GREENHOUSE GAS DYNAMICS OF SALINE LAKES: A STUDY ON THE IMPACTS OF ENVIRONMENTAL CHANGE

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ABSTRACT

GREENHOUSE GAS DYNAMICS OF SALINE LAKES: A STUDY ON THE IMPACTS OF ENVIRONMENTAL CHANGE

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Saline lakes, increasingly impacted by climate change and land use, play an important role in the global carbon and nitrogen cycles. This thesis study examined the complex factors influencing greenhouse gas (GHG) emissions from a diverse array of saline lakes, with a particular focus on those situated in semi-arid regions and experiencing increasing salinization pressures. Employing a combined approach of literature review, remote sensing methods, predictive models, field surveys, and controlled mesocosm experiments, we examined the interplay between salinity, temperature, climate effects and eutrophication on methane (CH_4), carbon dioxide (CO_2) and nitrous oxide (N_2O) emissions. Our findings reveal that saline lakes, particularly inland ones, are significant sources of CH_4 and N_2O, with ebullition emerging as a minor, but potentially significant emission pathway. Salinity exerted the primary inhibitory effect on CH_4 emissions, and the current salinization trend can further reduce CH_4 emissions from these ecosystems. However, organic matter availability partially counteracts the reducing impact of salinity. Temperature emerged as a primary driver of GHG emissions, tapping several biogeochemical pathways involved in GHG production and exhange, particularly stimulating ebullition, yet its influence varied across study sites, implicating the role of site specific factors. While temperature directly stimulated GHG production through enhanced microbial activity, it also altered ecosystem metabolism and nutrient cycling, which likely contributed to the observed variability. Unlike CH_4, which is strongly influenced by salinity, N_2O and CO_2 emissions are anticipated to increase in a likely future characterized by increased salinization, eutrophication, significant lake surface area losses, and frequent dry outs. This potentially mitigates the climate forcing benefit caused by the reduction of CH_4 emissions. This study underscores the vulnerability of saline lakes to land and water use changes, and emphasizes the interconnectedness of GHG emissions and ecological state of the ecosystem. Effective GHG mitigation strategies must address the underlying causes of ecosystem degradation, as increased emissions are symptomatic of broader environmental challenges.

Keywords: Saline Lakes, Freshwater Salinization, Eutrophication, Climate Change, Anthropogenic Pressures

ÖZ

TUZLU GÖLLERİN SERA GAZI DİNAMİKLERİ: İKLİM DEĞİŞİMİ VE İNSAN FAALİYETLERİNİN ETKİLERİNİ ANLAMAK

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Tuzlu göller, artan iklim değişikliği ve diğer insan faaliyetlerinden etkilenerek küresel karbon ve nitrojen döngülerinde önemli bir rol oynamaktadır. Bu çalışma, farklı coğrafi özelliklere sahip, özellikle artan tuzluluk baskısı altında olan yarı kurak bölgelerdeki tuzlu göllerde sera gazı salımlarını etkileyen faktörleri incelemektedir. Çalışmada literatür araştırması, uzaktan algılama yöntemleri, tahmin modelleri, saha çalışmaları ve kontrollü mezokozm deneylerini birleştiren çok yönlü bir yaklaşım benimsenmiştir. Araştırma, tuzluluk, sıcaklık, iklimsel etkiler, ötrofikasyon ve besin zenginleşmesinin metan (CH_4), karbondioksit (CO_2) ve azot protoksit (N_2O) emisyonları üzerindeki etkileşimini incelemiştir. Bulgularımız, özellikle iç kesimlerdeki tuzlu göllerin önemli CH_4 ve N_2O kaynakları olabileceğini, ve baloncuk yoluyla gaz salımının (ebullition) tuzlu göllerde küçük ancak potansiyel olarak önemli bir emisyon yolu olduğunu ortaya koymuştur. Tuzluluk, CH_4 emisyonlarını azaltırken, sıcaklık tüm sera gazı emisyonlarını artıran temel bir itici güç olarak ortaya çıkmıştır. Bununla birlikte, sıcaklığın etkisi çalışma alanlarına göre farklılık göstererek, ekosistem metabolizması ve besin döngüsü gibi ikincil faktörlerin rolünü vurgulamıştır. CH_4'ten farklı olarak, N_2O ve CO_2 emisyonlarının gelecekte artması beklenmektedir, bu da artan tuzluluk, ötrofikasyon, önemli göl alanı kayıpları ve sık görülen kuraklık dönemlerinin etkisiyle iklim zorlamasına neden olan CH_4 emisyonlarındaki azalmanın etkisini hafifletebilir. Bu çalışma, tuzlu göllerin çevresel değişime duyarlılığını vurgulamakta ve sera gazı emisyonları ile ekosistem sağlığı arasındaki bağlantının altını çizmektedir. Etkin sera gazı azaltma stratejileri, ekosistem bozulmasının temel nedenlerini ele almalıdır, çünkü artan emisyonlar daha geniş çevresel sorunların bir belirtisidir.

Anahtar Kelimeler: Tuzlu Göller, Göl Tuzlanması, Ötrofikasyon, İklim Değişimi, Antropojenik baskılar

To Sabahattin, Habibe and Barış, your support has been a constant source of strength for me.

Onward, to the Sun, onward!
We make a raid, bound sunward!
The Sun, we shall subdue its might,
Soon will come its surrender bright.

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INTRODUCTION

Aquatic ecosystems, including freshwater and saline lakes, ponds, streams, and wetlands, are essential for human life due to their valuable ecosystem services. These lentic ecosystems, while harboring a rich biodiversity, are also strategic resources for human societies, serving as sources of drinking water, irrigation, and other ecosystem services, and even minor changes in lake systems can have significant consequences for human well-being (Moss, 2012). These ecosystems are under threat from multiple stressors, including salinization, warming, and eutrophication, driven by factors such as increased agriculture, excessive water use, and climate change (Cunillera-Montcusi et al., 2022; Jeppesen et al, 2015; Meerhoff et al., 2022). These stressors can lead to ecosystem degradation, a decline in ecosystem services, biodiversity loss, and economic damage. Understanding and evaluating the external processes that influence the functioning of these ecosystems, identifying stress factors, and assessing the impacts of these factors have critical ecological and economic implications. By gaining insights into the future health of ecosystems, climate change mitigation strategies, and sustainability, we can develop effective measures to protect and restore these vital resources.

Salinization, climate change and eutrophication

Climate change and eutrophication are the two main stressors over aquatic ecosystems (Meerhoff et al., 2022). Threats posed by direct and indirect effects of climate change and agricultural intensification cause a series of cascading impacts on the health of lake ecosystems, one of the most immediate effect being salinization. Freshwater salinization is a significant global challenge, with numerous consequences and contributing factors. salinization (Cunillera-Montcusi et al., 2022). Overuse of surface- and groundwater resources as a result of agricultural intensification, urbanization, and the decline of lake systems due to water shortages are major drivers of salinization. Climate change, including warming and altered precipitation patterns, can exacerbate these trends, particularly in semi-arid regions (Cunillera-Montcusi et al., 2022), through various interacting effects (Figure 1). Increased evaporation because of climate warming is expected to increasingly contribute to negative water balance of the lakes, and in turn, salinization trend in both freshwater and brackish lakes (Williams, 2001). While this is the case for inland lakes, sea level rise, another consequence of climate change, can favor salinization in coastal brackish lakes through seawater intrusion (Scheffers and Kelletat, 2019). Numerous studies suggest that increased salinity is a major threat to the functioning and biodiversity of lakes, causing drastic and nonlinear reductions in taxon richness, food chain length, and trophic structure (Gutierrez et al., 2018; Lin et al., 2017). These nonlinear changes indicate the existence of salinity thresholds beyond which even minor changes can lead to drastic shifts in ecosystem structure (Jeppesen et al., 2007).

Beyond salinization, climate change has already impacted many aquatic environments globally and the extent of its impact will continue to intensify in the next century. The average surface temperature has risen by an average of 0.85 °C since the last century (IPCC, 2017), a significant part of this rise (0.55 °C) has occurred in the past 30 years. Between 1972 and 2009, the average temperature rise in Türkiye reached 1.6 °C while the average water temperature rise in the Mediterranean reached 0.9 °C. The Mediterranean basin, especially the Eastern Mediterranean, is one of the regions that are most sensitive to the negative effects of global climate change (Giorgi, 2006; Russo et al., 2019). These effects can be summarized as an increase in average temperature and evaporation, decrease in average precipitation (up to 25-30 %), increased interannual variation of temperature and precipitation, and a rise in the frequency and amplitude of extreme weather events (IPCC, 2007). Moreover, land drought is expected to double while a severe reduction of river runoff (up to 40 %) is also predicted in the Eastern Mediterranean (IPCC, 2014). Furthermore the alteration of wind patterns over land and oceans, are are significant changing (IPCC, 2021).

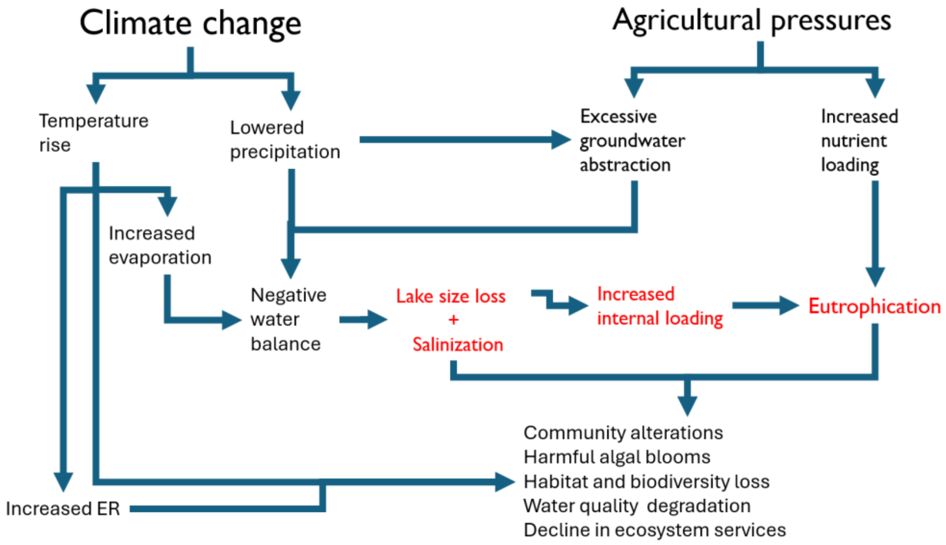

Fig. 1 Interactive effects of climate change and agricultural pressures on lake ecosystems in hot semiarid regions.

