytes in the ecosystem, its functioning and consequently in carbon balances.

Our results show that, despite high variability in storage and GHG emissions, fish ponds appear to be carbon sinks on average, without including the year where they are dried out. The majority of pond fish farming systems in Europe do not include this drying-out, as is the case in the Dombes region. As we have seen, this practice promotes carbon storage by stimulating primary productivity in the early years of the cycle, but also generates emissions when it is applied. The balances achieved therefore seem to be strongly influenced by this practice. It would therefore be interesting to study the balances on ponds left in water over longer time steps, in other systems where this practice is not applied, as well as studying other beneficial effects such as establishment of aquatic plants in species-poor or low plant cover ponds, or other ecosystem services such as biodiversity conservation.

Fish ponds can therefore play an important role in agricultural landscapes. The role and effects of management practices have yet to be studied. Nevertheless, by influencing the dynamics of primary production, drying-out and fertilization, applied in the right situations and conditions, can be levers for turning fish ponds into carbon sinks. Given this high temporal variability, and the dual role of the practice drying-out, it is all the more important to integrate monitoring over several years and production cycles in order to gain a better understanding of the role of fish ponds and the practices applied in carbon storage and emissions.

CRedit authorship contribution statement

Tuba BUCAK: Writing – review & editing, Validation, Software, Resources, Methodology, Investigation, Data curation. **Thomas A. DAVIDSON:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Vincent TOLON:** Writing – review & editing, Visualization, Validation, Software, Methodology, Formal analysis. **Léo GIRARD:** Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Joël ROBIN:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Soraya ROUIFED:** Writing – review & editing, Investigation, Conceptualization. **Alexander WEZEL:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 869296 – The PONDERFUL Project

We highly acknowledge the fish pond owners and managers allowing to sample their fish ponds. We further thank Mathieu GUERIN, Thomas LHUILLERY and Cyprien DUPONT for their help in data collection. Thanks also to Dennis HANSEN for all the sample analyses in Aarhus University.

Data Availability

Data will be made available on request.

References

- 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. *Glob. Biogeochem. Cycles* 26 (2), 2011GB004237 (Jun).
- AFNOR. ISO 10694 - Qualité du sol - Dosage du carbone organique et du carbone total après combustion sèche (analyse élémentaire). 1995.
- AFNOR. NF X31-160 - Qualité des sols - Détermination du phosphore soluble dans une solution à 20 g.l⁻¹ d'acide citrique monohydraté - Méthode Dyer. 1999.
- Archer, D., 2011. The Global Carbon Cycle [Internet]. Princeton University Press [cited 2024 Feb 1]. Available from: <https://www.degruyter.com/document/doi/10.1515/9781400837076/html>.
- Aubin, J., Robin, J., Wezel, A., Thomas, M., 2017. Agroecological management in fish pond systems. *Agroecological Practices for Sustainable Agriculture: Principles, Applications, and Making the Transition*, 1ère édition. World Scientific Europe Ltd.
- Audet, J., Carstensen, M.V., Hoffmann, C.C., Lavaux, L., Thiemer, K., Davidson, T.A., 2020. Greenhouse gas emissions from urban ponds in Denmark. *Inland Waters* 10 (3), 373–385. Jul 2.
- Audet, J., Neif, E.M., Cao, Y., Hoffmann, C.C., Lauridsen, T.L., Larsen, S.E., et al., 2017. Heat-wave effects on greenhouse gas emissions from shallow lake mesocosms. *Freshw. Biol.* 62 (7), 1130–1142 (Jul).
- Avocat, C., 1975. La Dombes, milieu naturel ou milieu en équilibre ? Introduction à une éco-géographie de l'espace dombiste. *geoca* 50 (1), 35–58.
- Ayub, M., Boyd, C.E., Teichert-Coddington, D., 1993. Effects of Urea Application, Aeration, and Drying on Total Carbon Concentrations in Pond Bottom Soils. *Progress. Fish. -Cult.* 55 (3), 210–213 (Jul).
