Limnetica, 42(2): 302-328 (2023). DOI: 10.23818/limn.42.22
 ISSN: 0213-8409

Understanding the fluxes of greenhouse gases in reservoirs under the inspiration of Margalef

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Received: 24/03/23 Accepted: 12/05/23

ABSTRACT

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Reservoirs are significant sources of greenhouse gases (GHG), such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), to the atmosphere. These systems receive and metabolize a larger amount of organic and inorganic carbon and nitrogen from their watersheds than lakes, resulting in the production of CO_2, CH_4 and N_2O. Despite their global relevance, there are still important uncertainties regarding the magnitude, variability and drivers of their emissions that undermine global estimates. Therefore, a comprehensive understanding of the origin of these emissions is required. Here, I investigate the fluxes of CO_2, CH_4 and N_2O and their concentrations in the water column of twelve Mediterranean reservoirs during the stratification and mixing periods to discern the main pathways involved in their production and the spatial and seasonal variability among these gases and their emissions and radiative forcing. Finally, I provide a theorical framework to understand GHG emissions as a response of reservoirs to eutrophication and external forcing. I integrate Margalef's ideas about how eutrophication perturbs the biogeochemistry of inland waters with the main findings of my previous work to analyze how the C, N and P inputs from reservoir watersheds modify the biogeochemical cycling of C, N, P and O, and determine the production and emission of CO_2, CH_4, and N_2O. This perturbation effect is especially notable for CH_4, and N_2O emissions, which increase significantly in eutrophic waters, even exceeding the climate forcing of CO_2. Therefore, emission of GHG should be seen as part of the reservoir response to the external forcing that displaces a fraction of the materials to the atmospheric boundary.

Key words: methane, nitrous oxide, carbon dioxide, GHG, reservoirs, eutrophication, greenhouse gases, Margalef

RESUMEN

Comprendiendo los flujos de gases de efecto invernadero en embalses bajo la inspiración de Margalef

Los embalses son fuentes significativas de gases de efecto invernadero (GEI), como dióxido de carbono (CO_2), metano (CH_4) y óxido nitroso (N_2O) a la atmósfera. Estos sistemas reciben y metabolizan una mayor cantidad de carbono orgánico e inorgánico, y de nitrógeno procedente de sus cuencas hidrográficas que los lagos, lo que determina la producción de CO_2, CH_4 y N_2O. A pesar de su relevancia mundial, sigue habiendo importantes incertidumbres en cuanto a la magnitud, variabilidad y factores ambientales que regulan estas emisiones, lo que compromete las estimaciones globales. Por lo tanto, se requiere una comprensión exhaustiva del origen de estas emisiones. En este trabajo estudio los flujos de CO_2, CH_4 y N_2O y sus concentraciones en la columna de agua de doce embalses mediterráneos durante los periodos de estratificación y mezcla, para discenir las principales vías implicadas en su producción y estudiar la variabilidad espacial y estacional entre gases y sus emisiones y forzamiento radiativo. Finalmente, proporciono un marco teórico para entender la emisión de GEI como una respuesta de los embalses a la eutrofización y al forzamiento externo. Aquí integro las ideas de Margalef sobre cómo la eutrofización afecta a la biogeoquímica de las aguas continentales, con los principales hallazgos de mis trabajos anteriores para analizar cómo los aportes de C, N y P de las cuencas de los embalses modifican los ciclos biogeoquímicos del C, N, P y O, y determinan la producción y emisión de CO_2, CH_4 y N_2O. Este efecto es especialmente notable en el caso de las emisiones de CH_4 y N_2O, que aumentan significativamente en aguas eutróficas, superando incluso el forzamiento climático del CO_2. Por lo tanto, la emisión de GEI debe considerarse como parte de la respuesta de los embalses al forzamiento externo, que desplaza una fracción de los materiales al límite atmosférico.

Palabras clave: *metano, óxido nitroso, dióxido de carbono, GEI, eutrofización, embalses, gases de efecto invernadero, Margalef*

RESERVOIRS ARE IDIOSYNCRATIC SYSTEMS

Reservoirs are frequently called artificial lakes, although they are not true lakes, but aquatic systems with their own idiosyncrasies (Margalef et al., 1976). They are an intermediate ecosystem between a river and a lake, with a tail that retains many river characteristics (shallower depth, predominance of horizontal transport, etc.), and an area near the dam where more lake-like characteristics are acquired (greater depth, possibility of thermal, chemical and biological stratification, etc.) (Margalef et al., 1976). Damming determines the reduction in flow and the increase in residence time, with subsequent changes in temperature and stratification, reduction in the turbulence due to particle settling, and sometimes an increase in autochthonous primary production, and alteration of oxygen conditions that can lead to hypoxia/anoxia events in deep waters. Damming also alters the delivery of nutrients, organic carbon and sediments downstream (Lehner et al., 2011). All of these changes affect carbon (C), nitrogen (N) and phosphorus (P) cycling (Friedl & Wüest, 2002), and the role of inland waters as active pipes in the landscape (Maranger et al., 2018).

Reservoirs, as other inland waters, can be seen as digesters that metabolize the elements they receive from the catchment; exchange the gaseous forms with the atmosphere (i.e., CO_2, CH_4, N_2O, and N_2); export one part downstream, and store another part in the sediments in globally significant quantities (Cole et al., 2007; DelSontro et al., 2018; Tranvik et al., 2009). However, reservoirs receive a larger amount of organic and inorganic matter and nitrogen from the catchment than do lakes, due to their higher catchment area, and higher drainage ratio (i.e., the catchment area : lake or reservoir surface area) (Harrison et al., 2009; Hayes et al., 2017; Knoll et al., 2015; Prats-Rodríguez et al., 2014; Thornton et al., 1990; Tong & Chen, 2002). Reservoirs also have larger rates of organic carbon burial in sediments than do lakes, as result of catchment instability and high erosion rates (Anderson et al., 2020; Mendonça et al., 2017). In addition, they can absorb or emit greenhouse gases, being sinks or sources of carbon dioxide (CO_2), methane (CH_4), or nitrous oxide (N_2O) to the atmosphere. CH_4 and N_2O are particularly relevant despite their lower abundance in the atmosphere, because they have a warming potential of 34 and 298 times higher than CO_2 in a 100 year timescale (IPCC, 2013). Depending on the balance among all these processes, reservoirs will act as net sinks or sources for the different biogeochemical elements.

In this context, several studies have pointed out that reservoirs are significant sources of CO_2, CH_4 and N_2O to the atmosphere (Bastviken et al., 2011; Deemer et al., 2016; León-Palmero, et al., 2020a; Soued et al., 2015; Tranvik et al., 2009). Further discussion about how to quantify all the changes induced by damming to account for the net reservoir C footprint can be found in Prairie et al. (2018). In the present work, I focus on the fluxes of GHG from reservoirs on an annual scale regardless of whether these reservoirs are net sources or sinks of C or N at longer time scales.

Emissions of CO_2, CH_4 and N_2O from reservoirs is a topic of growing interest due to the prevalence of reservoirs worldwide. Although dams and reservoirs have been built for thousands of years, their number has increased significantly worldwide since the 1950s, reaching more than 58,000 large dams (i.e., $\geq$ 15 m height or 5-15 m height and impounding more than 0.003 m^3 of storage) by 2020 (https://www.icold-cigb.org/GB/world_register/general_synthesis.asp). Small reservoirs are more abundant than large dams, although there have been rarely investigated. Lehner et al. (2011) estimated that there are more than 2.8 million impoundments larger than 0.001 km^2, and 16.7 million larger than 100 m^2, representing a total storage volume over 8000 km^3 and a surface area of around 306 000 km^2, and increasing the

terrestrial freshwater surface by more than 7 %. Some of these dams will probably be decommissioned in the coming years, as they will reach their designed lifespan by the middle of the 21st century (Perera & North, 2021).

Reservoirs are preponderant aquatic systems in the Mediterranean biome, and in the Iberian Peninsula in particular, where they were primarily constructed to provide drinking and irrigation water (Barros et al., 2011; Deemer et al., 2016; Lehner et al., 2011; Morales-Pineda et al., 2014; Naselli-Flores, 2003). In recent years, the need of more clean energy has switched the main purpose to hydropower dams, especially in countries with emerging economies, where over 3500 reservoirs are either planned or under construction (Zarfl et al., 2015). In particular, the Ganges-Brahmaputra (396 future dams), Amazon (368) and Mekong (120) are the basins with the highest number of hydropower dams under construction or planned (Zarfl et al., 2019). A better understanding of the emission of greenhouse gases, and their drivers is necessary to improve the global GHG estimates and reduce or prevent the impact of existing and future reservoirs. Here, I discuss the (1) main pathways involved in the production of CO_2, CH_4 and N_2O in reservoirs, (2) the spatial and seasonal variability among the gases and their emissions and radiative forcing, and finally, I provide a (3) theorical model to understand the emission of GHG as the response of reservoirs to external forcing and eutrophication. In this model, I apply Margalef's ideas about how eutrophication perturbs the biogeochemical cycling of C, N, P and O in inland waters and determines the partitioning of elements, and integrate them with the main findings of my PhD work on the CO_2, CH_4, and N_2O fluxes, concentrations, and productions in the water column of twelve reservoirs in southeastern Spain (León Palmero, 2021). These reservoirs will be referred in this work as "study reservoirs".