Temperature changes lead to enhanced evaporation, which in turn expedites the decline of lake size and water levels. Reduction of water volume also causes concentration of dissolved matter, potentially leading to increased salinity levels while lower precipitation can contribute to the water stress, pushing the lake ecosystems towards desiccation (Jeppesen et al., 2015). Beyond the sole physical changes, warmer water temperatures directly influence the biological communities. Elevated water temperatures can increase metabolic rates for aquatic organisms, while heightened metabolic activity leads to enhanced ecosystem respiration (ER), the process by which organisms break down organic matter and release carbon dioxide (CO_2), causing dissolved oxygen (DO) concentrations to drop in the water column. Acute or chronic hypoxia events cause oxygen stress in aquatic environments, particularly for fish and other organisms with high oxygen demands, potentially causing fish kills (Rao et al., 2014). In addition, agricultural activities in semi-arid regions often and increasingly rely on irrigation (Yano et al., 2007) which is achieved by damming of the natural streams and groundwater use. Surface- and ground water abstraction for irrigation purposes exerts a strain on lake water inputs, further reducing water levels beyond those caused by evaporation (Yano et al., 2007). The extreme water use is especially detrimental in closed basins, which have sensitive water balances as in the case of western Anatolia (Konya Closed Basin and Burdur Closed Basin), causing significant reduction and complete dry out of lakes (Yılmaz et al., 2021; Çolak et al., 2022), potentially leading to habitat loss and fragmentation, biodiversity loss and ecosystem degradation for aquatic organisms including fish and birds (Korkmaz et al., 2022).

Nutrient enrichment through agricultural runoff is another major threat to aquatic environments worldwide, growing alongside increasing agricultural demands (Jeppesen et al., 2014). This enrichment stimulates eutrophication by creating favorable conditions for primary producers, potentially leading to algal blooms, negatively affecting the natural submerged vegetation which are crucial to ecosystem functioning (Sondergard et al., 2010; Zhang et al., 2016). Excessive phytoplankton growth also consumes DO during decomposition, which creates a synergistic effect with increased ER, further exacerbating oxygen stress (Rao et al., 2014.). Nutrient enrichment in the lakes frequently leads to harmful algal blooms, decreasing water quality and ecosystem health.

The increasing frequency of extreme weather events adds another dimension of stress to lentic ecosystems. Heatwaves can trigger acute hypoxia and biological stress in aquatic environments (Shinohara et al., 2023), while heavy precipitation events can introduce intense nutrient loads (Li et al., 2015), both potentially exacerbating the impacts discussed. These events can have significant impacts due to their intensity, although their temporal scale is shorter.

Additionally, there is evidence suggesting a global decline in wind speeds since the 1980s, a phenomenon known as “global stilling” (IPCC, 2021), that can potentially alter many processes including GHG dynamics of lakes and coastal environments.

Overall, climate change is predicted to exacerbate the effects of eutrophication in lakes and other aquatic systems (Jeppesen et al., 2014). As a result of this “allied attack" on the ecosystem functioning and structure of lake ecosystems, range contraction or complete habitat loss, drastic changes in species distribution and composition, food chain structure, system photosynthesis and respiratory dynamics are expected to occur (Moss, 2012), diminishing the overall health and resilience of lake ecosystems. The anticipated changes in these ecosystems will have impacts beyond their boundaries. Lakes and wetlands serve important functions within the global carbon (C) and nitrogen (N) cycles, significantly contributing to greenhouse gas (GHG) emissions. Thus, alterations to these aquatic environments have implications on a planetary scale. Understanding how these changes affect lake biogeochemistry and GHG dynamics is important for developing realistic and insightful mitigation strategies, i.e. "fighting back."

Greenhouse gases, climate change, lakes, salinization

GHGs and climate change

GHGs play a central role in the heat budget of the atmosphere. It has been demonstrated by various scientists since the mid-19th century that GHGs, the most important ones being carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and water vapor, in terms of their atmospheric concentration and effects, heat the Earth's surface by absorbing heat from the sun and make the Earth suitable for life. As early as Tyndall (1861), it has been suggested that the changes observed in the geological time in the climate were directly related to the ratio of water vapor and carbon dioxide in the atmosphere while Arrhenius (1896) attempted to quantify the relation of surface temperatures with the atmospheric mixing ratio of carbon dioxide (see. Anderson, 2016). Callendar (1938), showed the warming caused by the change in carbon dioxide concentration in the last 50 years. A climate sensitivity value of 2 °C calculated by Callendar corresponds to the lower end of the IPCC's forecast range today.

Modern discussions concerning climate change often utilize the concepts of climate forcing, or radiative forcing, to quantify the influence of various atmospheric components, such as GHGs, aerosols, water vapor and cloud density, on Earth's energy balance. Radiative forcing, simply put, is the difference between the energy of the sunlight that reaches to the Earth's surface and the heat reflected from it and is expressed in J/s m^2 or W/m^2. This value reflects the observed or projected changes in climate and average surface temperatures in the long run. In other terms, *"Radiative forcing is a measure of the influence a factor has in altering the balance of incoming and outgoing energy in the Earth-atmosphere system and is an index of the importance of the factor as a potential climate change mechanism"* (IPCC 2007).

The concentrations of CO_2, N_2O, and CH_4 in the atmosphere have increased 40 %, 150 % and 20 %, respectively, compared to the pre-industrial revolution values (~1750), with CO_2 increased from 280 ppm to 400 ppm, CH_4 from 700 ppb to 1900 ppb, and N_2O increased from 280 ppb to 325 ppb (IPCC 2013). GHGs contribute a total of 2.8 W/m^2 to the net climate forcing, which is 2.3 $W/\ m^2$, and constitute the main component of the total heating effect (IPCC 2013).

Lentic ecosystems and GHGs

Serving as an important nexus in the global C and N cycles, lakes and wetlands perform a multitude of biogeochemical functions including nutrient cycling and carbon sequestration/release. They contribute a disproportionately high percentage to the global greenhouse gas (GHGs) budget compared to their relatively small surface areas (DelSontro, 2018; Bastviken, 2011). Although the estimations vary, emissions from the wetlands, rice paddies, and lakes constitute roughly the half of the total global methane (~250 Tg y^{-1}) and 5 % of the nitrous oxide emissions (Saunois et al., 2016; Tian et al., 2020). Overall, they are equivalent to ~20 % of global fossil fuel CO_2 emission and this ratio is predicted to rise even further with the continued eutrophication (DelSontro, 2018). While their role as significant sources of GHG emissions underscores their importance in the Earth's climate system, the intertwined relationship between eutrophication, salinization and climate warming creates complex impacts on the GHG dynamics of these ecosystems, rendering them permanent climate hotspots (Fig. 2). While these stressors are key in shaping GHG dynamics of lakes, in turn, GHG emissions from lentic environments can reinforce warming and salinization trends globally in longer timescales.

Temperature is a key factor in the abiotic and biotic processes, including its direct effect on the metabolism of the lake ecosystems (Yvon-Durocher, 2014; Wik et al., 2014). Higher temperatures result in higher metabolic rates, including respiration and methanogenesis, i.e., bacterial sedimentary production of CH_4 under anoxic conditions (Wik et al., 2014). Eutrophication through nutrient enrichment is the other factor driving GHG emissions through stimulating various pathways that lead to production of GHGs (DelSontro et al., 2016). Nutrient enrichment stimulates primary production, leading to increased organic matter availability, which in turn fuels aerobic and anaerobic decomposition pathways. In hypoxic and anoxic conditions nutrient enrichment and eutrophication can stimulate N_2O production through different pathways, further contributing to GHG emissions of lentic environments (Kortelainen et al., 2020; Tian et al., 2018).

A frequently overlooked aspect of climate change is the alteration of wind patterns. lower wind speeds can reduce the diffusion of gases from lakes, potentially slowing down emissions. Gas diffusion from lakes is heavily dependent on gas transfer velocity, which is influenced by temperature, barometric pressure, and wind stress over the surface. Wind intensity can dramatically alter gas transfer velocity, making it a crucial factor for gas diffusion from lakes (Cole and Caraco, 1998; Schilder et al., 2013). While slower average wind speeds may reduce diffusive gas fluxes, the overall impact on GHG emissions will depend on the balance between reduced diffusion and changes in gas production.

Salinity and salinization, introduces further complications to the production of GHGs, especially associated with methanogenesis. While CH_4 production is potentially stimulated by the combined effects of temperature and organic matter availability (Davidson et al., 2018; DelSontro et al., 2016), salinity can cause biological stress and alter the bacterial community (Zhou et al., 2022), potentially affecting the GHG dynamics. However, more importantly, the sulfate ion (SO_4^{2-}), a component of salt in the natural saline systems, effectively inhibits CH_4 production through competition, and also contributes to the anaerobic oxidation of CH_4 in water column through coupled processes (Barnes and Goldberg, 1976; Bartlett et al., 1987). This poses a complication for assessment and quantification of the multiple stressors (eutrophication, temperature etc.) impacts on the CH_4 in the ecosystems.

Accurate assessment of CH_4 emissions from aquatic environments is further hindered by the episodic nature of ebullition, the intermittent and rapid release of CH_4 gas from sediments. Ebullition is the alternative emission pathway of CH_4, in which CH_4 produced in the sediment accumulates to supersaturation, followed by conversion to gas phase due to its low solubility and consequential release from the sediment upon the effect of a physical trigger (e.g., a drop in the atmospheric pressure, bioturbation, etc.) (eg., Wik et al., 2014). Although the early research primarily focused on the diffusional, continuous flux of CH_4 from aquatic ecosystems, ebullition events are often the major pathway in lentic ecosystems, contributing up to 70 % of total CH_4 emissions from lakes (Bastviken et al., 2004). Consequently, earlier research, primarily focused on diffusive fluxes, significantly underestimated CH_4 emissions from these ecosystems. To capture the full extent of CH_4 emissions, extended and continuous monitoring protocols and specific methodologies are required, especially in saline lakes, where the effects of ebullition is even less studied.