- Barko J.W., James W.F. Effects of Submerged Aquatic Macrophytes on Nutrient Dynamics, Sedimentation, and Resuspension. In: Jeppesen E, Sondergaard M, Sondergaard M, Christoffersen K, editors. *The Structuring Role of Submerged Macrophytes in Lakes* [Internet]. New York, NY: Springer New York; 1998 [cited 2024 Feb 27]. p. 197–214. (Caldwell MM, Heldmaier G, Lange OL, Mooney HA, Schulze ED, Sommer U, editors. *Ecological Studies*; vol. 131). Available from: http://link.springer.com/10.1007/978-1-4612-0695-8_10.
- Bartosiewicz, M., Laurion, I., MacIntyre, S., 2015. Greenhouse gas emission and storage in a small shallow lake. *Hydrobiologia* 757 (1), 101–115 (Sep).
- Bartosiewicz, M., Laurion, I., Clayer, F., Maranger, R., 2016. Heat-wave effects on oxygen, nutrients, and phytoplankton can alter global warming potential of gases emitted from a small shallow lake. *Environ. Sci. Technol.* 50 (12), 6267–6275. Jun 21.
- Bastviken, D., Nygren, J., Schenk, J., Parellada Massana, R., Duc, N.T., 2020. Technical note: Facilitating the use of low-cost methane (CH₄) sensors in flux chambers – calibration, data processing, and an open-source make-it-yourself logger. *Biogeosciences* 17 (13), 3659–3667. Jul 14.
- Bastviken, D., Sundgren, I., Natchimuthu, S., Reyier, H., Gålfalk, M., 2015. Technical Note: Cost-efficient approaches to measure carbon dioxide (CO₂) fluxes and concentrations in terrestrial and aquatic environments using mini loggers. *Biogeosciences* 12 (12), 3849–3859. Jun 24.
- Bastviken, D., Tranvik, L.J., Downing, J.A., Crill, P.M., Enrich-Prast, A., 2011. Freshwater methane emissions offset the continental carbon sink. *Science* 331 (6013), Jan 7.
- Battin, T.J., Kaplan, L.A., Findlay, S., Hopkinson, C.S., Marti, E., Packman, A.I., et al., 2008. Biophysical controls on organic carbon fluxes in fluvial networks. *Nat. Geosci.* 1 (2), 95–100 (Feb).
- Battin, T.J., Luyssaert, S., Kaplan, L.A., Aufdenkampe, A.K., Richter, A., Tranvik, L.J., 2009. The boundless carbon cycle. *Nat. Geosci.* 2 (9), 598–600 (Sep).
- Bernard A., Lebreton P. Les oiseaux de la Dombes: une mise à jour. 2007;
- Biggs, J., Corfield, A., Walker, D., Whitfield, M., Williams, P., 1994. *N. Approaches Manag. ponds* 15.

- Borges, A.V., Abril, G., Darchambeau, F., Teodoru, C.R., Deborde, J., Vidal, L.O., et al., 2015. Divergent biophysical controls of aquatic CO₂ and CH₄ in the World's two largest rivers. *Sci. Rep.* 5 (1), 15614. Oct 23.
- 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. *Environ. Pollut.* 158 (8), 2537–2540 (Aug).
- Brothers, S.M., Hilt, S., Meyer, S., Köhler, J., 2013. Plant community structure determines primary productivity in shallow, eutrophic lakes. *Freshw. Biol.* 58 (11), 2264–2276 (Nov).
- Céréghino, R., Biggs, J., Oertli, B., Declerck, S., 2007. The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. In: Oertli, B., Céréghino, R., Biggs, J., Declerck, S., Hull, A., Miracle, M.R. (Eds.), *Pond Conservation in Europe* [Internet]. Springer Netherlands, Dordrecht [cited 2022 Nov 29]. p. 1–6. Available from: http://link.springer.com/10.1007/978-90-481-9088-1_1.
- Chen, J., Jin, Q., Shi, R., Xu, X., Zhao, S., Ji, M., et al., 2020. Synchronous nutrient controlled-release of greenhouse gases during mineralization of sediments from different lakes. *Bull. Environ. Contam. Toxicol.* 105 (1), 76–85 (Jul).