DESCRIPTION OF STUDY RESERVOIRS

The study reservoirs, located in watersheds with diverse lithology and land uses (detailed maps are shown in León-Palmero et al., 2020a), were sampled during the stratification and mixing periods between July 2016 and August 2017. They were chosen to represent a broad spectrum of size, age, and morphometry. They were built between 1932 and 2003, and their surface area varied from 1.18 km^2 for El Portillo reservoir to 26.13 km^2 for Iznájar reservoir. The volume ranged from 18.74 hm^3 for Cubillas reservoir to 981.12 hm^3 for Iznájar reservoir (Table S1, available at https://www.limnetica.net/en/limnetica). The reservoirs also differed in chemical and trophic characteristics and presented a range of chlorophyll-*a* concentration from 0.6 to 17.8 µg/L, a range of dissolved organic carbon (DOC) concentration from 0.82 to 4.80 mg C/L; and from 17.90 to 52.85 mg C/L for dissolved inorganic carbon (DIC) concentration (i.e., mean values for the water column). Total nitrogen (TN) concentration ranged from 0.24 to 4.18 mg N/L, while total phosphorus (TP) concentration varied from 4.6 to 57.0 µg P/L (Table S2, https://www.limnetica.net/en/limnetica). Gross primary production (GPP), net ecosystem production (NEP) and respiration (R) rates were only measured in the epilimnion during the stratification period, as described in León-Palmero et al. (2020b). GPP varied from 0.16 to 2.40 g O_2 m^{-3} d^{-1} in terms of O_2 production, and from 0.35 to 7.50 g C m^{-2} d^{-1} in terms of C fixation. The NEP, measured as O_2 and C production, ranged from -0.07 to 0.32 g O_2 m^{-3} d^{-1}, and from -1.41 to 0.21 g C m^{-2} d^{-1} (Table S3, https://www.limnetica.net/en/limnetica). The fluxes of CO_2, CH_4, and N_2O from these twelve reservoirs are presented in Table S4 (https://www.limnetica.net/en/limnetica), and they were previously described in León-Palmero et al. (2020a). The dissolved CH_4 and N_2O concentrations and saturations in the water column and their drivers were described by León-Palmero et al. (2020b), and León-Palmero et al. (in press), respectively. The methods used for the physical, chemical, and biological characterization of the water column, including the primary production measurements, are described in detail in León-Palmero et al. (2020b) and in León-Palmero et al. (in press). More details about these twelve reservoirs can also be found in León-Palmero et al. (2019, 2021). All raw data were deposited in the PANGAEA database (León-Palmero et al., 2020c, 2020d, 2020e).

PRODUCTION OF GHGs

CO_2 production

Lakes and reservoirs are usually CO_2 supersaturated (Cole et al., 1994), and they release 0.32 Pg C/yr globally (Raymond et al., 2013). They are often heterotrophic systems, i.e., the CO_2 production by microbial mineralization of dissolved organic carbon (DOC) exceeds the CO_2 uptake by photosynthesis (Tranvik et al., 2018). DOC is the most abundant form of organic carbon in most lakes and reservoirs, and it is commonly dominated by DOC of terrestrial origin coming from the watershed (i.e., allochthonous DOC) (Tranvik et al., 2018). The rate at which DOC mineralization occurs depends on its reactivity and the local hydrological regime (Vachon et al., 2017). Rantakari & Kortelainen (2005) described a positive relationship between the CO_2 fluxes and the mean annual precipitation in boreal lakes, suggesting that CO_2 production is enhanced by the decomposition of terrestrial organic matter previously transported by precipitation. In addition, they also found that TP concentration and the proportion of agricultural land in the watershed had significant positive correlations with CO_2 saturation (Rantakari & Kortelainen, 2005). Roehm et al. (2009) suggested that DOC concentration is a good predictor for CO_2 concentration in lakes, although the relationship differs among regions. Moreover, CO_2 supersaturation is frequently attributed to the net heterotrophy of the system, although there are other important sources of CO_2 in aquatic systems, such as DOC photomineralization. Sunlight decomposes dissolved organic matter in inorganic molecules, releasing CO_2 (Johannessen & Miller, 2001; Reche, 2003). Besides, photobleaching reactions break complex and recalcitrant organic molecules into smaller ones, which enhances microbial DOC mineralization and, consequently, CO_2 production (Ortega-Retuerta et al., 2007; Reche et al., 1998). Koehler et al. (2014) calculated that up to 10 % of the global CO_2 emissions from inland waters are photochemically induced.

On the other hand, the studies on lake metabolism have been traditionally conducted in carbonate-poor systems, and have ignored lakes and reservoirs located in calcareous watersheds, where inorganic carbon loading during weathering contributes significantly to CO_2 supersaturation (López et al., 2011; Marcé et al., 2015; McDonald et al., 2013; Ran et al., 2022; Weyhenmeyer et al., 2015). I must note that inorganic carbon loading is not a production pathway, as this CO_2 is not produced in the aquatic system, but it should be considered as a relevant source of CO_2 in inland waters. In León-Palmero et al. (2020a), we found that dissolved inorganic carbon (DIC) concentration was a negative function of the non-calcareous area in the reservoir watershed (i.e., igneous rocks and metamorphic rocks with less capacity to leach DIC). Marcé et al. (2015) showed that CO_2 supersaturation in lakes is directly related to carbonate weathering in the watershed when the alkalinity exceeds 1 mEq. /l, which corresponds to 57 % of the surface area occupied by lakes and reservoirs, mostly in tropical and temperate latitudes. Calcite precipitation also occurs at water alkalinities above 1 mEq. /L, acting as a carbon sink in the sediments and a CO_2 source to the atmosphere on the short-term. However, this emission represented a negligible fraction of the CO_2 emissions from lakes and reservoirs (< 0.5 %) (Khan et al., 2020). Although less studied than CO_2, inland waters also produce significant amounts of CH_4 and N_2O (Bastviken et al., 2011; Soued et al., 2015; Tranvik et al., 2009).

CH_4 production

Rivers, lakes and reservoirs are also supersaturated in CH_4, and they emit up to 77.5 – 134.4 Tg C/yr on a global basis (Bastviken et al., 2011; Deemer et al., 2016; Stanley et al., 2016), representing more CH_4 than is emitted from the ocean surface (Saunois et al., 2016). The decomposition of organic matter by methanogenic archaea in anoxic sediments is a primary source of CH_4 in inland waters (Segers, 1998). This methanogenesis could also occur in the anoxic water column, and is affected by temperature, and by the quantity and quality of the organic matter (León-Palmero et al., 2020b; Marotta et al., 2014; Sepulveda-Jauregui et al., 2018; Thanh-Duc et al., 2010; West et al., 2012; Yvon-Durocher et al., 2014). A fraction of the methane produced in the anoxic layers

is oxidized by methanotrophs to CO_2 in the presence (Oswald et al., 2015, 2016; Schubert & Wehrli, 2018; Tang et al., 2016; Thalasso et al., 2020) or absence (Su et al., 2022; Weber et al., 2017) of oxygen. However, CH_4 supersaturation has been consistently detected in the oxic waters of reservoirs (León-Palmero et al., 2020b) and lakes (Bogard et al., 2014; Donis et al., 2017; Grossart et al., 2011; Murase et al., 2003; Schmidt & Conrad, 1993; Tang et al., 2014). The diffusion and ebullition of CH_4 from the anoxic bottom and littoral sediments to the oxic layers can partially explain CH_4 supersaturation, especially in shallow systems (e.g., Encinas Fernández et al., 2016; León-Palmero et al., 2020a; Peeters et al., 2019). However, CH_4 transport does not fully explain CH_4 supersaturation in large reservoirs and lakes. The occurrence of methanogenesis in micro-anoxic zones in the guts of fishes and zooplankton, in fecal pellets, and within sinking particles has been also reported (Bianchi et al., 1992; de Angelis & Lee, 1994; Karl & Tilbrook, 1994; Oremland, 1979), although CH_4 production rates in these microenvironments were too low to sustain the observed CH_4 supersaturation (Schmale et al., 2018; Tang et al., 2014).