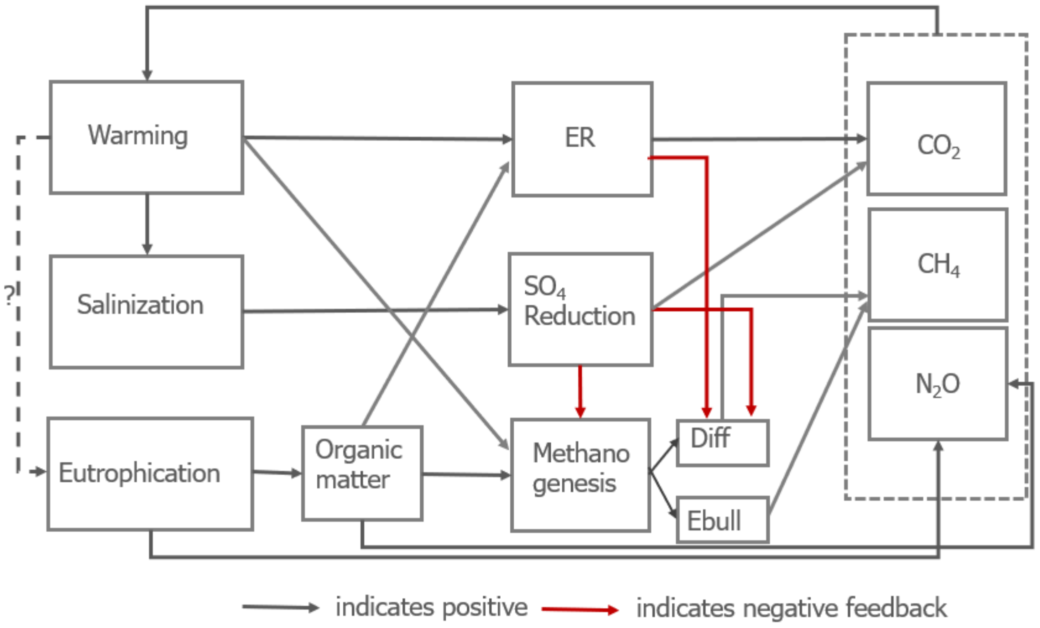

Fig. 2. An (over)simplified diagram of the feedback mechanisms between climate change, eutrophication and greenhouse gas emissions through various pathways in the aquatic ecosystems. Dashed line between warming and eutrophication suggests a less direct positive association.

Carbon dioxide

Carbon dioxide (CO_2**)** is the major GHG driving climate warming, with a radiative forcing of ~1.8 W m^{-2}, constituting more than 60 % of the net forcing (IPCC, 2014). CO_2 dynamics of lentic ecosystems are shaped fundamentally by biotic processes, i.e., photosynthesis and respiration, although abiotic factors, including groundwater seepage (Perkins et al., 2015), mineral dissolution (Vargas-Sánchez et al., 2022) also contribute to the emissions.

The role of lakes as sources or sinks of CO_2 is determined via a multitude of complex and dynamic factors. Earlier studies often reported CO_2 supersaturation in lake water, suggesting a net CO_2 emission (Cole et al., 1994). Moreover, lentic and riparian wetland ecosystems are generally considered as sources of CO_2 and global net emission from lakes and rivers are estimated to be 0.14 and 0.03 Gt C y^{-}, respectively (Cole et al., 1994; Duarte and Prairie, 2005). However, subsequent research suggests that many lentic ecosystems exhibit CO_2 undersaturation, indicating a net CO_2 uptake (Balmer and Downing, 2011). This apparent contradiction likely arises from the dynamic nature of CO_2 exchange between aquatic ecosystems and the atmosphere. The amount and direction of CO_2 flux is determined by the result of many processes including photosynthesis, respiration, and physical factors such as temperature, light availability, gas transfer rates and hydrology. These factors show significant variability across both spatial and varying temporal scales, from diurnal to seasonal to the interannual (Chiu et al., 2020), making generalizations about the CO_2 dynamics of the lakes difficult.

Temperature is a primary factor influencing CO_2 dynamics (Kosten et al., 2010). Seasonal and interannual oscillations and long-term climate warming exerts a significant influence on the ecosystem metabolism. Elevated temperatures often lead to higher respiration, and accelerate decomposition of organic matter, stimulating CO_2 emissions (Kosten et al., 2010) In the context of climate change, projected rise of global temperatures will likely alter the carbon balance of the lakes, pushing their metabolism to a more heterotrophic state, potentially intensifying their role as sources, and diminishing their capacity as sink (Kosten et al., 2010). The latter could be especially important for coastal wetlands, which are famously known for their carbon sequestration potential (Brown et al., 2016; Fourqurean et al., 2012; Serrano et al., 2021).

Eutrophication, driven by nutrient enrichment, can stimulate primary production and can temporarily enhance CO_2 uptake (Balmer and Downing, 2011). However, increasing organic matter in the water column would eventually stimulate decomposition, leading to elevated CO_2 emissions (Ollivier et al., 2019; Zhang et al., 2023). Reservoirs in particular show higher CO_2 emissions due to terrestrial inputs (Mackling et al., 2018). Similarly, inland lakes, particularly saline lakes endorheic basins, are also more prone to generally elevated CO_2 emissions as they are accumulating endpoints for nutrients and organic matter (Duarte et al., 2008).

Hydrology of the lakes, including residence time, water balance and nutrient transport also play a key role impacting GHG dynamics. Climate change, a critical factor tapping many processes related to carbon cycle in lakes including not only temperature but also hydrology, lake size and morphology through its various direct and indirect effects (Fig. 1). Together with agricultural stressors, it can alter water balance and residence time of the water bodies. Fluctuating lake levels, with temporary and permanent dry outs, influenced by seasonal and long-term climate change, can significantly alter CO_2 emissions. As lakes shrink, exposed lake sediments undergo rapid oxidation as they contact the atmospheric oxygen, releasing substantial CO_2 to the atmosphere in pulses (Keller et al., 2020). This phenomenon, particularly relevant in shallow lakes and wetlands, can further contribute to the emissions from lakes. The increasing frequency and severity of droughts associated with climate change potentially increases temporary and permanent lake dry outs, amplifying the potential for carbon release from these ecosystems (Keller et al., 2020).

Salinity also plays a role in various ways in ecosystem metabolism, thus can have significant effects on carbon cycling. Increasing salinity linked to climate change and anthropogenic activity can lead to lower primary production as it exerts biological stress on the plankton communities (Jeppesen *et al*., 2007; 2015; Ollivier *et al*., 2019) and potentially can alter the emissions. However, the complex interaction of physical, chemical, and biological processes governs CO_2 emissions from lentic ecosystems, for accurately assessing and predicting the carbon dynamics and future trajectory of these ecosystems, these factors must be taken into account together.

Methane

Methane (CH_4**)** is the simplest hydrocarbon and the most abundant organic gas in the atmosphere. CH_4, whose GHG potential is 25-40 times higher than that of CO_2, has a lifetime of 10 years in the atmosphere and causes both direct and indirect radiative forcing of around 0.58 W/ m^2, which accounts for almost 25 % of the total net radiative forcing (Lelieveld et al., 1998; IPCC 2013). The concentration of CH_4 in the atmosphere increases around 5 ppb per year, with an annual emission of 460-600 Tg (IPCC 2007; Wuebbles and Hayhoe 2002). 70 % of the atmospheric CH_4 is of anthropogenic origin while 30 % of originates from natural sources (Table 1). Natural wetlands and terrestrial aquatic systems are the main natural resources of methane with ~100 Tg y-1 (Fowler et al., 2009; IPCC, 2007) and paddy farming, cattle husbandry, energy production, biomass combustion and waste management are the main sources of human origin. The main mechanism removing CH_4 from the atmosphere is oxidation via hydroxyl (OH) radicals, the soil and stratosphere are secondary CH_4 sinks with a contribution of 6-7 %. (van Amstel and Swart, 1994; Fowler et al. 2009).

In wetlands CH_4 is produced by microbial processes under sub- and anoxic conditions, either sediment pore water or sediment water column interface, where oxygen becomes depleted. Methanogenesis is the ultimate step of organic matter degradation, occuring in environments where no other electron acceptors such as nitrate (NO_3), ferric ion (Fe^{3+}), manganese (IV) ion or SO_4^{2-} are available, and responsible for the oxidation of a significant amount of organic matter in wetlands and shallow lakes. In wetlands, 2-7 % of the carbon fixed as organic matter (net primary production) is emitted as CH_4 (Aselmann and Crutzen, 1989) estimate the percentage to be 5 % (Whiting and Chanton, 1993). Eutrophic conditions (increased nutrient loading and production) can cause enhanced CH_4 emission (Beaulieu, 2019; Davidson, 2015; DelSontro, 2016; Zhou, 2019). In addition, since respiration and methanogenesis are more temperature-dependent than photosynthesis (Allen et al, 2005, Yvon-Durocher et al, 2014; 2017), emissions of GHGs from wetlands are expected to increase with changing temperature. Indeed; even though other factors such as substrate availability or productivity complicate the relationship between microbial level temperature-dependence of methane production and its ecosystem scale results, i.e., CH_4 ultimately released to the atmosphere (Davidson 2015; DelSontro, 2016), many studies show that increasing temperature alone is associated with increased methanogen activity from microbial to ecosystem level (Yvon-Durocher, 2014; Wik et al., 2014; Duc et al., 2010; Bridgham et al. 2013). Moreover, climate warming has a potential of increasing the proportion of primary production emitted as CH_4 instead of carbon dioxide; a warming of 4 °C has been demonstrated to increase CH_4 efflux 20 % and 9 % more with respect to the rise of gross primary production (GPP) and ER, respectively (Yvon-Durocher, 2011). This suggests that there might be a previously unknown positive feedback mechanism that exists between aquatic ecosystems and warming. In addition to these, a few research conducted in recent years suggested that nutrient enrichment and warming may interact to exert a combined effect on the CH_4 emission from the wetlands (DelSontro, 2016; 2018; Davidson, 2018). Davidson et al. reported that in a mesocosm experiment nutrient enrichment without temperature treatment caused doubling of the total mean methane flux from 266 to 552 mg-CH_4 yr^{-1}, while nutrient enrichment combined with + 2-5 °C heating resulted 6- to 17-fold increase in the methane flux (2018).