- Cole, J.J., Caraco, N.F., Kling, G.W., Kratz, T.K., 1994. Carbon Dioxide Supersaturation in the Surface Waters of Lakes. *Science* 265 (5178), 1568–1570. Sep 9.
- Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., et al., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10 (1), 172–185 (Feb).
- David, F.S., Proença, D.C., Flickinger, D.L., Wolff Bueno, G., Valenti, W.C., 2021. Carbon budget in integrated aquaculture systems with Nile tilapia (*Oreochromis niloticus*) and Amazon river prawn (*Macrobrachium amazonicum*). *Aquac. Res.* 52 (11), 5155–5167 (Nov).
- Davidson, T.A., Audet, J., Jeppesen, E., Landkildehus, F., Lauridsen, T.L., Søndergaard, M., et al., 2018. Synergy between nutrients and warming enhances methane ebullition from experimental lakes. *Nat. Clim. Change* 8 (2), 156–160 (Feb).
- Davidson, T.A., Audet, J., Svenning, J.C., Lauridsen, T.L., Søndergaard, M., Landkildehus, F., et al., 2015. Eutrophication effects on greenhouse gas fluxes from shallow-lake mesocosms override those of climate warming. *Glob. Change Biol.* 21 (12), 4449–4463 (Dec).
- Davidson, T.A., Søndergaard, M., Audet, J., Levi, E., Esposito, C., Bucak, T., et al., 2024. Temporary stratification promotes large greenhouse gas emissions in a shallow eutrophic lake. *Biogeosciences* 21 (1), 93–107. Jan 3.
- Deacon, E.L., 1981. Sea-air gas transfer: The wind speed dependence. *Bound.-Layer Meteor.* 21 (1), 31–37 (Aug).
- Deemer, B.R., Harrison, J.A., Li, S., Beaulieu, J.J., DelSontro, T., Barros, N., et al., 2016. Greenhouse Gas Emissions from Reservoir Water Surfaces: A New Global Synthesis. *BioScience* 66 (11), 949–964. Nov 1.
- DelSontro, T., Beaulieu, J.J., Downing, J.A., 2018. Greenhouse gas emissions from lakes and impoundments: Upscaling in the face of global change. *Limnol. Oceanogr. Lett.* 3 (3), 64–75 (Jun).
- Dillon, P.J., Molot, L.A., 1997. Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments. *Water Resour. Res.* 33 (11), 2591–2600 (Nov).
- Dong, B., Xi, Y., Cui, Y., Peng, S., 2023. Quantifying Methane Emissions from Aquaculture Ponds in China. *Environ. Sci. Technol.* 57 (4), 1576–1583. Jan 31.
- Downing, J.A., 2010. Emerging global role of small lakes and ponds. *Little things Mean. a Lot. Limn. ética.* 29 (1).
- Duarte, C.M., Prairie, Y.T., 2005. Prevalence of Heterotrophy and Atmospheric CO₂ Emissions from Aquatic Ecosystems. *Ecosystems* 8 (7), 862–870 (Nov).
- EFSE. La séquestration de carbone par les écosystèmes en France. 2019 p. 102.
- Esposito, C., Nijman, T.P.A., Veraart, A.J., Audet, J., Levi, E.E., Lauridsen, T.L., et al., 2023. Activity and abundance of methane-oxidizing bacteria on plants in experimental lakes subjected to different nutrient and warming treatments. *Aquat. Bot.* 185, 103610 (Mar).
- Finlay, K., Vogt, R.J., Simpson, G.L., Leavitt, P.R., 2019. Seasonality of pCO₂ in a hard-water lake of the northern Great Plains: The legacy effects of climate and limnological conditions over 36 years. *Limnol. Oceanogr.* [Internet] 64 (S1). Jan [cited 2023 Sep 11];
- Flickinger, D.L., Costa, G.A., Dantas, D.P., Proença, D.C., David, F.S., Durbin, R.M., et al., 2020. The budget of carbon in the farming of the Amazon river prawn and tambaqui fish in earthen pond monoculture and integrated multitrophic systems. *Aquac. Rep.* 17, 100340 (Jul).