There are alternative explanations based on the consistent link detected between dissolved CH_4 concentration and autotrophic organisms, primary production, and chlorophyll-*a* concentration (Bogard et al., 2014; Grossart et al., 2011; León-Palmero et al., 2020b; Owens et al., 1991; Schmidt & Conrad, 1993; Tang et al., 2014). This link may rely on the degradation of methylphosphonates by cyanobacteria (Wang et al., 2017; Yao et al., 2016) or may be directly related to photosynthesis in algae and cyanobacteria (Bižić et al., 2020; Hartmann et al., 2020; Klintzsch et al., 2019; Lenhart et al., 2016). We previously showed that the dissolved CH_4 in oxic waters of reservoirs was mainly coupled to photosynthetic picoeukaryote abundance, but also to cyanobacteria abundance (León-Palmero et al. 2020b). The mean depth of the reservoirs, as a proxy for vertical CH_4 transport from sediments to the oxic waters, also contributed notably to the CH_4 concentration in oxic waters. Overall, the explanation of the CH_4 supersaturation in surface waters and its subsequent emission relies on the interaction of several processes, with a central role for phytoplankton, since phytoplankton directly determined CH_4 concentration in oxic waters, and indirectly provided high-quality C sources for production of CH_4 in anoxic layers, which can be subsequently transported to oxic waters.

N_2O production

Anthropogenic addition of nitrogen to the biosphere has increased the inputs of this nutrient into inland waters, boosting the production and emission of N_2O (Beaulieu et al., 2011; León-Palmero et al., 2020a; Mulholland et al., 2008; Seitzinger et al., 2000). N_2O has 298 times the warming effect of CO_2 in a 100-year time horizon (IPCC, 2013), and is the primary driver of stratospheric ozone depletion (Ravishankara et al., 2009). DelSontro et al. (2018) calculated that lakes and reservoirs may emit about ~ 0.3 Tg N-N_2O/yr, although this estimation is based on a limited dataset. Microbial transformations that lead to the production and consumption of N_2O include ammonia oxidation, nitrifier denitrification, and denitrification, and they are strongly dependent on N and oxygen availabilities (Beaulieu et al., 2015; Codispoti, 2010; Ji et al., 2018; León-Palmero et al., in press). Nevertheless, few studies have characterized microbial N_2O cycling in reservoirs.

N_2O is a side product during ammonia oxidation to nitrite (i.e., first step of nitrification) in well-oxygenated waters, which is performed by ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) (Könneke et al., 2005; Kowalchuk & Stephen, 2001). At low oxygen concentrations nitrifiers increase the yield of N_2O production by nitrifier denitrification (i.e., AOB), by hybrid formation (i.e., AOA), or hydroxylamine oxidation (i.e., AOA) (Wan et al., 2023), although some details remain controversial (Stein, 2019; Wan et al., 2023; Ward, 2013). In AOB and AOA, N_2O production rates reached maxima under suboxic conditions (Hink et al., 2017). On the other side, denitrification consists of the sequential reduction of nitrate to nitrite, nitric oxide, nitrous oxide, and dinitrogen, and it is responsible for the production of significant amounts of N_2O in inland waters (Seitzinger et al., 2000). N_2O can accumulate in the waters if

the rate of N_2O production exceeds the N_2O reduction to N_2. Conversely, denitrification can be a N_2O sink if the rate of N_2O reduction to N_2 is higher than the rate of N_2O formation. Although denitrification is usually considered facultative anaerobic respiration, these bacteria also occur in the oxic waters of lakes (Junier et al., 2008; Kim et al., 2011; Pajares et al., 2017) and reservoirs (León-Palmero et al., in press). Denitrifying bacteria were ubiquitous in the water column of the study reservoirs, and more abundant than ammonia oxidizing archaea and bacteria. Interestingly, we also found that P inputs and cumulative Chl-*a*, as a proxy for autochthonous organic matter exported from the water column, increased denitrifier abundance. N_2O concentration was a function of the abundance of denitrifying bacteria and the main substrate for denitrification (i.e., nitrate). N_2O was consumed or produced depending on the N availability under suboxic conditions. That is, at low oxygen conditions, there was consumption when nitrogen concentration was low, and production when nitrogen concentration was high. A similar trend was found in the reservoirs studied by Beaulieu et al. (2015). Yet, our knowledge on the production and consumption of N_2O in reservoirs is still very limited, despite the relevance of these systems for N removal at landscape scale, especially in areas subjected to high N inputs (McCrackin & Elser, 2011).

VARIABILITY AND RADIATIVE FORCING OF GHG EMISSIONS

According to the global estimates of Deemer et al. (2016), reservoirs release 36.8 Tg C/yr as CO_2, 13.3 Tg C/yr as CH_4, and 0.03 Tg N/yr as N_2O. Other estimates for hydroelectric reservoirs calculated that they may emit between 48 - 82 Tg C/yr as CO_2 and between 3 - 14 Tg C/yr as CH_4 (Barros et al., 2011; Li & Zhang, 2014). Nevertheless, the existing estimates are highly uncertain because they are based on limited datasets. The global studies of Barros et al. (2011) and Deemer et al. (2016) showed that GHG fluxes had been seldom measured in the Mediterranean biome (latitudinal band 30° – 45°), and in the Iberian Peninsula in particular, despite being one of the regions with the highest number of reservoirs, coinciding with the low number of natural lakes (Lehner & Döll, 2004). This latitudinal lack of direct measurements seriously limits the confidence on the global estimates of GHG emissions. In León-Palmero et al. (2020a) we quantified the fluxes of CO_2, CH_4, and N_2O in twelve reservoirs during the summer stratification and the winter mixing in southeastern Spain. This work represented the first inventory of direct and simultaneous fluxes of the three main greenhouse gases (CO_2, CH_4, and N_2O) in reservoirs located in the Mediterranean biome, and it demonstrated the great range in GHG emissions that Mediterranean reservoirs exhibit. We found that GHG fluxes varied by several orders of magnitude among them and between seasons. Some reservoirs were sinks (fluxes < 0) while others were sources (fluxes > 0) for CO_2 and N_2O, but all reservoirs were CH_4 sources. CO_2 fluxes ranged from -131.97 to 393.11 mg C m^{-2} d^{-1} during the stratification period, and from -52.51 to 149.62 mg C m^{-2} d^{-1} during the mixing period. CH_4 fluxes varied from 0.51 to 678.84 mg C m^{-2} d^{-1} during the stratification period, and from 0.10 to 4.41 mg C m^{-2} d^{-1} during the mixing period. N_2O fluxes ranged from -154.03 to 3600.88 µg N m^{-2} d^{-1} during the stratification period, and from -238.08 to 313.44 µg N m^{-2} d^{-1} during the mixing period (table S4). The median values for both periods were 114.0 mg C-CO_2 m^{-2} d^{-1}, 1.6 mg C-CH_4 m^{-2} d^{-1}, and 0.0 µg N-N_2O m^{-2} d^{-1}; while the weighted averages according to the reservoir surfaces were notably higher (i.e., 104.2 mg C-CO_2 m^{-2} d^{-1}, 14.2 mg C-CH_4 m^{-2} d^{-1}, and 591.4 µg N-N_2O m^{-2} d^{-1}) due to the differences in area among reservoirs (Fig. 1). The weighted average for CH_4 emissions in the study reservoirs is close to the value estimated before by Álvarez-Cobelas & Sánchez-Carrillo (2019) (e.g., 10.2 mg C m^{-2} d^{-1}) for Iberian reservoirs, and higher than the estimation for N_2O by the same authors (e.g., 192.4 µg N m^{-2} d^{-1}).