The early studies regarding the effect of salinity on GHG emissions from the aquatic environments mainly focused on marine sediments and coastal/estuarine wetlands, where effects of salinity could be observed across a gradient. It is established that salinity strongly inhibits CH_4 emissions from marine sediments (Barnes and Goldberg, 1976) and salt marshes (DeLaune et al., 1983; Bartlett et al, 1987). It is understood through *in situ* observations and incubation experiments that presence of SO_4 ion favors sulfate reducing bacteria, which in turn outcompetes CH_4 producers, constituting the most dominant control over the CH_4 efflux (Barnes and Goldberg, 1976; DeLaune et al., 1983; Bartlett et al, 1987; Wang, 1996). This relationship, however, is subject to complication with other external factors. There are examples where CH_4 efflux increases upon intrusion of saline water to the medium (Weston, 2011) and there is evidence, or lack of evidence that suggests a non-linear relationship between salinity and CH_4 inhibition (DeLaune, 1983; Huertas, 2019). In context of extreme weather events, surges of freshwater addition (through heavy episodes of precipitation and flooding) can effectively lower salinity in wetland and shallow lake environments, eliciting a pulse of GHG emissions (Capooci, 2019). In addition, more recent studies reveal that the relationship of CH_4 emissions to salinity is modulated by temperature (Chamberlain et al., 2020) and the availability of organic matter (Soued et al., 2024). In certain cases, CH_4 production persists despite increasing salinity, to the shift of microbial community as a response to the salinization (Zhou et al., 2022). Nevertheless, annual log-transformed CH_4 flux from wetlands could be modeled against salinity with a linear fit (Bartlett, 1987; Poffenbarger, 2011). These findings show that saline and brackish wetlands and shallow lakes might be contributing relatively low yet significant amounts of GHGs, between salinity levels 5-20 ppb. Further studies demonstrate that a wetland ecosystem can act as a sink of CH_4 rather than a source as a response to an increasing salinity in an coastal wetland (Livesley and Andrusiak 2012; Welti et al., 2017). Few studies focusing on the GHG emissions from saline lakes report similar results: Verma et al. (2002) denote the dramatic difference of emissions between two adjacent lagoon lakes: while freshwater lake emitted 193.2 ± 24.5 mg m^{-2} h^{-1} brackish lake only emitted 9.3 ± 9.6 mg m^{-2} h^{-1}. Likewise, a recent hyper-saline lakes study demonstrated only minimal CH_4 efflux, with the exception of the ones whose salinity is altered (reduced) by external factors (Camacho et al., 2017), while another study suggested that hyper-saline lakes act as sinks for CH_4 (Sokolov and Tretsenko, 1995).

Table 1-1 Global annual budgets of N_2O and CH_4 (Fowler et al., 2009)

Source	N_2O **(Tg/Y)**	**Source**	CH_4 **(Tg/Y)**
Natural Sources			
Ocean	3.8 (1.8-5.8)	Ocean	4 (0.2-20)
Atmosphere	0.6 (0.3-1.2)	Termites	20 (2-22)
Soil	6.6 (3.3-9)	Wetlands	100 (92-232)
		Other	21 (10.4-48.2
Anthropogenic sources			
Agriculture	2.8 (1.7-4.8)	Rice paddies	60 (25-90)
Biomass burning	0.7 (0.2-1)	Biomass burning	50 (27-80)
Energy production	0.7 (0.2-1.8)	Energy production	106 (46-174)
Other	2.5 (0.9-4.1)	Cattle husbandry	81 (65-100)
		Waste management	61 (40-100)

Total Sources	**17.7 (8.5-27.7)**		**503 (410-660)**
Sinks			
Stratosphere	12.5 (10-15)	Stratosphere	40 (32-48)
Soil	1.5-3	Soil	30 (15-45)
		Tropospheric OH	445 (360-530)
Total sinks	14 (11.5-18)		515 (430-600)

Nitrous oxide

Nitrous Oxide (N_2O**)** has a current concentration of 325 ppb (IPCC 2013) and its atmospheric concentration increases by 0.25% (0.7-1.0 ppb) annually (Law, 2018). Despite its relatively low concentration, it has a heat absorption capacity 150-300 times higher than that of CO_2 on a molecular basis (van Amstel and Swart, 1994) and is therefore the third most important greenhouse gas with a radiative forcing of about 0.18 W/ m^2. Oceans (3.8 Tg y-1) and soil (6.6 Tg y-1) constitute the largest natural resources of N_2O, which has an annual emission of 18 Tg, while agriculture and wastewater are the main anthropogenic resources (Table 1).

Wetlands are significant, although not primary, source of N_2O. In aquatic ecosystems, N_2O is produced as a by-product of nitrification and intermediate of denitrification which optimally occur in (sub)oxic and anoxic conditions, (Kortelainen et al., 2020) respectively. Main controls on the nitrous oxide production therefore are oxygen level, nutrient availability and temperature. It can be generalized that increase of nutrient levels cause more N_2O emissions (Audet, 2014; Wang, 2009), while on the other hand, many research suggested that oxygen level poses a more dominant control over denitrification, and thus N_2O efflux (Liikanen and Martikainen, 2003; Wang, 2009). Relatively undisturbed (riparian) wetlands emit relatively low N_2O, and not usually considered “hotspots” (Audet et al., 2014) while eutrophic wetlands and lakes, especially shallow lakes and littoral regions of deep lakes are “hotspots” of N_2O (Wang, 2006). For example, in Lake Taihu, a hyper-eutrophic lake in China, littoral emissions range from -278 to 2101 μg N_2O m^{-2} h^{-1} and more than 40 % of its emissions is coming from its littoral zone, which covers only 5.4 % of total lake area. These findings are in line with previous studies (Huttunen et al., 2003), which suggests that N_2O emissions from the pelagic zone of lakes are negligible due to the low NO_3 inputs while littoral zones act as a buffer for NO_3 and contribute to the N_2O emissions. It is suggested that ammonium coming in groundwater affect N_2O emission positively (Audet et al., 2014) while experimental studies reveal that nitrate addition enhance denitrification and consequent N_2O release, regardless of their previous N-deposition level (McCrackin and Elser, 2010). This suggests that lake sediments have a high and unsaturated capacity of NO_3 uptake, and another study showed that anthropogenic inorganic N becomes a primary control only on heavy eutrophication conditions (Wang, 2009). In addition, relationship between temperature and N_2O efflux draws a complex picture. While emissions correlate strongly with seasonal temperature variation, observations from different regions do not reflect this (Davidson et al., 2015). Similar to the relationship of temperature and CH_4, the discrepancy between molecular level temperature dependence and ecosystem level outcomes also seem to be at play in N_2O evolution (Davidson et al., 2015), with the implication that the impact of temperature rise in the given range (2-5 °C) is either insignificant or nonlinear and other factors are influencing gas emissions.

Relationship of N_2O production with salinity seems more complex and less understood: although one early research suggests N_2O emissions tend to be lower in higher salinity areas (Smith et al, 1983); many mangrove studies show that saline wetlands may act as minor sources or sinks (with emission rates between -5 and 20 mg N m^{-2} h^{-1}), depending on other factors such as soil temperature, pH, oxygen availability, NO_3^- and organic carbon levels, rather than salinity (Livesley and Andrusiak, 2012).

Spatiotemporal variability arising from dynamic interactions of these interconnected factors require site-specific studies which must be complemented by comprehensive, long-term and experimental approaches to achieve a better understanding of GHG dynamics of saline lakes. This knowledge is crucial for constructing a more accurate image of the future in a changing climate and informing mitigation strategies.

GHG emission pathways and measurement methods

Aquatic ecosystems release GHGs into the atmosphere through various pathways, including ebullitive and diffusive fluxes, storage or turnover fluxes, and plant-mediated transport. This research focuses primarily on diffusive and ebullitive fluxes from lentic environments, although the other pathways can also significant contributors to GHG emissions from these ecosystems. Main emission patterns are as follows:

1. Diffusive flux: Diffusion refers to the gradual transport of dissolved gases from the water column to the atmosphere. The earliest studies focus on diffusive emission and it is the most frequently estimated component of total GHG emissions (Sanches et al., 2019). Diffusion is influenced by factors such as temperature, dissolved concentration, lake characteristics such as size and morphology, and weather conditions which affects the gas transfer rate, such as barometric pressure, partial pressure of the gas, wind stress (Bastviken et al., 2004). Majority of CO_2 and N_2O, and CH_4 that escapes oxidation in the water column can be emitted through this pathway.

Diffusive flux, a continuous process that changes gradually, can be estimated through short-term measurements. Two primary methods are used to measure diffusive fluxes are floating chambers and headspace measurements. Floating chamber methods (e.g., Bastviken et al., 2015) relies on the direct measurement of flux and involves placing a floating chamber on the lake surface and periodically sampling the gas concentration within the chamber. The increase in gas concentration over time is used to calculate the diffusion rate and flux, in snapshot study this method is adopted (see Chapter 2 for details). Headspace method utilizes Henry’s law to estimate diffusive gas flux based on the dissolved gas concentration in the water. The headspace method was employed in the mesocosm studies presented in Chapters 3 and 4.

2. Ebullitive Flux: This pathway involves the release of greenhouse gases, particularly CH_4, as bubbles directly from anoxic sediments into the atmosphere. CH_4 produced in the sediment is relatively readily converted to gaseous phase, due to its low solubility and starts to accumulate. After a certain threshold is passed, or a physical effect triggers its mobilization, such as a change in barometric pressure (Wik et al., 2013) the gas is released to the atmosphere as bubbles. It is considered one of the most important contributors to CH_4 emissions in surface waters, as it allows for a rapid escape of gas with minimal loss due to oxidation or biological interaction in the water column. It is estimated that globally 70 % of the CH_4 is emitted as ebullition (Bastviken et al., 2004; 2011).

Ebullitive flux is a stochastic process leading to episodic emissions irregular in terms of period and concentration. Accurate quantification of ebullition requires continuous sampling using chambers or bubble traps, or use of sensor based devices such as continuous sampling devices or real time GHG monitors. More details are given in Chapter 3, and 4 and see Caveats chapters in the discussion (5. 3. 2).

3. Storage/Turnover flux: Storage flux occurs when dissolved GHG accumulates in the water column during stratification periods or when ice cover prevents gas exchange with the atmosphere. This accumulated GHG, especially CH_4 can be released suddenly during events like seasonal lake overturn (Davidson et al., 2023) or ice melting (Sanches et al., 2019), resulting in significant emissions.

4. Plant mediated transport: Emergent aquatic vegetation can also play a role in emissions, particularly CH_4 emissions. This pathway involves the transport of CH_4 produced in sediments through plant tissues to the atmosphere, which is particularly relevant in ecosystems with abundant macrophytes (Yang et al., 2022).