- Fontanilles A., Robin J., Rouifed S., Guerin M., Vanacker M., Arthaud F., et al. Disturbance and resilience of aquatic plant communities in fish ponds after temporary dry periods. 2023;
- Fusé, V.S., Priano, M.E., Williams, K.E., Gere, J.L., Guzmán, S.A., Gratton, R., et al., 2016. Temporal variation in methane emissions in a shallow lake at a southern mid latitude during high and low rainfall periods. *Environ. Monit. Assess.* 188 (10), 590 (Oct).
- Girard, L., Wezel, A., Robin, J., 2023. Drying out fish ponds, for an entire growth season, as an agroecological practice: maintaining primary producers for fish production and biodiversity conservation. *Open Res Eur.* 3, 125. Aug 18.
- Gregg, R., Elias, J., Alonso, I., Crosher, I., Muto, P., Morecroft, M., 2021. Carbon storage and sequestration by habitat: a review of the evidence, (second edition). 2nd ed. Natural England, UK.
- Grinham, A., Albert, S., Deering, N., Dunbabin, M., Bastviken, D., Sherman, B., et al., 2018. The importance of small artificial water bodies as sources of methane emissions in Queensland, Australia. *Hydrol. Earth Syst. Sci.* 22 (10), 5281–5298. Oct 15.
- Hilt, S., Brothers, S., Jeppesen, E., Veraart, A.J., Kosten, S., 2017. Translating Regime Shifts in Shallow Lakes into Changes in Ecosystem Functions and Services. *BioScience* 67 (10), 928–936. Oct 1.
- Holgerson, M.A., Ray, N.E., Russ, C., 2021. High rates of carbon burial linked to autochthonous production in artificial ponds. *Limnol. Oceanogr. Lett.* 16(10). Aug 18.
- Holgerson, M.A., Raymond, P.A., 2016. Large contribution to inland water CO₂ and CH₄ emissions from very small ponds. *Nat. Geosci.* 9 (3), 222–226 (Mar).
- Horvath, L., Tamas, G., Seagrave, C., 2002. *Carp and Pond Fish Culture*, Seconde Edition. John Wiley & Sons.
- Huttunen, J.T., Alm, J., Liikanen, A., Juutinen, S., Larmola, T., Hammar, T., et al., 2003. Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. *Chemosphere* 52 (3), 609–621 (Jul).
- Hwang, Y., Ryu, Y., Huang, Y., Kim, J., Iwata, H., Kang, M., 2020. Comprehensive assessments of carbon dynamics in an intermittently-irrigated rice paddy. *Agricultural and Forest Meteorology* 285, 107933. <https://doi.org/10.1016/j.agrformet.2020.107933>.
- IPCC. Synthesis report of the IPCC sixth assessment report. 2023.
- Kortelainen, P., Pajunen, H., Rantakari, M., Saarnisto, M., 2004. A large carbon pool and small sink in boreal Holocene lake sediments. *Glob. Change Biol.* 10 (10), 1648–1653 (Oct).
- Lapierre, J., Seekell, D.A., Filstrup, C.T., Collins, S.M., Emi Fergus, C., Soranno, P.A., et al., 2017. Continental-scale variation in controls of summer CO₂ in United States lakes. *JGR Biogeosciences* 122 (4), 875–885 (Apr).
- Lin, Q., Liu, E., Zhang, E., Bindler, R., Nath, B., Zhang, K., et al., 2022. Spatial variation of organic carbon sequestration in large lakes and implications for carbon stock quantification. *CATENA* 208, 105768 (Jan).
- McPhillips, L., Walter, M.T., 2015. Hydrologic conditions drive denitrification and greenhouse gas emissions in stormwater detention basins. *Ecol. Eng.* 85, 67–75 (Dec).