To address the total radiative forcing and the relative contribution of each GHG, I converted the fluxes of CO_2, CH_4, and N_2O from León-Palmero et al. (2020a) to CO_2 equivalents using their warming potentials (IPCC, 2013) (Fig. 1). Most of the study reservoirs had a positive radiative forcing in the study period (i.e., acted as GHG sources). In some cases, the CO_2 and N_2O inflow totally

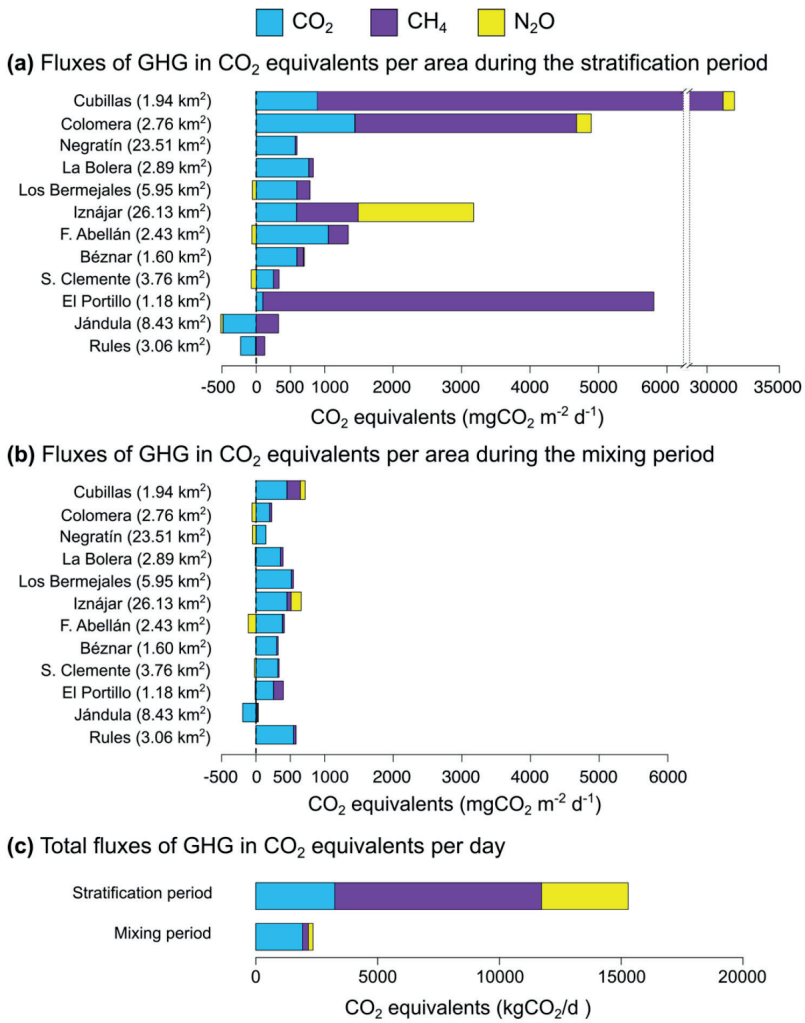

Figure 1. The study reservoirs act as GHG sinks (< 0 values) or sources (> 0 values) of GHG. Fluxes of CO_2, CH_4 and N_2O expressed in CO_2 equivalents (mg CO_2 m^{-2} d^{-1}) during the stratification (a) and mixing (b) periods. The total fluxes in CO_2 equivalents (kg CO_2/d) are shown in (c). Note the x-axis has a break in the panel (a). The CO_2 equivalents were calculated by multiplying the mass-based flux by the 100-year global warming potential of each gas (1 for CO_2, 34 for CH_4 and 298 for N_2O) (IPCC, 2013). *Los embalses estudiados actúan como sumideros (valores < 0) o como fuentes de GEI (valores > 0). Los flujos de CO_2, CH_4 y N_2O expresados en equivalentes de CO_2 (mg CO_2 m^{-2} d^{-1}) durante el periodo de estratificación (a) y mezcla (b). Los flujos totales en equivalentes de CO_2 (kg CO_2/d) se muestran en (c). Nótese que el eje x tiene un corte en el panel (a). Los equivalentes de CO_2 se calcularon multiplicando el flujo basado en la masa por el potencial de calentamiento global a 100 años de cada gas (1 para el CO_2, 34 para el CH_4 and 298 para el N_2O) (IPCC, 2013).*

or partially compensated the CH_4 emissions, as shown in figure 1a and b. During the stratification period, the radiative forcings ranged from 125 mg CO_2 equivalents m^{-2} d^{-1} to 31 884 mg CO_2 equivalents m^{-2} d^{-1} and were dominated by the CH_4 emissions (Fig. 1a). Conversely, during the mixing period the radiative forcings ranged from 29 mg CO_2 equivalents m^{-2} d^{-1} to 722 mg CO_2 equivalents m^{-2} d^{-1} and were dominated by CO_2 emissions (Fig. 1b). The higher radiative forcings during the stratification than during the mixing period is related to the significant differ-

ences in CH_4 emissions between seasons (Fig. 1c). These emissions are much affected by temperature (e.g., Yvon-Durocher et al., 2014).

The contribution of each greenhouse gas to the total radiative forcing was more variable during the summer stratification (Fig. 1c). For example, CH_4 emission represented 97 % of the radiative forcing in Cubillas reservoir during the stratification period, but a 28 % during the winter mixing. In Iznájar reservoir, the radiative forcing by N_2O emissions exceeded the forcing by CO_2 and CH_4 together during the stratification period (i.e., 53 %). On average per system, and only considering reservoirs with a final radiative forcing per area > 0 (i.e., sum of CO_2, CH_4, and N_2O measured in mg CO_2 equivalents m^{-2} d^{-1}), the fluxes of CO_2, CH_4, and N_2O determined 59 %, 39 %, and 2 %, respectively, of the radiative forcing during the stratification period, and 97 %, 12 %, and -9 % during the winter mixing, respectively.

The large differences in the surface area of these reservoirs (i.e., from 1.94 km^2 to 26.13 km^2, Fig.1) affects their radiative forcing. Therefore, I also accounted for the radiative forcing of all reservoirs and their areas by multiplying the flux of each gas by the area occupied by the reservoir (e.g., kg CO_2 equivalents/d, Fig. 1c). CO_2, CH_4, and N_2O fluxes contributed 21 %, 56 %, and 23 % to the total radiative forcing during the stratification period, and 82 %, 10 %, and 8 % during the mixing period, respectively. Deemer et al. (2016) suggested that CH_4 emissions from reservoirs may be responsible for the majority of the radiative forcing of reservoirs (i.e., 79 % of the CO_2 equivalents), while CO_2 and N_2O fluxes contributed only 17 % and 4 %, respectively. In our dataset CH_4 emissions were responsible for the majority of the radiative forcing (i.e., 56 %) during the summer stratification, while CO_2 fluxes determined 82 % of the radiative forcing during the winter mixing. Nitrous oxide fluxes even exceeded CO_2 forcing during summer stratification when considering the total area of the reservoirs. These results emphasize the need of considering the three GHG fluxes and their differences at intersystem and temporal scales.

The hypolimnion of the study reservoirs presented important accumulations of DIC, CH_4 and N_2O during the stratification period, whose potential emission would significantly increase their C footprint (León-Palmero et al., 2020b; León-Palmero et al., in press). The GHG stored in deeper waters may be emitted to the atmosphere via other pathways, such as the autumn overturn, or by degassing at the dam outflow or further downstream (i.e., indirect emissions). Previous work detected higher fluxes of CO_2 and CH_4 during the overturn period, but they also demonstrated that most of the accumulated CH_4 was oxidized in the water column during the overturn in lakes (Encinas Fernández et al., 2014; Kankaala et al., 2007; López Bellido et al., 2009; Schubert et al., 2012). However, less is known about the N_2O fluxes during the overturn. León-Palmero et al. (in press) detected that N_2O supersaturation reached up to 1449 % in Iznájar reservoir, while the water columns presented both supersaturation and undersaturation at different depths. A better temporal resolution may capture these emissions derived from the water column mixing in fall. The GHG stored in deep waters may be also released to the atmosphere at the hydroelectricity turbines and downstream when the water is released to the river course (i.e., degassing and downstream emissions), representing a relatively small fraction of the CO_2 emissions (Teodoru et al., 2012), but a significant fraction for CH_4 (Abril et al., 2005; Diem et al., 2012; Kemenes et al., 2007; Maeck et al., 2013; Okuku et al., 2019; Teodoru et al., 2012) and N_2O emissions (Okuku et al., 2019).

Moreover, GHG emissions may differ not only among seasons, but also on a spatial scale. Montes-Pérez et al. (2022) found that the riverine zone was a sink for CO_2, while the lacustrine zone was a source, at the annual scale. Both areas emitted CH_4 to the atmosphere. Exposed sediment beds on the shores of reservoirs should be also considered to achieve a holistic approach to GHG emissions from these ecosystems. These sediments emerge temporarily to the surface due to hydrological changes (i.e., during the dry season) and human hydraulic management. When that happens, organic carbon that was previously buried in submerged sediments is exposed to the atmosphere, leading to an increase in the aerobic respiration of the organic matter, and the subsequent significant release of CO_2 (Almeida et al., 2019; Gómez-Gener et al., 2015; Jin et al., 2016; Marcé et al., 2019; Pozzo-Pirotta et al., 2022).