5. Anaerobic production of CH_4: Recent studies have demonstrated that CH_4 can also be produced under oxic conditions, a possible explanation to the phenomenon known

as the “methane paradox”. The CH_4 produced in the oxic surface waters constitutes a small but distinct source of CH_4 in the lake environments (Grossart et al., 2011; Perez-Coronel and Beman, 2022)

Scope and aim of the thesis

Saline lakes, both inland and coastal, are crucial components of the global biosphere, playing vital roles in biogeochemical cycles, harboring a wide biodiversity, and providing ecosystem services. However, these ecosystems face a growing threat from environmental change. This thesis study investigates the complex interplay between several pressures and their present and future impacts on GHG dynamics in saline lakes. Specifically, it focuses on the effects of salinity and salinization, temperature rise, eutrophication, and other anticipated changes in the aquatic ecosystems in semi-arid regions. These regions are characterized by having sensitive water balances, rendering their lake ecosystems particularly vulnerable to ongoing water abstractions for agriculture, temperature rise and alteration of precipitation patterns (Cunillera-Montcusi et al., 2022). The combined effects of agriculture and climate change are expected to exacerbate habitat loss, water quality degradation, and biodiversity loss that many lakes have already begun to experience. As a result of this, GHG dynamics in these lakes are also anticipated to alter significantly. This doctoral research aims to disentangle the effects of these interacting forces to elucidate the potential changes impacting saline lakes, particularly those affecting their GHG dynamics.

To achieve this, we seek to answer the following research questions:

1. What are the general trends of GHG emissions in saline lentic environments?

2. What drives GHG emissions in these ecosystems?

3. How do GHG emissions respond to environmental change?

4. How will ongoing change shape the future of GHG dynamics in such ecosystems?

To answer these questions a multifaceted approach that integrates (i) the evaluation of existing literature, which provides a foundation for historical trends in the saline lakes from the main study region; (ii) remote sensing and hydrological modeling techniques, which allow basin-scale analysis of ongoing and future changes in the studied lakes, such as changes in lake surface area, salinity levels, and surrounding vegetation; (iii) field surveys, comprising direct measurements of physicochemical and environmental variables along with GHG fluxes from a diverse range of saline lake ecosystems, providing crucial data for understanding spatial variability; and (iv) experimental studies, which consist of controlled mesocosm experiments and enable the isolation and investigation of specific factors, such as salinity changes or extreme weather events, on GHG emissions from saline lakes.

The thesis is organized into four complementary but independent chapters to tackle different aspects of the subject matter. The first chapter, titled "Decadal changes in size, salinity, waterbirds, and fish in lakes of the Konya Closed Basin, Turkey, associated with climate change and increasing water abstraction for agriculture" establishes the context for subsequent research by providing a comprehensive overview of the KCB's historical and contemporary environmental conditions. Drawing upon long-term data and remote sensing techniques, the chapter analyzes decadal changes in climate patterns, agricultural patterns, water use for agriculture, groundwater levels, lake surface area, and salinity. This analysis reveals a concerning trend of decreasing water availability and increasing salinity in KCB lakes, suggesting potential disruptions to their ecological balance and GHG dynamics. The chapter was published in the journal *Inland Waters* in 2021.

Building upon the foundation laid in Chapter one, Chapter two, titled, "Contrasting Greenhouse Gas Emissions in Coastal and Inland Mediterranean Saline Lakes" specifically investigates GHG emissions from saline lakes. This chapter presents a snapshot field survey conducted in the early summer 2021 and 2022, comparing diffusive fluxes of methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (N_2O) across 33 coastal and inland saline lakes in Anatolia, Turkey, with 19 of them being in KCB. The study reveals a striking difference between the two lake types. Coastal lakes, characterized by lower nutrient and organic matter content, exhibit minimal CH_4 and N_2O emissions, potentially acting as net sinks. Conversely, inland endorheic saline lakes associated with higher nutrient concentrations sustained CH_4 and N_2O emissions even at high salinity levels. These findings emphasize the importance of lake type, nutrient composition, and potential interactions with salinity when evaluating the overall GHG dynamics of saline lakes. This chapter was submitted to the journal *Science of the Total Environment* (20 July 2024) and is currently under review (as of 25 September 2024).

The third chapter, titled "Temperature Drives Minor Methane and Nitrous Oxide Ebullition: A Synchronized Salinity Gradient Experiment in Shallow Lake Mesocosms in Contrasting Climate" utilizes a controlled mesocosm experiment to further explore the relationship between temperature, salinity and GHG emissions, particularly focusing on the ebullition (episodic bubbling events from the sediment) pathway of CH_4 emissions, which is relatively understudied in saline aquatic ecosystems. This chapter describes an experiment employing a salinity gradient design within large outdoor mesocosms to simulate a range of freshwater to hypersaline conditions with fixed nutrient loading, while the weather and seasonality represents the natural conditions. The experiment investigates how salinity affects the diffusive fluxes and total fluxes of CH_4, CO_2, and N_2O. The observed pattern of decreasing diffusional CH_4 flux with lower temperatures potentially reflects biological activity and temperature dependence of metabolic processes. More importantly, the study reveals a significant difference between the diffusive and total CH_4 fluxes. The total flux exhibited greater variation irrespective of temperature or salinity, suggesting that ebullition may be a significant but understudied emission pathway for CH_4 in saline lakes, particularly at higher salinities.

Chapter four, titled "Impact of Heatwaves on Greenhouse Gas Fluxes in Shallow Saline Lakes: A Synchronized Mesocosm Study Across Contrasting Climates" is the continuation of the experimental approach using mesocosms. The chapters aim to explore the potential interplay of temperature and salinity on the GHG dynamics in shallow saline lakes under different salinity regimes. We performed two coordinated mesocosm experiments in two sites (Ankara and Mersin, Turkey) in 2022, with contrasting climate zones (semiarid hot, and semiarid cold, respectively) to elucidate the effects of short-term extreme weather events (i.e., heatwaves) and long-term temperature alterations in different climate conditions and salinity regimes.

Finally, the discussion chapter (chapter five) tries to make a synthesis of disclosed research in the previous chapters; by investigating the interaction of intensifying anthropogenic pressures and the other factors influencing GHG dynamics in saline lakes, and the limitations of the study.

By combining field observations and controlled experiments, the research seeks to comprehensively understand the production dynamics, emission pathways, and overall balance of GHGs within these ecosystems. It investigates how environmental variables like salinity, temperature, and nutrient composition influence GHG production, and further explores how projected shifts in these variables will alter the overall GHG balance. Understanding these dynamics is crucial, as they have the potential to significantly impact the global climate system.

The research presented in this thesis lays the groundwork for further investigations. Future studies can explore the long-term impacts of salinization on GHG emissions, including seasonal variations through continuous monitoring efforts in natural ecosystems. Additionally, modeling approaches can be incorporated to predict future emission scenarios under various climate change and water management projections.

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CHAPTER 1

DECADAL CHANGES IN SIZE, SALINITY AND BIOTA IN LAKES IN KONYA CLOSED BASIN, TURKEY, SUBJECTED TO INCREASING WATER ABSTRACTION FOR AGRICULTURE AND CLIMATE CHANGE

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ABSTRACT

The Konya Closed Basin (KCB) in Turkey has a cold semi-arid to warm Mediterranean climate and hosts the largest Turkish freshwater lake, Lake Beyşehir, in the upstream, and the iconic saline Lake Tuz in the downstream of the basin. Using published as well as own ground-truth and remote sensing data, we give a brief description of the paleo-environmental changes in KCB, followed by a detailed description of the changes in land use, crop production, groundwater and surface water levels and climate, and the implications that the changes have had for the lake water surface area, salinity, and biotic (waterbird and fish) communities during the past 40 years. KCB is intensively farmed, and crop production has increased substantially, especially since 2000 with mainly water thirsty crops. This, combined with climate warming, has led to a substantial reduction of the groundwater level (up to 1 m/year) as well as of the surface area of the lakes and wetlands, followed by salinisation, and some have already dried out completely. Three globally threatened waterbird species face extinction in the basin, while 18 out of 62 breeding species have already been lost. Similarly, KCB has 38 fish species of which 74% of endemic, and 61% of those are considered threatened or near threatened. Modelling projections using various climate and land use scenarios indicate serious additional reductions in water level in the future due to climate change, which will cause serious damage to the lake ecosystems and the services that they provide.

INTRODUCTION

Globally, temperature and precipitation patterns are predicted to change markedly as a result of climate change (IPCC 2007, 2014). Particularly regions with a cold or hot semi-arid to arid and Mediterranean climate are expected to be strongly affected. In the Mediterranean region, major reductions in net precipitation are anticipated by the end of the 21st century together with a dramatic increase of land in drought (Pegion 2012; Russo et al. 2019) Moreover, water abstraction, not least for irrigation purposes, is expected to increase markedly in the years to come (Yano et al. 2007; Rodriguez Diaz et al. 2007) in the Mediterranean and dry climate zones due to both the reduction in net precipitation and an increase in evapotranspiration, but also a global increase in the demand for food by a growing population and a shift to more thirsty crops will accelerate the salinisation of lakes and soils.

The magnitude of the future changes poses a major threat to the functioning and biodiversity of inland aquatic ecosystems, and as temperature increases, many lakes may even dry out temporarily or permanently. Increasing salinity in the remaining water bodies may lead to reduced biodiversity (Williams et al 1990, Schallenberg et al. 2003; Flöder et al. 2004, Jeppesen et al. 2015) and loss of ecosystem functioning (Lin et al. 2017; Vidal et al. this volume).

However, so far knowledge of the effects of warming on saline lakes as well as the effects of salinization on the structure and functioning of freshwater lakes is fragmented and far from at the level achieved for freshwater lakes (Cañedo-Argüells et al. 2019; Jeppesen et al. 2015). This is unfortunate as the proportion of saline lakes is expected to increase substantially in the near future.