- Natchimuthu, S., Panneer Selvam, B., Bastviken, D., 2014. Influence of weather variables on methane and carbon dioxide flux from a shallow pond. *Biogeochemistry* 119 (1–3), 403–413 (Jun).
- Oertli, B., Biggs, J., Céréghino, R., Grillas, P., Joly, P., Lachavanne, J.B., 2005. Conservation and monitoring of pond biodiversity: introduction. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 15 (6), 535–540 (Nov).
- Oertli, B., Frossard, P.A., 2013. *Mares et étangs: Ecologie, conservation, gestion, valorisation*. PPUR Presses polytechniques.
- Oliveira Junior, E.S., Temmink, R.J.M., Buhler, B.F., Souza, R.M., Resende, N., Spanings, T., et al., 2019. Benthivorous fish bioturbation reduces methane emissions, but increases total greenhouse gas emissions. *Freshw. Biol.* 64 (1), 197–207 (Jan).
- Ollivier, Q.R., Maher, D.T., Pitfield, C., Macreadie, P.I., 2019. Punching above their weight: Large release of greenhouse gases from small agricultural dams. *Glob. Change Biol.* 25 (2), 721–732 (Feb).
- Panneer Selvam, 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. *Glob. Change Biol.* 20 (11), 3397–3407 (Nov).
- Parsons, T.T., Strickland, J.D.H., 1963. Discussion of Spectrophotometric Determination of Marine-Plant Pigments, with Revised Equations for Ascertaining Chlorophylls and Carotenoids. *J. Mar. Res.* 21, 155–163.
- Peacock, M., Audet, J., Bastviken, D., Cook, S., Evans, C.D., Grinham, A., et al., 2021. Small artificial waterbodies are widespread and persistent emitters of methane and carbon dioxide. *Glob. Change Biol.* 27 (20), 5109–5123 (Oct).
- Peacock, M., Audet, J., Jordan, S., Smeds, J., Wallin, M.B., 2019. Greenhouse gas emissions from urban ponds are driven by nutrient status and hydrology. *Ecosphere* 10 (3), e02643 (Mar).
- Petersen, S.O., Hoffmann, C.C., Schäfer, C.M., Blicher-Mathiesen, G., Elsgaard, L., Kristensen, K., et al., 2012. Annual emissions of CH₄ and N₂O, and ecosystem respiration, from eight organic soils in Western Denmark managed by agriculture. *Biogeosciences* 9 (1), 403–422. Jan 23.
- Praetzel L.S.E., Plenter N., Schilling S., Schmiedeskamp M., Broll G., Knorr K.H. Organic matter and sediment properties determine in-lake variability of sediment CO₂ and CH₄ production and emissions of a small and shallow lake [Internet]. *Biogeochemistry: Greenhouse Gases*; 2019 Aug. Available from: <https://bg.copernicus.org/preprints/bg-2019-284/bg-2019-284.pdf>.
- Prairie, Y.T., Alm, J., Beaulieu, J., Barros, N., Battin, T., Cole, J., et al., 2018. Greenhouse Gas Emissions from Freshwater Reservoirs: What Does the Atmosphere See? *Ecosystems* 21 (5), 1058–1071 (Aug).
- Rabaey, J.S., Holgerson, M.A., Richardson, D.C., Andersen, M.R., Bansal, S., Bortolotti, L. E., 2024. Freshwater Biogeochemical Hotspots: High Primary Production and Ecosystem Respiration in Shallow Waterbodies. *Geophys. Res. Lett.* 51 (15). <https://doi.org/10.1029/2023GL106689>.
- Rantakari, M., Kortelainen, P., 2005. Interannual variation and climatic regulation of the CO₂ emission from large boreal lakes. *Glob. Change Biol.* 11 (8), 1368–1380 (Aug).
- Ray, N.E., Holgerson, M.A., 2023. High Intra-Seasonal Variability in Greenhouse Gas Emissions From Temperate Constructed Ponds. *Geophys. Res. Lett.* 50 (18), e2023GL104235. Sep 28.
- Raymond, P.A., Caraco, N.F., Cole, J.J., 1997. Carbon Dioxide Concentration and Atmospheric Flux in the Hudson River. *Estuaries* 20 (2), 381 (Jun).