The degradation of the organic matter also determines the higher emission of CH_4 in exposed sediments than in adjacent uphill soils (Paranaíba et al., 2022). Future climatic scenarios for the Mediterranean region project an increase in the occurrence of extreme heat and drought events (Giorgi & Lionello, 2008), enhancing CO_2 emissions from the episodically exposed sediments of reservoirs (Gómez-Gener et al., 2015), and CH_4 emissions due to the reduction in the reservoir depth (León-Palmero et al., 2020a).

DRIVERS OF GHG EMISSIONS

In general terms, GHG emissions depend on the budget between their production and consumption, and their storage capacity in the water column. GHG storage is closely linked to water mean depth, because deep reservoirs can accumulate more GHG in the hypolimnion during the thermal stratification, due to the high hydrostatic pressure, and the thermocline that acts as a barrier to the hypolimnetic GHG diffusion toward the surface layers (Keller & Stallard, 1994; West et al., 2016). In contrast, shallow systems have less capacity to store GHG, and they usually have warmer waters, decreasing the solubility of gases (i.e., less storage capacity) and increasing the production of GHG, especially methane (Aben et al., 2017; Keller & Stallard, 1994; Marotta et al., 2014). West et al. (2016) found that CH_4 ebullitive fluxes most frequently occurred at sites less than 6 m deep. Both the mean depth, and the water temperature were important drivers explaining CH_4 emissions and concentrations in Iberian reservoirs (León-Palmero et al., 2020a; León-Palmero et al., 2020b; Montes-Pérez et al., 2022).

Other variables affect the net production of GHG in the water column and in the sediments. As explained previously, the decomposition of organic matter determines the production of CO_2 in oxic conditions, and the production of CH_4 (and CO_2) in anoxic conditions by archaeal methanogenesis. Therefore, reservoirs may present the highest emissions of CO_2 and CH_4 during the early years after the flooding event, due to the decomposition of the flooded vegetation and soil organic matter, but C emissions would stabilize after this first stage (Abril et al., 2005;

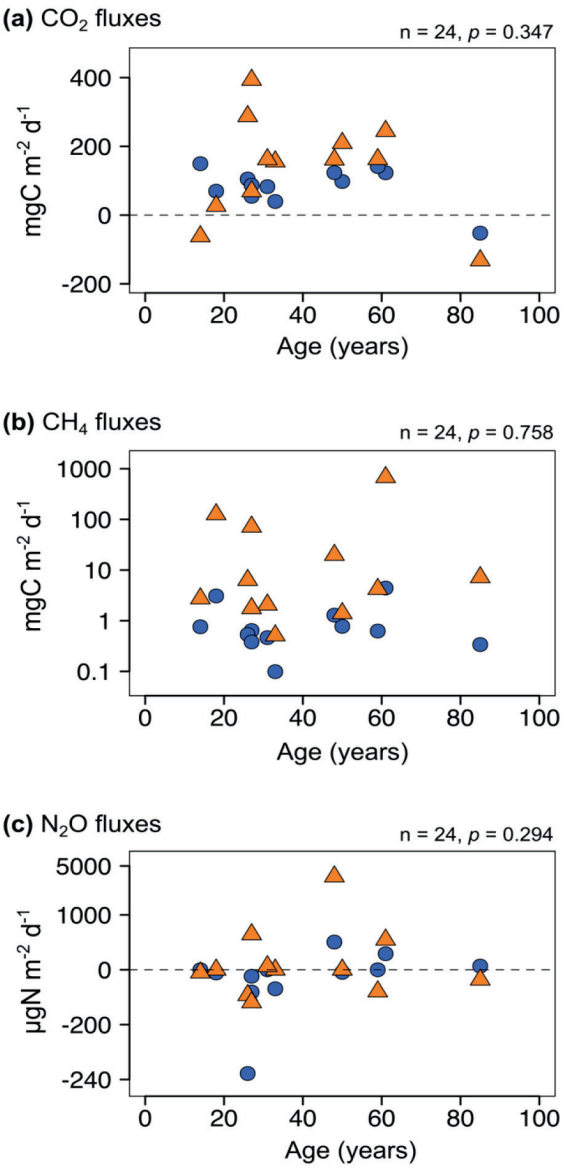

Figure 2. Scatterplot of the GHG fluxes and the age of the study reservoirs. (a) CO_2 fluxes, mg C m^{-2} d^{-1} (b) CH_4 fluxes, mg C m^{-2} d^{-1} (c) N_2O fluxes, µg N m^{-2} d^{-1}. The orange triangles represent fluxes during the stratification period (n = 12), and the blue dots represent fluxes during the mixing period (n = 12). *p* values for the regression analysis are provided. Note the logarithmic scales in the y axis of (b) and (c). *Gráfico de dispersión de los flujos de GEI y la edad de los embalses estudiados. (a) Flujos de CO_2, mg C m^{-2} d^{-1} (b) Flujos de CH_4, mg C m^{-2} d^{-1} (c) Flujos de N_2O, µg N m^{-2} d^{-1}. Los triángulos naranjas representan los flujos durante el periodo de estratificación (n = 12), y los círculos azules representan los flujos durante el estado de mezcla (n = 12). Se muestran los valores* p *obtenidos en el análisis de regression. Nótese la escala logarítmica en el eje y de (b) y (c).*

Barros et al., 2011; Tremblay et al., 2005). Teodoru et al. (2012) found the highest emissions of CO_2, and the lowest of CH_4 during the first five years after the flooding event. To test the effect of the reservoir age in their emissions, twelve reservoirs covering a wide range of ages were selected, from 14 years (i.e., Rules reservoir) to 85 years (i.e., Jándula reservoir). However, I did not detect any significant relationship between the CO_2, CH_4, or N_2O fluxes and the age of the study reservoirs based on the regression analysis (Fig. 2). I also tested the effect of the reservoir age on the concentrations of DOC, DIC, CH_4 and N_2O in the hypolimnion/bottom waters of the reservoirs using a regression analysis. DOC concentration in deep waters increased with the age of the reservoir (Fig. 3a, $p < 0.001$), which is the opposite of the expected trend, and it indicates that the reservoirs are accumulating organic matter in deep waters over time. The reservoir age did not affect the concentration of DIC, CH_4, or N_2O (Fig. 3b, c, d). These twelve reservoirs are located in the stabilization region described by Teodoru et al. (2012) (i.e., five years from the flooding event), and that may explain the absence of relationship between GHG emissions and reservoir age. Regarding the flood event, it is important to notice that different landscapes contain different types of vegetation and amounts of organic carbon stored in soils, and that will affect the GHG emissions during the first years (Brothers et al., 2012). For instance, a reservoir that flood peatlands will presumably emit more C to the atmosphere, because these ecosystems store large amounts of organic carbon in the peat (Kelly et al., 1997; Louis et al., 2000).

Nevertheless, reservoirs are dynamic ecosystems that evolve in time and space, and after the

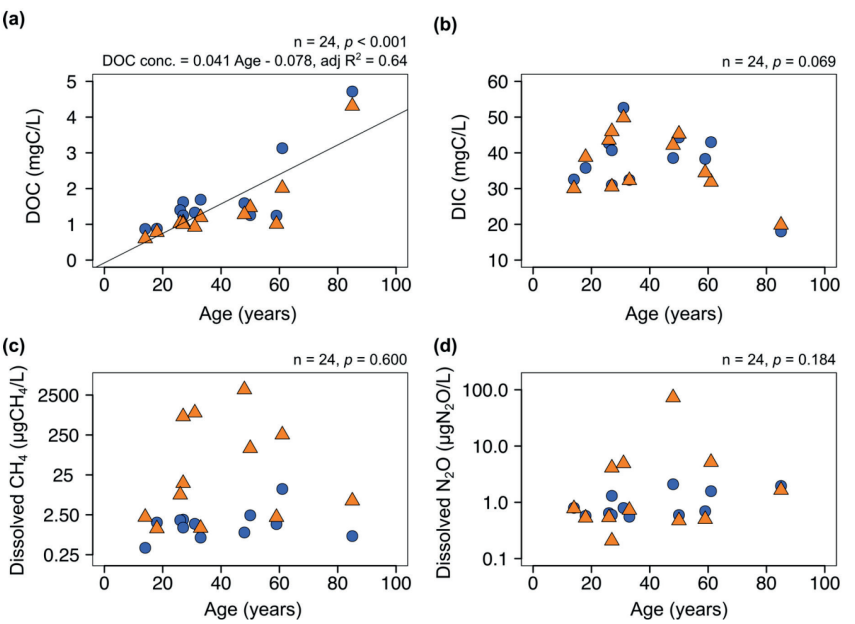

Figure 3. Scatterplot of the dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), CH_4, and N_2O concentrations in hypolimnetic/bottom waters and the age of the reservoir. (a) DOC, mg C/L; (b) DIC, mg C/L; (c) CH_4, µg CH_4/L; (d) N_2O, µg N_2O/L. The orange triangles represent values during the stratification period (n = 12), and the blue dots represent values during the mixing period (n = 12). *p* values for the regression analysis are provided. Note the logarithmic scales in the y axis of (c) and (d). *Gráfico de dispersión de las concentraciones de carbono orgánico disuelto (DOC), carbono inorgánico disuelto (DIC), CH_4, y N_2O en el hipolimnion de los embalses y la edad de éstos. (a) DOC, mg C/L; (b) DIC, mg C/L; (c) CH_4, µg CH_4/L; (d) N_2O, µg N_2O/L. Los triángulos naranjas representan los flujos durante el periodo de estratificación (n = 12), y los círculos azules representan los flujos durante el estado de mezcla (n = 12). Se muestran los valores* p *obtenidos en el análisis de regresión. Nótese la escala logarítmica en el eje y de (c) y (d).*