Closed basins in semi-arid or arid regions respond relatively rapidly to geological and climatic changes since any slight alteration may have significant consequences for their water balance. For instance, a few years of prolonged drought may lead to enhanced salinity and, consequently, alter the ecosystem characteristics of the lakes (Beklioğlu et al. 2018; Levi et al. 2016). Here, we focus on the semiarid Konya Closed Basin (KCB), which is the largest closed basin of Turkey, spanning almost 50,000 km^2 and covering 7% of the country’s land area. It has a population of 3.2 million and supports extensive agricultural activities that depend heavily on surface water and groundwater abstraction, implying that many natural streams have been regulated and channeled for dam construction to provide water for irrigated crop farming. Despite this, KCB exhibits an astonishing biodiversity and a high rate of endemism of its plants and freshwater fish, which can mainly be ascribed to its role as a refuge during the ice ages in the quaternary period (Eken et al. 2006; Şenkul and Kaya, 2017). The basin is also home to several globally threatened waterbird species and is an important area for breeding, wintering and migrating waterbirds in Turkey and the Mediterranean region as a whole due to its central location that also constitutes a major migratory bottleneck (Kirwan et al. 2010). KCB is famous for its spectacular freshwater lakes, extensive marshes and saline lakes of which some are the remnants of a paleolake, Lake Konya, which dried out during the Holocene (Kirwan et al. 2010). The region is located in the intersection of 3 ecoregions and comprises important biodiversity and protected areas. Within the basin, there are 2 national parks, 1 strict nature reserve, 2 Ramsar sites, 10 “Important Plant Areas” (IPAs) (Özhatay et al. 2003), 11 NATURA 2000 areas (Republic of Turkey Ministry of Agriculture and Forestry 2018) and 16 “Important Bird Areas” (IBAs). The basin also intersects 3 more IBAs (Eken et al. 2006; Kirwan et al., 2010; BirdLife International, 2020).

In this overview paper, we first provide a brief paleoecological description of the KCB since the last glacial maximum. Then, we describe the changes in meteorology, land use (mainly agriculture) and groundwater level during the past four to six decades and how these changes have affected the lakes both in terms of size and physico-chemical variables, including salinity and biota (fish and waterbirds), based on remote sensing data and data derived from a 2020 field sampling campaign as well as literature and existing databases. Included are also a few case studies focusing on the recent drastic transformations occurring in the iconic Lake Meke Maar and the large wetlands, the Ereğli, Eşmekaya and Hotamış Marshes, as well as the future of Lake Beyşehir, the largest freshwater lake in the basin and the whole Mediterranean region. Finally, we discuss the future of the KCB lakes seen in the light of global change, with emphasis on the need for mitigation initiatives.

MATERIALS AND METHODS

Lakes sampled in 2020

We sampled 19 natural lakes and 22 dams in the Konya Closed Basin (KCB) between 21 and 27 June 2020 to analyse surface water chemistry variables and chlorophyll-*a* (Chl-*a*) concentrations (Fig. 1). Lake Tuz was sampled at three different stations due to its large size. The samplings were conducted along the shore using a sampling pole (4 m). Temperature, dissolved oxygen, electrical conductivity and turbidity were determined using a YSI ProDSS Multiparameter Water Quality Meter. The 1-2 L water samples were filtered through GFC filters for Chl-*a* analyses on site, and 500 ml water samples were taken for analysis of water chemistry variables. All samples were kept frozen until analysis. We used the acetone extraction method for Chl-*a* analyses (Strickland and Parsons 1972; UNEP/MAP 2005). Nutrient (PO_4, NO_3+NO_2 and $Si(OH)_4$) analyses were performed with standard methods using a Technicon A II model auto-analyser.

Remote sensing analyses

We used Sentinel-2 MSI and Landsat data from the long-term monitoring and mapping of lake surface area and salinity of Lakes Düden, Little Düden and Uyuz, which – because of their high salinity – were selected to serve as examples of the changes that have occurred in KCB over the last 40 years. Optical satellite images (Landsat and Sentinel data) included 80 non-cloudy Landsat 1-3 MSS, Landsat 4-5-7-8 TM, ETM+, OLI data and 6 non-cloudy Sentinel 2A images (for the period 2016-2019) downloaded from www.earthexplorer.usgs.gov. The Sentinel images were processed applying Sen2Cor (software processing Sentinel 2 data, ESA). For the Landsat image series, Dark-Object Subtraction (DOS) atmospheric correction technique was applied using the Semi-Automatic Classification (SCA) plugin in QGIS (Congedo 2018). Pre-procession (radiometric and geometric corrections) of the images was done before determination of lake surface areas. The Normalized Water Index and the Modified Normalized Water Index (MNDWI) (Xu 2006) were used to assign the water pixels, which were subsequently checked for correctness against the normalised vegetation index (NDVI) for the vegetation-covered lake surface area. Shortwave infrared and red-edge spectral bands were used to improve the salinity detection of the spectral indices (Bannari et al. 2018, Wang 2019). Thus, SWIR bands (2.2 µm of Landsat 8, 2.205 µm of Landsat 5 and 2.194 µm of Sentinel data), NIR bands (0.865 µm of Landsat 8, 0.835 µm of Landsat 5) and a Red-edge band (0.78 µm) of Sentinel data were used to create the salinity index.

Monthly mean temperature and total precipitation data were obtained from Turkish State Meteorological Service (TSMS) for the period 1970-2020. After testing the normality and homogeneity of the data, Mann Kendal and Şen's trend analysis (Şen, 2011) were applied. For estimation of evapotranspiration, the Thornthwaite method (Thornthwaite and Mather 1955) was used. We used the standardised precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010) for the time scales 3, 9, 12, 24, 36 and 48 months to determine which time periods best described the hydrologic response of small waterbodies in the study area. The groundwater levels at the observation wells located in the basin were obtained from DSI (State Hydraulic Works).

Agriculture data

Data on agricultural land area, crop patterns and their biomass production (i.e. crops, vegetables, fruits) for 1980-2019 were obtained from the database of the Turkish Statistical Institute (TUIK 2020).

Populations of globally threatened waterbird species

We compiled population estimates and observation records for globally threatened waterbird species in the region for period 1960-2020, including common pochard (*Aythya ferina*), marbled teal (*Marmaronetta angustirostris*), white-headed duck (*Oxyura leucocephala*), slender-billed curlew (*Numenius tenuirostris*) and red-breasted goose (*Branta ruficollis),* supplemented with sighting records in Cornell Lab of Ornithology's databases (Cornell Lab of Ornithology) as well as mid-winter waterbird censuses (DKMP, 2019a) to evaluate population changes. For a full list of the resources used and a detailed description of the methodology followed for our final abundance estimates see Supporting Material S1.

We also quantified the change in the species richness of breeding waterbirds in KCB by analysing data gathered in two breeding bird atlases from the period 1998-2018 when the wetlands of the basin underwent substantial degradation. The first breeding bird atlas was conducted in KCB in 1998 (Eken and Magnin, 2000). The second atlas was conducted at national scale between 2014 and 2018 (Boyla et al., 2019). As the two atlases used the same coordinate and grid systems and similar methodologies, they are practically comparable. We chose 50x50 km spatial resolution because the most recent atlas did not report results at the finer 10x10 km scale. For the peripheral squares, we only considered registrations within the borders of the KCB. See Supporting Material S2 for detailed descriptions of the methods followed in the atlases.

Fish

We collected information on fish species and their status in KCB from a wide range of literature, which is listed in supporting material S3. The validityn of fish names were checked using Fishbase (Froese and Pauly 2020) and Catalog of Fishes (Fricke et al. 2020). The conservation status of species was classified according to their IUCN Red List Categories (IUCN 2020).

RESULTS

Konya basin – paleo-environmental history

The Konya Closed Basin (KCB) is located at a mean altitude of 900-1050 m in the south of the Central Anatolian Plateau (Fig. 1). The flat and mostly marl and limestone terrain of the basin, formed as a result of lacustrine deposition during the quaternary period (Roberts 1983), is enclosed by the Taurus Mountains (>3,000 m) to the south and the west and the uplands of the Anatolian plateau to the east and the north. The basin housed the extensive paleolake Lake Konya (Fig 1) during most of the quaternary until the end of the last glacial period, but with intermittent dry outs. Although the basin is endorheic with no surface outflows, the southern basin has a few karstic outlets to the deeper strata, which probably prevented complete salinisation of the basin during the paleo-history (Roberts 1983; Kuzucuoğlu et al. 1999).

The lakes in the KCB display complex responses to climate change. High water levels have appeared in cold and dry periods when evaporation was low with prominent ice cover (Roberts 1983). In addition, despite the limited precipitation in the basin in the cold periods, the seasonal snow build-up and consequent thawing of the glacial formations in the Taurus Mountains in the south, where precipitation was presumably higher than in the northern basin, have contributed to the positive water balance of the lakes (Fontugne et al. 1999). Whether the water levels are principally determined by changes in precipitation or evaporation is the subject of long debate (Roberts et al. 1999), but recent research using stable isotope signals indicates a strong role of evaporation, especially during the interglacial periods and at the beginning of the Holocene (Roberts et al. 2016).

In the last glacial maximum (25-20 ka BP), paleolake Lake Konya reached its highest stand with a surface area > 4,000 km^2 and a maximum depth of 30 m (Roberts 1983; Roberts et al. 1999; Fontugne et al. 1999), and the stand of Lake Tuz was 15 m higher than today (Kashima 2002). The lakes started to recede between 17 to 13 ka BP (Roberts 1983; Kuzucuoğlu et al. 1999; Roberts et al. 1999) but exhibited markedly higher water levels during the Younger Dryas (13 ka BP). The cold intermittent period marked the last high stand of paleolake Lake Konya that fragmented into smaller, isolated water bodies in the following millennia, not least when warmer conditions predominated at the beginning of the Holocene (Roberts 1983).