- Raymond, P.A., Hartmann, J., Lauerwald, R., Sobek, S., McDonald, C., Hoover, M., et al., 2013. Global carbon dioxide emissions from inland waters. *Nature* 503 (7476), 355–359. Nov 21.
- Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F.T., Gruber, N., Janssens, I.A., et al., 2013. Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nat. Geosci.* 6 (8), 597–607 (Aug).

- Robin, J., Wezel, A., Bornette, G., Arthaud, F., Angélibert, S., Rosset, V., et al., 2014. Biodiversity in eutrophicated shallow lakes: determination of tipping points and tools for monitoring. *Hydrobiologia* 723 (1), 63–75 (Feb).
- Rosentreter, J.A., Borges, A.V., Deemer, B.R., Hølgerson, M.A., Liu, S., Song, C., et al., 2021. Half of global methane emissions come from highly variable aquatic ecosystem sources. *Nat. Geosci.* 14 (4), 225–230 (Apr).
- Rutegwa, M., Gebauer, R., Veselý, L., Regenda, J., Strunecký, O., Hejzlar, J., et al., 2019a. Diffusive methane emissions from temperate semi-intensive carp ponds. *Aquacult Environ. Inter.* 11, 19–30. Jan 24.
- Rutegwa, M., Potužák, J., Hejzlar, J., Drozd, B., 2019b. Carbon metabolism and nutrient balance in a hypereutrophic semi-intensive fishpond. *Knowl. Manag Aquat. Ecosyst.* (420), 49.
- Saunio, M., Jackson, R.B., Bousquet, P., Poulter, B., Canadell, J.G., 2016. The growing role of methane in anthropogenic climate change. *Environ. Res Lett.* 11 (12), 120207. Dec 1.
- Sceau, R., 1980. Les étangs de la Dombes, fondements socio-économiques d'un système hydraulique. *geoca* 55 (2), 129–159.
- Schlumberger, O., Girard, P., 2020. Memento de la pisciculture d'étang. 5ième édition mise à jour. Quae, Versailles.
- Sobek, S., Tranvik, L.J., Cole, J.J., 2005. Temperature independence of carbon dioxide supersaturation in global lakes. *Glob. Biogeochem. Cycles* 19 (2), 2004GB002264 (Jun).
- Soussana, J.F., Tallec, T., Blanfort, V., 2010. Mitigating the greenhouse gas balance of ruminant production systems through carbon sequestration in grasslands. *Animal* 4 (3), 334–350.
- Stadmark, J., Leonardson, L., 2005. Emissions of greenhouse gases from ponds constructed for nitrogen removal. *Ecol. Eng.* 25 (5), 542–551 (Dec).
- Sun, K., Chen, X., Dong, X., Yang, X., 2020. Spatiotemporal patterns of carbon sequestration in a large shallow lake, Chaohu Lake: Evidence from multiple-core records. *Limnologia* 81, 125748 (Mar).
- Sun, H., Lu, X., Yu, R., Yang, J., Liu, X., Cao, Z., et al., 2021. Eutrophication decreased CO₂ but increased CH₄ emissions from lake: A case study of a shallow Lake Ulansuhai. *Water Res.* 201, 117363 (Aug).
- Taylor, S., Gilbert, P.J., Cooke, D.A., Deary, M.E., Jeffries, M.J., 2019. High carbon burial rates by small ponds in the landscape. *Front. Ecol. Environ.* 17 (1), 25–31 (Feb).
- Thioulouse J., Dray S., Dufour A.B., Siberchicot A., Jombart T., Pavoine S. *Multivariate Analysis of Ecological Data with ade4*. 2018.
- Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., Striegl, R.G., Ballatore, T.J., et al., 2009. Lakes and reservoirs as regulators of carbon cycling and climate. *Limnol. Oceanogr.* 54 (6part2), 2298–2314 (Nov).