very first years, their biogeochemistry may not depend on the initial organic matter stock. Instead, GHG production and emissions may rely on the autochthonous and the allochthonous organic C processing, and on the nutrient inputs that they receive from their watersheds. In this regard, the global synthesis by Deemer et al. (2016) pointed out that factors related to productivity may be better predictors for reservoir emissions than latitude or reservoir age. To analyze in more detail how the inputs of organic and inorganic carbon, and specially the N and P loading (i.e., external forcing) and the concomitant water eutrophication, impact CO_2, CH_4, or N_2O production and emission in reservoirs, I apply Margalef's ideas and integrate them with the main findings of my PhD work in twelve reservoirs in southeastern Spain (León Palmero, 2021).

Greenhouse gas emissions in response to external forcing

Forty years ago, Margalef (1983) explained that inland waters are forced by the terrestrial ecosystems in their watersheds, receiving organic and inorganic carbon, major nutrients (as nitrogen and phosphorus), and micronutrients. The eutrophication of inland waters is a response to this external forcing, and limnologists have extensively studied it. Eutrophication is a common phenomenon occurring in inland and coastal waters globally, and it is characterized by excessive plant and algal growth (Chislock et al., 2013). Eutrophication occurs naturally when sediments fill a lake over centuries (Carpenter, 1981), but also occur when human activities, such as agriculture, industry, and sewage disposal, increase the loading of limiting nutrients into inland waters, and, in this case, is termed cultural eutrophication (Carpenter et al., 1998). P is often the limiting nutrient in inland waters (Schindler, 1977), while N is more commonly the limiting nutrient in estuarine and coastal marine waters (Nixon, 1995; Ryther & Dunstan, 1971). Human activities increase the loading of both nutrients, but P compounds are less mobile and retained in the soils more efficiently than N-compounds during runoff, which is reflected in higher N:P ratios in lakes (Downing & McCauley, 1992), or in the higher increase in N than in P concentration in reservoirs affected by agricultural runoff (León-Palmero et al., 2021). Some consequences of cultural eutrophication include cyanobacterial blooms, hypoxia events, and the degradation of drinking water supplies, fisheries, and recreational areas (Chislock et al., 2013).

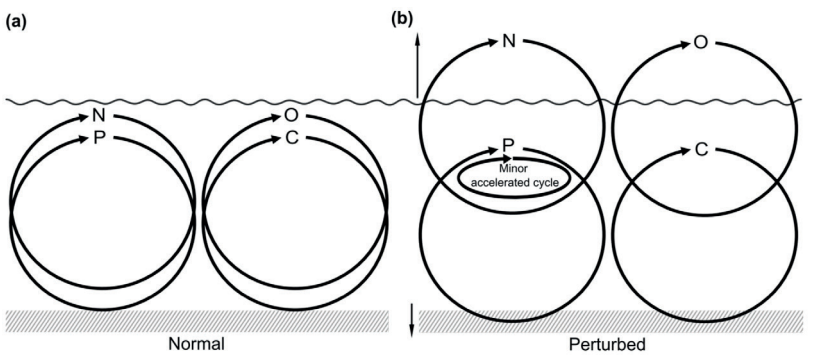

Figure 4. A lake or reservoir suffering from external forcing accelerates its renewal rate, displaces part of its components at its boundaries, or removes them. Nitrogen (N) and oxygen (O) migrate to the atmosphere, while phosphorus (P) and carbon (C) migrate to the sediments. A minor cycle is generated in which the internal load recycling and release of P into the water column is accelerated. (a) Normal, (b) Perturbed. Redrawn from the original model proposed by Margalef (1983). *Un lago o embalse forzado acelera su velocidad de renovación, desplaza parte de sus componentes a sus fronteras, o los elimina. El nitrógeno (N) y el oxígeno (O) migran a la atmósfera, mientras que el fósforo (P) y el carbono (C) migran a los sedimentos. Se genera un ciclo menor en el que se acelera el reciclado de la carga interna y liberación de P en la columna de agua a) Normal, (b) Perturbado. Redibujado a partir del modelo original propuesto por Margalef (1983).*

Reservoirs are particularly threatened by eutrophication and external inputs. Since eutrophication is a problem mostly linked to human activities, it could be said that the reservoirs, born as a consequence of civilization, are already fatally doomed to eutrophication from the beginning (Margalef et al., 1976). The accumulation of both soluble nutrients and insoluble sediments at the bottom of the reservoir are frequently associated, as a consequence of poor soil conservation in the reservoir watershed (Margalef et al., 1976). Reservoirs receive more inorganic and organic matter and nitrogen from the catchment than do lakes, due to their higher catchment area, and higher drainage ratio (Harrison et al., 2009; Hayes et al., 2017; Knoll et al., 2015; Prats-Rodríguez et al., 2014; Thornton et al., 1990; Tong & Chen, 2002). While carbonate weathering in calcareous watersheds produce significant inputs of inorganic carbon, the agricultural and urban areas export nitrogen and phosphorus to the watercourses, increasing significantly their concentrations in reservoirs (León-Palmero et al., 2021; León-Palmero et al., 2020a; López et al., 2011; Marcé et al., 2015; Weyhenmeyer et al., 2015).

In response to the external forcing, inland waters modify their functioning to minimize the consequences of stress by accelerating some internal processes and displacing a fraction of the materials to their boundaries, i.e., to the atmosphere

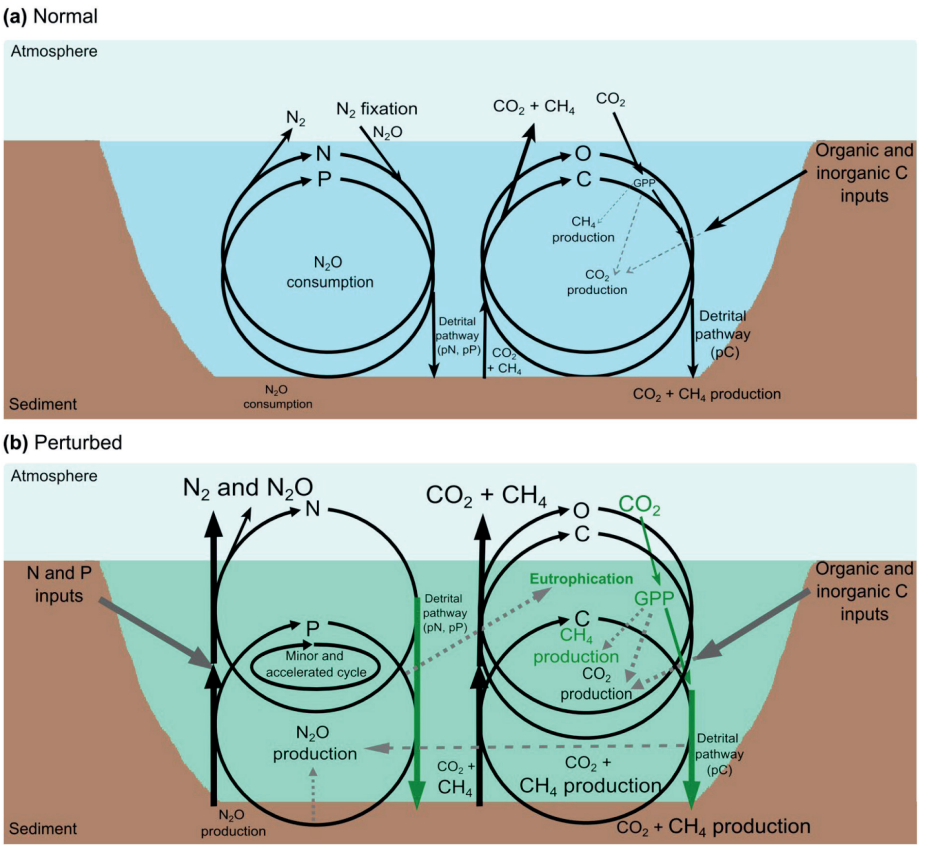

Figure 5. Eutrophication in lakes and reservoirs alters the biogeochemical cycles of N, P, C, and O, promoting the emission of GHG. Inspired by the model of Margalef (1983) that is shown in figure 4. (a) Normal, (b) Perturbed. pC/N/P stands for particulate C/N/P. The arrows symbolize connections, and their thickness or letters size is proportional to the importance of the process. *La eutrofización de lagos y embalses altera los ciclos biogeoquímicos del N, P, C, y O, promoviendo la emisión de GHG. Inspirado en el modelo de Margalef (1983) que se muestra en la figura 4. (a) Normal, (b) Perturbado. pC/N/P significa C/N/P particulado. Las flechas simbolizan conexiones, y su grosor o tamaño de las letras es proporcional a la importancia del proceso.*