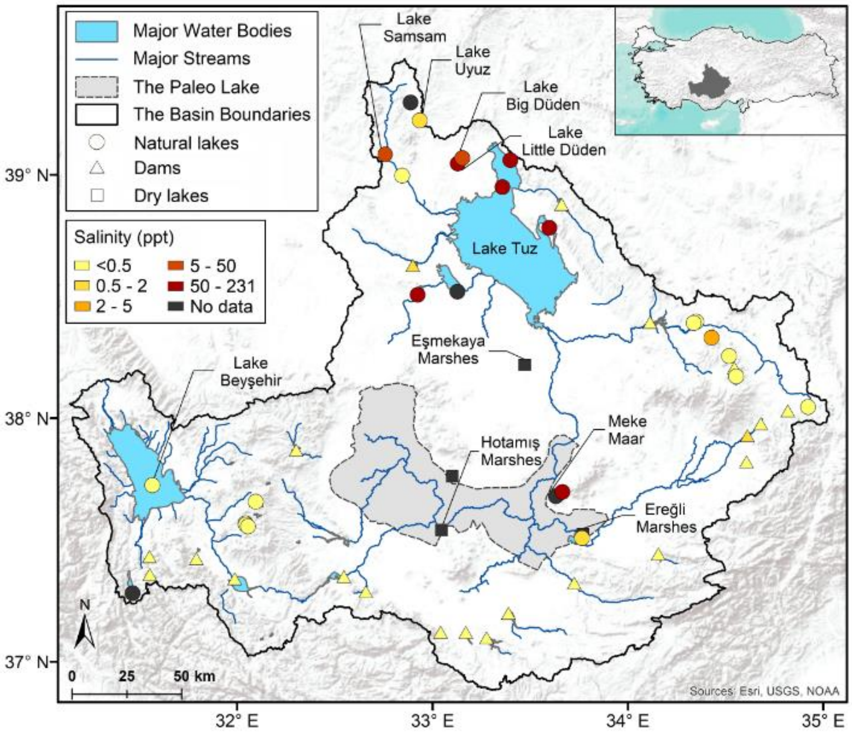

Figure 1-1 Map of Konya Closed Basin (KCB) showing the boundaries, the major water bodies, and the salinities (ppt) of the lakes and dams sampled in June 2020, and the greatest extent of the paleolake Lake Konya in the last glacial maximum (source: Esri and Garmin 2014).

In the early Holocene, warmer and wetter conditions prevailed in the region (Dean et al. 2015; Roberts et al. 2016), and the landscape shifted from steppe plant dominance (e.g. *Chenopodiaceae*, *Artemisia*) (Roberts et al. 2016; Woodbridge et al. 2019) to (oak) tree dominance (Roberts et al. 2011). However, the simultaneous dry out of Lake Konya suggested that the precipitation pattern changed less than the temperature-induced increase in evaporation (Roberts 1983). The early Holocene was also the first period in which human activity had unequivocal impact on the environmental landscape and altered the vegetation (Assouti and Hather 2001), likely as a result of animal herding and early crop farming activities. Çatalhöyük, which was one of the most populous Neolithic settlements so far discovered with a population of 10,000 at its highest, was founded in the southern alluvial margins of the basin and remained there for more than one millennium (Hodder 1996; Roberts et al. 2002, 2011; Asouti and Kabukcu 2014). After the Holocene climatic optimum (9000-5000 BP), a period of gradual aridification occurred in the mid-Holocene (Dean et al. 2015). The late Holocene witnessed a climatic amelioration accompanied by an increase in settlement numbers (Allcock and Roberts 2014) in the region, called the Beyşehir Occupation (BO) phase (c. 3,000-1,300 BP). The basin was repopulated, with widespread arboreal agricultural areas with fruit trees (Eastwood et al. 1999). Following the centennial hiatus after the BO phase, agricultural activities regained momentum in the area, but this time with a greater emphasis on cereal agriculture and pastoralism during the last millennia (England et al. 2008). This pattern of agro-pastoralism remained stable well into the modern period; thus, by the mid-19th century and afterwards in the Republic period, cereals, especially rye (*Secale cereale*), markedly increased in the pollen record (England et al. 2008). In the more recent past, with the development of irrigation, water thirsty crops (e.g. sugar beet and legumes) increased their share, while livestock production became restricted to the mountainous regions where irrigation was not available (Fontugne et al. 1999).

Konya Closed Basin – recent history

Climate, precipitation, evaporation and temperature changes

Today, the KCB has a diverse climate. Thus, in the south of the basin the climate is Mediterranean, while a cold-dry steppe climate prevails in the northern basin and a desert climate in the central Karapınar region. Long-term annual mean precipitation in the basin was 340 mm during 1970-2020. The lowest mean annual precipitation of 289 mm was observed in the Karapınar and the maximum annual precipitation (747 mm) in the Seydişehir region (for location see Fig. 1). Mann Kendal and Şen's trend analysis (Şen, 2011) of existing data indicated an increase in the annual mean temperatures (~0.045 ^{o}C/year) at most of the stations used in our study and a decrease in annual precipitation at some, but not all sites (Fig. 2). Moreover, open surface evaporation occurred between April-October, with a maximum of 262 mm in July and a minimum of 100 mm in October for the period 1970-2013.

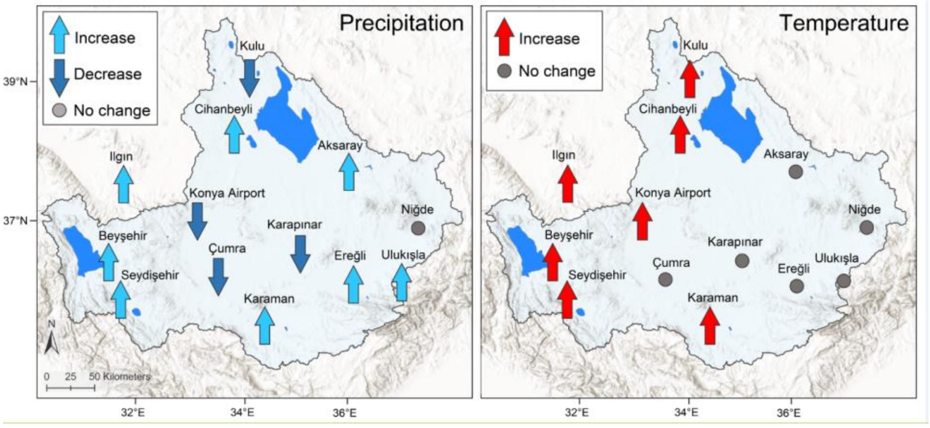

Figure 1-2 Precipitation and temperature trend analyses of selected meteorological stations for the period of 1970-2020 of Konya Closed Basin.

Changes in land and water use

According to CORINE 2012 first-level classification, approximately 56% of the KCB area was used for crop farming (27×10^3 km^2) and 8×10^3 km^2 were irrigated (Republic of Turkey Ministry of Agriculture and Forestry 2018). Although a semi-arid climate prevails in most of the KCB, and 70% of the precipitation occurs outside the growing period, cultivation of water thirsty crops has been widespread in the KCB farmlands (Berke et al. 2014).

The municipalities of Konya and Karaman cover most of the KCB (40×10^3 km^2 and 9×10^3 km^2, respectively). From 1995 to 2019, the total agricultural area of Konya and Karaman decreased from approximately 30×10^3 to 22×10^3 km^2 (TUIK 2020). Despite these reductions in cultivated area, the crop production increased substantially after 2000, coinciding with increased utilisation of fertilizer and enhanced water use for irrigation (Konya Directorate of Provincial Agriculture and Forestry 2019) (Fig. 3). In 2019, the dominant crops were sugar beet, maize, wheat, alfalfa and barley, which accounted for 28%, 18%, 9%, 9% and 6%, respectively, of the >22 mill. tons of agricultural production (TUIK 2020). Although an average 74% of the arable land in the two provinces has been cultivated with winter cereals since 2010, the yield of winter cereals was lower than of other crops such as sugar beet and maize (TUIK 2020).

As the total production increased, the extent of irrigated land and water use also increased (Fig. 3). In 2019, more than 3×10^3 hm^3 water were used to irrigate 6×10^3 km^2 in Konya (EIA 2019). In 2018, 1×10^3 km^2 of the Karaman area was irrigated, corresponding to 31% of the agricultural land (EIA 2018). In 2008, sprinkler and drip methods were introduced for irrigation as a water saving potential at the expense of the more primitive surface irrigation (EIA 2019).

Although sugar beet is one of the thirstiest cultivated crops in KCB, its production has been promoted in various ways such as via establishment of new sugar factories (i.e. Konya, Çumra Sugar Factory with a capacity of 0.3 mill tons/year) and privatisation of sugar factories (i.e. Konya Sugar Factory in 1991 and Turkish Sugar Factory in 2008). Besides, in 2001, a new “Sugar Law” was passed, which supported privatisation and increased the sugar beet-based production in Turkey (Türkşeker 2020), creating a major increase in sugar beet production and a consequent demand for water for irrigation in KCB (Fig. 3).

By contrast, from 1980-2009, the total number of livestock (i.e., goat, sheep, cattle, buffalo) first decreased from approximately 4.5 to 2 mill. but then increased to around 4 million due to government subsidies (Fig. 3) (Republic of Turkey Ministry of Agriculture and Forestry 2013; TUIK 2020).

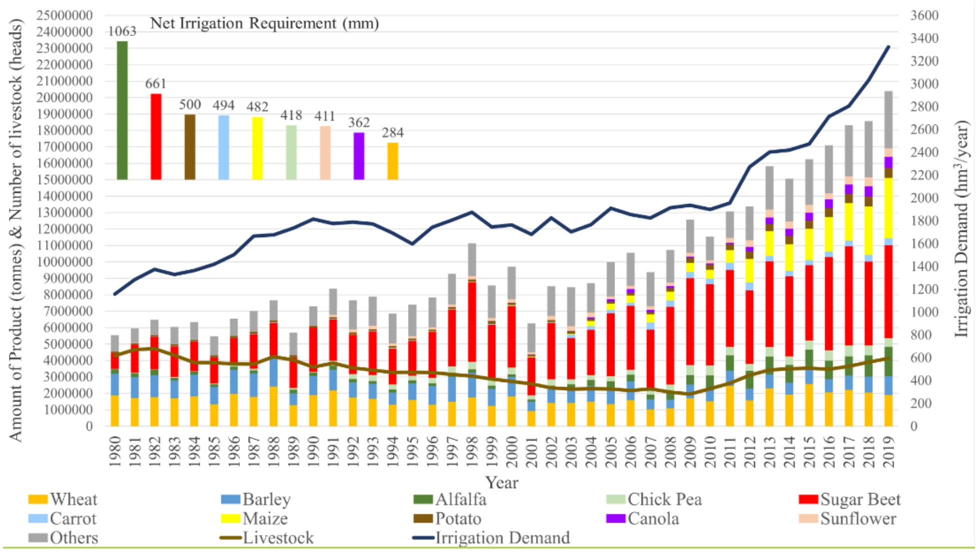

Figure 1-3 Total agricultural products (tons), number of livestock (heads) and estimated irrigation amount (hm3/year) in Konya and Karaman provinces between 1980 and 2019 (data taken from TUIK 2020). Also shown (upper left) is the net amount of irrigation water (mm) for crops largely cultivated in the Konya Closed Basin (Berke et al. 2014). Estimated irrigation demand includes total irrigation of winter cereals, alfalfa, sunflower, maize, bean, cow vetch, potato, chickpea, sainfoin and sugar beets. Estimations were obtained by multiplying the area in which the crop was cultivated with the net irrigation requirements, assuming that 85% of KBC’s winter cereals were fed by rainfall (Topak et al. 2008).