- Trolle, Dennis, Peter, A.Staehr, Davidson, Thomas A., Bjerring, Rikke, Lauridsen, Torben L., Søndergaard, Martin, Jeppesen, Erik, 2012. "Seasonal Dynamics of CO₂ Flux Across the Surface of Shallow Temperate Lakes." *Ecosystems* 15 (2), 336–347. (<http://www.jstor.org/stable/41413047>).
- Vanni, M.J., 2002. Nutrient Cycling by Animals in Freshwater Ecosystems. *Annu Rev. Ecol. Syst.* 33 (1), 341–370 (Nov).
- Villa, J.A., Bernal, B., 2018. Carbon sequestration in wetlands, from science to practice: An overview of the biogeochemical process, measurement methods, and policy framework. *Ecol. Eng.* 114, 115–128 (Apr).
- Waldemer, C., Koschorreck, M., 2023. Spatial and temporal variability of greenhouse gas ebullition from temperate freshwater fish ponds. *Aquaculture* 574, 739656 (Sep).
- Wanninkhof, R., 1992. Relationship between wind speed and gas exchange over the ocean. *J. Geophys Res* 97 (C5), 7373.
- Webb, J.R., Hayes, N.M., Simpson, G.L., Leavitt, P.R., Baulch, H.M., Finlay, K., 2019. Widespread nitrous oxide undersaturation in farm waterbodies creates an unexpected greenhouse gas sink. *Proc. Natl. Acad. Sci. USA* 116 (20), 9814–9819. May 14.
- Weiss, R.F., 1974. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. *Mar. Chem.* 2 (3), 203–215 (Nov).
- Weiss, R.F., Price, B.A., 1980. Nitrous oxide solubility in water and seawater. *Mar. Chem.* 8 (4), 347–359 (Feb).
- Wezel, A., Arthaud, F., Dufloux, C., Renoud, F., Vallod, D., Robin, J., et al., 2013. Varied impact of land use on water and sediment parameters in fish ponds of the Dombes agro-ecosystem, France. *Hydrol. Sci. J.* 58 (4), 854–871 (May).
- Wickham H. *ggplot2: elegant graphics for data analysis*. 2016.
- Wiesenburg, D.A., Guinasso, N.L., 1979. Equilibrium solubilities of methane, carbon monoxide, and hydrogen in water and sea water. *J. Chem. Eng. Data* 24 (4), 356–360 (Oct).
- Willeit, M., Ganopolski, A., Calov, R., Brovkin, V., 2019. Mid-Pleistocene transition in glacial cycles explained by declining CO₂ and regolith removal. *Sci. Adv.* 5 (4), eaav7337. Apr 5.
- Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., et al., 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biol. Conserv.* 115 (2), 329–341 (Feb).
- Yang, P., Zhang, L., Lin, Y., Yang, H., Lai, D.Y.F., Tong, C., et al., 2024. Significant inter-annual fluctuation in CO₂ and CH₄ diffusive fluxes from subtropical aquaculture ponds: Implications for climate change and carbon emission evaluations. *Water Res.* 249, 120943 (Feb).
- Yue, X.L., Gao, Q.X., 2018. Contributions of natural systems and human activity to greenhouse gas emissions. *Adv. Clim. Change Res.* 9 (4), 243–252 (Dec).
- Zhang, L., He, K., Wang, T., Liu, C., An, Y., Zhong, J., 2022. Frequent algal blooms dramatically increase methane while decrease carbon dioxide in a shallow lake bay. *Environ. Pollut.* 312, 120061 (Nov).
- Zhang, D., Tian, X., Dong, S., Chen, Y., Feng, J., He, R., et al., 2020. Carbon budgets of two typical polyculture pond systems in coastal China and their potential roles in the global carbon cycle. *Aquacult Environ. Inter.* 12, 105–115. Mar 26.
- Zimmer, K.D., Hobbs, W.O., Domine, L.M., Herwig, B.R., Hanson, M.A., Cotner, J.B., 2016. Uniform carbon fluxes in shallow lakes in alternative stable states: Uniform carbon fluxes in shallow lakes. *Limnol. Oceanogr.* 61 (1), 330–340 (Jan).