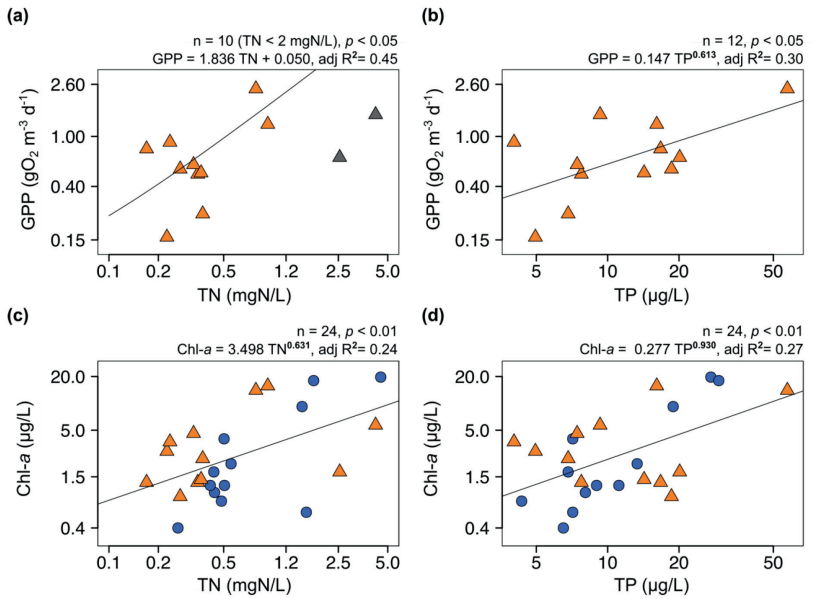

Figure 6. Effect of TN and TP on GPP and Chl-*a* concentrations in the epilimnion of the study reservoirs. GPP as function of (a) TN and (b) TP concentrations. Chl-*a* concentration as function of (c) TN and (d) TP concentrations. In (a), only values with TN < 2 mgN/L were included in the analysis. The orange triangles represent values during the stratification period, and the blue dots represent values during the mixing period. Note the log scales. *Efecto del NT y PT en la PPB y la concentración de Chl-*a *en el epilimnion de los embalses estudiados. La PPB es una función de la concentración de (a) NT y de (b) PT. La concentración de Chl-*a *es una función de la concentración de (c) NT y de (d) PT. Los triángulos naranjas representan los flujos durante el periodo de estratificación, y los círculos azules representan los flujos durante el estado de mezcla. En (a) sólo los valores con TN < 2 mgN/L fueron incluidos en el análisis. Nótense las escalas logarítmicas.*

and the sediments. A perturbed system removes a fraction of its C and P from the water column to the sediment, while a fraction of the O and N is displaced to the atmosphere (Fig. 4). Thanks to several regulation mechanisms, the system deviates from its previous situation less than expected (Margalef, 1983). Based on the clear feedbacks between eutrophication and GHG emissions, I propose that the production of CO_2, CH_4, and N_2O are parts of the response of reservoirs in particular, but inland waters in general, to the human external forcing. Besides N and P causing eutrophication, I will also consider carbon inputs from the watersheds as part of the external forcing. I show this response in figure 5, which is inspired by the model proposed by Margalef for perturbed ecosystems in his book "Limnología" (Fig. 4) (Margalef, 1983).

N and P loadings from the watershed produce eutrophication, leading to the increase of gross primary production (GPP) to the limit defined by the light absorption of chlorophyll. The effect of TN and TP increasing GPP and Chl-*a* concentrations in the epilimnion of the study reservoirs is shown in figure 6. This increase in GPP incorporates more CO_2 into the system (i.e., autochthonous organic matter, green arrows in figure 5), and increases the production of CH_4 in oxic conditions, which is linked to phytoplankton growth and the photoautotrophic carbon fixation of algae and cyanobacteria, as discussed above (Bižić et al., 2020; Hartmann et al., 2020; Klintzsch et al., 2019; Lenhart et al., 2016; León-Palmero et al., 2020b). Consequently, the concomitant CO_2 production by respiration (i.e., organic C mineralization) also increases in the photic zone and in deeper layers due to the higher availability of organic matter. In addition, the higher availability of nutrients allows more efficient decomposition of the autochthonous and the allochthonous

organic matter in eutrophic waters (Rantakari & Kortelainen, 2005). In the study reservoirs the respiration rate during the stratification period was a function of the chlorophyll-*a* concentration in surface waters, and the respiration rate was the second variable driving the CO_2 fluxes (León-Palmero et al., 2020a). In addition, the decomposition of organic carbon compounds and further CO_2 production in surface waters also occurs by photomineralization (Ortega-Retuerta et al., 2007; Reche et al., 1998).

Nevertheless, the respiration rate only explained 9.4 % of the deviance in the fitted model for CO_2 fluxes in these reservoirs (León-Palmero et al., 2020a). Autochthonous and allochthonous organic matter mineralization may be the main driver of CO_2 emissions in carbonate-poor systems. However, in lakes and reservoirs with an alkalinity exceeding 1 mEq/l, which represents the 57 % of the surface area occupied by lakes and reservoirs worldwide, carbonate weathering explains the CO_2 supersaturation and CO_2 fluxes (Marcé et al., 2015). In our fitted model, the watershed lithology was the main driver of CO_2 fluxes, explaining 90.7 % of the deviance (León-Palmero et al., 2020a). This result also suggests that an increase in the erosion and weathering rates in reservoir watersheds may also increase CO_2 emissions.

During eutrophication, a higher amount of OM is produced in the photic zone, and a significant fraction of this autochthonous OM will follow the sediment's detrital pathway as particulate C, N, and P (pC/N/P in Fig. 5). Throughout the water column and in the sediments, the microbial community degrades a fraction of the organic C, while another fraction is sequestered by sediment burial. OM decomposition by microbial activity consumes the oxygen in the water column and may lead to hypoxia/anoxia events during the stratification period. In other words, an oxygen fraction is displaced to the atmosphere (Margalef, 1983). The deoxygenation process affects biodiversity and nutrient biogeochemistry, and it has been linked to climate warming and human activities in coastal and ocean waters (Breitburg et al., 2018). Deoxygenation is also a widespread phenomenon in temperate lakes, and the decline in the oxygen concentration in inland waters is 2.75 to 9.3 times greater than observed in the world's oceans (Jane et al., 2021).

Low oxygen events enhance GHG production by archaeal methanogenesis, nitrifier denitrification, and denitrification, increasing the production of CH_4, N_2O, and CO_2. Anoxia particularly enhances the production of CH_4 over CO_2, because CH_4 is the dominant product of OM mineralization in low oxygen conditions (Liikanen et al., 2002). Importantly, this autochthonous organic matter exported from the photic zone not only increases the quantity but also the quality of the organic substrates reaching deeper layers and sediments, positively affecting the production of GHGs more than from allochthonous inputs (Grasset et al., 2018; West et al., 2012). In the study reservoirs, the production that follows the detrital pathway, which was accounted as cumulative Chl-*a*, promoted CH_4 production in low oxygen layers (León-Palmero et al., 2020b), and N_2O production in the water column (León-Palmero et al., in press). Therefore, phytoplanktonic sources appear to determine the CH_4 concentration in reservoirs at two levels: in oxic waters by direct CH_4 production by phytoplankton, and in anoxic waters by the decomposition of the phytoplanktonic biomass exported from surface layers (León-Palmero et al., 2020b). Previous studies also related CH_4 emissions to Chl-*a* concentrations in lakes and reservoirs, and highlighted that eutrophication is the primary driver of CH_4 emissions (Bastviken et al., 2004; Deemer et al., 2016; DelSontro et al., 2018).

According to Margalef (1983) a perturbed system removes a C fraction to the sediment (Fig. 4). Carbon burial rates in reservoirs are usually high due to the watershed instability and high erosion rates, and contribute substantially to aquatic C sequestration (Anderson et al., 2020). Due to the higher nutrient availability, the global C sequestration in lake and reservoir sediments has increased significantly (Anderson et al., 2020), although it is still unclear how the proportion of C emitted versus C buried changes in response to eutrophication. Most studies evaluating the C burial (and emission) in lakes and reservoirs didn't consider how the water level fluctuations can expose sediments to the atmosphere (i.e., drawdown areas) and alter the C balance in these areas. In this regard, Keller et al. (2021) showed that reservoirs

may act as net carbon sources when these drawdown areas are taken into account, because they emit more carbon (as CO_2, and CH_4) than they bury. Accounting for the episodically exposed sediments, the ratio between carbon emissions and carbon burial in sediments would increase from 1.26 (0.66–2.58) to 2.02 (1.04 – 4.26).

Overall, the CO_2 and CH_4 emissions in inland waters determine the release of an important fraction of C to the atmosphere, while the organic C burial determines the movement to the sediment. This C that is released or buried comes from CO_2 fixation (autochthonous OM), allochthonous OM, or inorganic inputs. There is general agreement that eutrophic reservoirs emit more CH_4 than oligotrophic ones, and the increase is not linear, but rather exponential (Deemer et al., 2016; DelSontro et al., 2018). However, it is not clear if eutrophication may reverse the carbon budget of reservoirs, that is, shifting the ecosystem from net heterotrophy to net autotrophy due to the large amount of CO_2 converted to organic material, as some studies in lakes suggested (e.g., Pacheco et al., 2014), while others found the opposite trend (e.g., Zhou et al., 2020). Inland waters are often heterotrophic systems (Tranvik et al., 2018), and this net heterotrophy can also be found in eutrophic systems (Prairie et al., 2002). In this study, reservoirs exposing the highest TN and TP concentrations (i.e., Colomera and Iznájar) showed a negative NEP in the epilimnion (i.e., g O_2 m^{-3} d^{-1}), while the ones with the positive NEP (i.e., San Clemente and Rules) showed low nutrient concentrations (i.e., g O_2 m^{-3} d^{-1}, table S3). The global analysis by Deemer et al. (2016) in reservoirs indicated that eutrophication did not affect the net carbon balance of reservoirs very much, but increased significantly the atmospheric radiative forcing of reservoirs due to the higher global warming potential of CH_4. Our results in Mediterranean reservoirs are in line with those of Deemer et al. (2016). CO_2 emissions were mostly driven by the lithology of the watershed, instead of the biological CO_2 production in the system. Regarding the model shown in figure 5, and in view of the current knowledge, I consider that it is necessary to add another deviation in the C cycle to the atmosphere, in order to include CO_2 and CH_4 emissions, as a significant part of reservoir response to eutrophication. This deviation of C to the atmosphere also includes C emissions from drawdown areas in the model. Water level oscillations due to climate change or human management of reservoirs may increase the C deviation to the atmosphere at the same time that decrease the deviation to the sediment.

Moreover, the excess of P in the reservoir water column is also displaced to the sediment, that acts as a P trap (Margalef, 1983). The burial of P in inland water sediments represents 56 % of terrestrial P inputs into inland waters, and reservoirs are particularly effective in P sedimentation (Maranger et al., 2018). A fraction of the P that is buried, is bound to Fe and Al hydroxydes, and it can return to the water column under reductive conditions (i.e., anoxic conditions) due to the dissolution of the Fe-bound P in the sediments (Nürnberg, 1984). Additionally to the role of P promoting phytoplankton growth, we also found that P promoted denitrifying bacterial abundance in the study reservoirs, thus impacting the production of N_2O (León-Palmero et al., in press). Interestingly, Finlay et al., (2013) found that the higher availability of P increased nitrogen removal rates and efficiency based on a global lake dataset. These results support an important feedback between the P and N cycles.

Finally, the N cycle is the most complex biogeochemical cycle on Earth (Thamdrup, 2012), and it remains the most poorly constrained of the three elements (i.e., C, P, and N) in inland waters due to the complexity of the cycle, and the bias towards C and P (Maranger et al., 2018). Nitrogen appears in diverse chemical forms and undergoes a variety of transformations mediated by specialized microorganisms, which can increase, maintain or remove N from the system (Stein & Klotz, 2016; Thamdrup, 2012). Similarly to P, I believe that there might be an equilibrium concentration of N for each system, which should depend on the physico-chemical characteristics of the water. Inland waters can increase the N inventory through N_2 fixation from the atmosphere, which is the biggest pool of N (Margalef, 1983). They can also drive the excess N to the atmosphere by producing significant amounts N_2 and to a lesser extent N_2O. Maranger et al. (2018) calculated that up to the 75 % of N loss in inland waters is

as gas to the atmosphere. Denitrification produces N_2 and N_2O, while other microbial pathways, such as annamox, only produce N_2 (Thamdrup, 2012). Zhu et al. (2015) estimated that anammox could be responsible for 11.4 % of the total N loss from China's inland waters. Aerobic ammonia oxidizing organisms can also produce N_2O as by-product, with the higher rates at suboxic conditions (Codispoti, 2010), although we did not detect a significant contribution by them to the N_2O pool in the study reservoirs (León-Palmero et al., in press). In contrast, we did find that denitrifying bacteria were ubiquitous and very abundant in the water column of the study reservoirs, as well as significantly related to the N_2O concentration (León-Palmero et al., in press).

Reservoirs are more efficient at removing N than lakes per unit area (Harrison et al., 2009), and it was estimated that up to 6.5 Tg N/yr is lost from reservoirs to the atmosphere through denitrification (Beusen et al., 2016; Harrison et al., 2009). Based on the changes observed in the dissolved inorganic N (DIN) concentrations, we estimated that Cubillas and Iznájar reservoirs removed 468 and 5337 kg N/d from July to September in 2018, representing a 45 % and 11 % decrease, respectively, in the DIN concentration in the water column (León Palmero, 2021). The study reservoirs were sinks and sources of N_2O to the atmosphere depending on the N availability (León-Palmero et al., 2020a), which is in agreement with previous studies (Baulch et al., 2011; Beaulieu et al., 2011, 2015; Seitzinger et al., 2000). Denitrification acted as an N_2O sink, reducing N_2O to N_2 at low N concentrations, while it was a significant source of N_2O at high N concentrations. The consumption and the production of N_2O were enhanced at low oxygen conditions, where we detected the lowest and the highest saturation values (León-Palmero et al., in press). Denitrification was also favored by P inputs, and autochthonous organic matter, which are typical components of a eutrophication scenario, as if the process fed back on itself to maximize nitrogen loss. Therefore, denitrification may act as an ecosystemic regulation mechanism to minimize the consequences of stress by releasing the excess N back into the atmosphere, from where it was extracted first of all by human activities.

FINAL REMARKS

The changes undergone by an aquatic ecosystem during eutrophication are much more profound than simply excessive phytoplankton growth. The increase in nutrient availability causes deep changes in the biogeochemical cycling of basic elements for life (i.e., C, N, P, and O) and affects biodiversity and the ecosystem services provided to humans (e.g., drinking water in the case of reservoirs). Recent studies have shown that eutrophication also increases the production and emission of greenhouse gases, especially methane and nitrous oxide. These two gases represent a very significant portion of the total radiative forcing in the study reservoirs, even exceeding the forcing by CO_2 during the stratification period. As ecologists, we should address eutrophication as a whole ecosystem reaction, considering the multiple interconnections and feedbacks. That includes GHG emissions as a part of the response, not as a consequence. To explain this idea, Margalef's original model on perturbed inland waters provided me with the perfect canvas.

ACKNOWLEDGMENTS

The financial support was provided by the Ministerio de Economía y Competitividad (HERA project, grant no. CGL2014-52362-R), and the Ministerio de Ciencia, Innovación y Universidades (CRONOS project, RTI2018- 098849-B-I00) of Spain. EL-P was supported by a PhD fellowship from the Ministerio de Educación, Cultura y Deporte of Spain (grant nos. FPU014/02917), and a postdoctoral contract from CRONOS project at the University of Granada, and later from Danmarks Frie Forskningsfond (DFF, 1026-00428B) at the University of Southern Denmark. The author thanks Isabel Reche and Rafael Morales-Baquero for their supervision during her PhD, and Bess B. Ward for her thoughtful comments and for proofreading the English version of this manuscript. The author also thanks the Iberian Association of Limnology (AIL) for the award to the best Iberian thesis in the field of limnology 2021, and for their invitation to present the research in a plenary talk at the SIBECOL-AIL congress in Aveiro and to contextualize this manuscript.

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