Change in groundwater resources

The water potential of the basin is estimated to 4,679 hm^3/year, of which 42.8% comes from groundwater resources (Dolsar 2015). There are 22 dams in the basin, mostly designed and operated for irrigation purposes. In 2015, the annual amount of water used in the KCB was 4,996 hm^3, of which 95% was used for irrigation, 4% for domestic water supply and 1% for industrial purposes. The extra water needed was provided by transfer from neighbouring catchments (Gembos and Blue Tunnel Projects, 540 hm^3/year) (Dolsar 2015). It is estimated that a 5-10% decrease in precipitation will result in a 34% decrease in surface water (Dolsar 2015). Of the 88,394 wells in KCB used for irrigation, 41% were unlicensed in 2013 (Dolsar 2015). Overall, the average groundwater level decrease from the wells has been 1 m/year during the last 20 years (1995-2015) (Fig. 4), although there are a few exceptions from this general pattern (data from selected wells are presented in Figure 4).

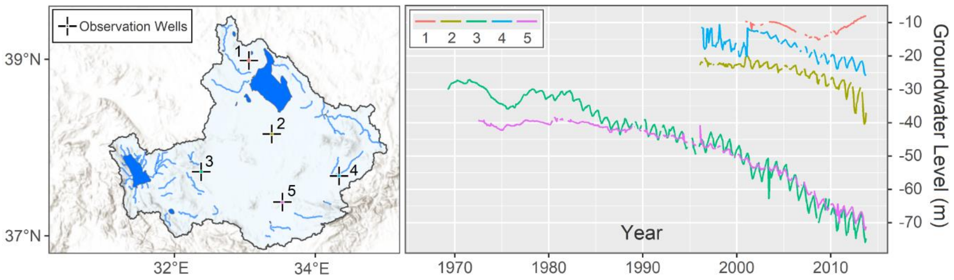

Figure 1-4 a) The map of the five selected observational wells numbered from 1 to 5 and b) Long-term changes in the groundwater levels of the five of the selected wells of KCB.

Change in lake surface area

KCB holds many lakes including the iconic saline Lake Tuz and the largest Turkish freshwater lake, Lake Beyşehir. To illustrate the changes in lake surface areas during the last 35 years due to the reduction in groundwater and surface waters levels, as well climate change, we used surface area data derived from remote sensing from May (wettest month) and August (driest month) on four lakes situated in the northern-most and dry part of the KCB together with monthly temperature and precipitation data on the entire lake catchment (Fig, 5). About 50% of the lake surface area of the three lakes studied has been lost during the last 35 years, the decrease being most prominent in the dry season and largest in Lake Düden.

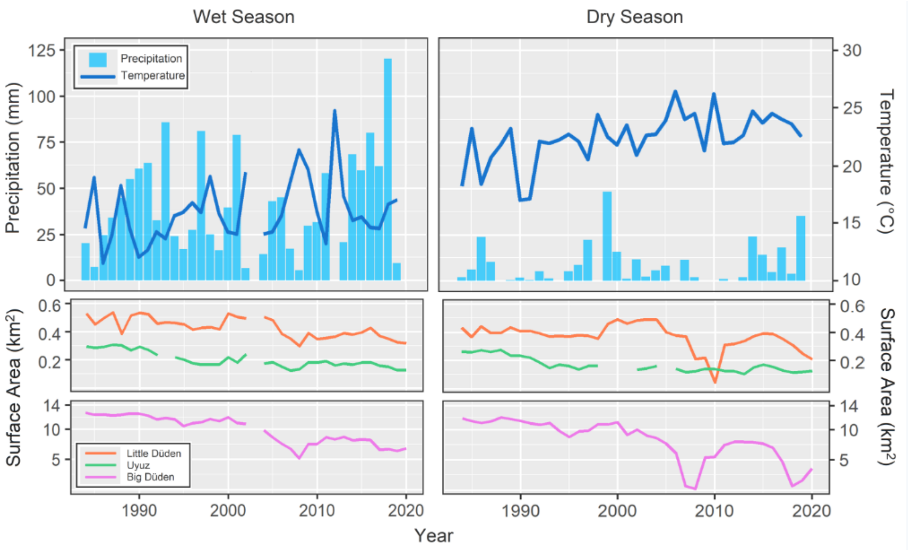

Figure 1-5 Changes given in the surface areas of Lakes Düden, Little Düden and Uyuz, monthly total precipitation and average temperature recorded at nearby stations both in the a) dry and b) wet seasons.

Among the calculated Standardised Precipitation Evapotranspiration Indices (SPEI), we found a 36 month-period (SPEI 36) to be optimal. SPEI 36 values and surface areas of the lakes are presented in Fig. 6. Water stress effects on the lakes were seen after 2000 where the surface area began to decrease. The groundwater level increased again after 2008 in the well close to Lake Düden and Lake Little Düden (Fig. 4) followed by an increase in lake area, emphasising the importance of groundwater input. The aquifer system of Lake Uyuz is different from that of Lake Düden. An effect of water stress, indicated by SPEI 36, is reflected by the surface area changes in Lake Uyuz, but an increase in surface area was observed in the wet season in 2002 and in the dry season in 2004 and 2015, suggesting a lower dependency of than groundwater input in this than in the two other lakes.

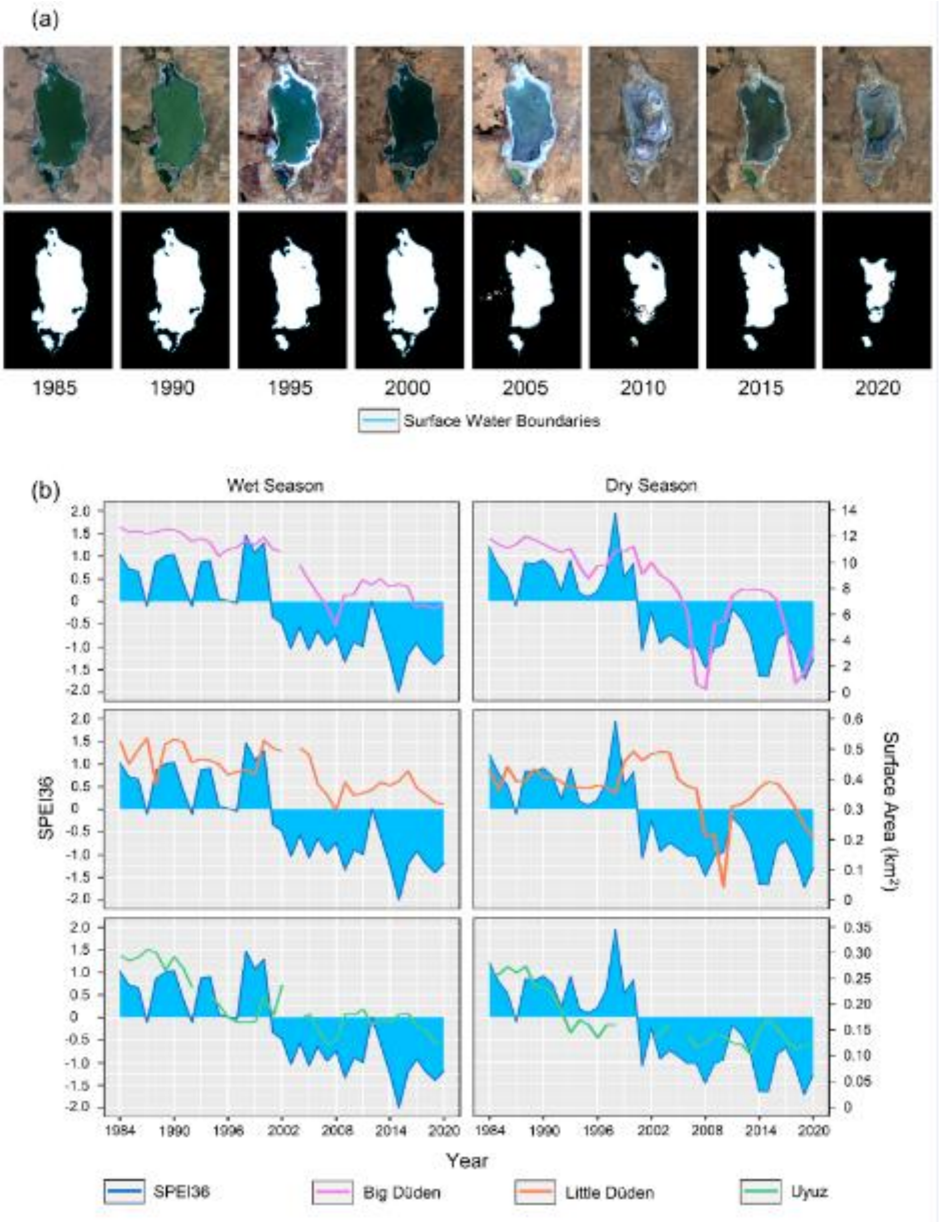

Figure 1-6 a) Landsat RGB images of Lake Düden (upper larger one) and Lake Little Düden (lower small one) from 1985 to 2020 with five years of interval, b) Changes in the SPEI (36 month) and surface area retrieved from satellite images for the period 1985-2020 of Lakes Düden, Little Düden and Uyuz from 1985 to 2020 with five years of interval.

Snapshot lake survey

The snapshot survey included 19 natural and 22 dams. Although located at similar elevations, the median areas of the natural lakes were lower than the dams' (Table 1). Also, the natural lakes had a higher median salinity than the dams and exhibited a two order of magnitude higher variability among sites. The natural lakes tended to have higher median PO_4-P, SiO_4 and Chl-*a* concentrations but lower median NO_3 concentrations than the dams.

A salinity index ((B7-B5) / (B7+B5)) was calculated from Landsat and Sentinel images using the near-infrared and shortwave-infrared bands for the period 1985-2020 for Lake Duden and Lake Little Duden. The calculated index was tested against the collected field salinity (ppt) data in June 2020, yielding a correlation coefficient of 0.92. Salinity increases in the dry season (August) in all three lakes. The salinity index values are relatively lower in the wet (May) than in the dry season due to less evaporation and a higher contribution of surface water to the lakes (Fig. 7).

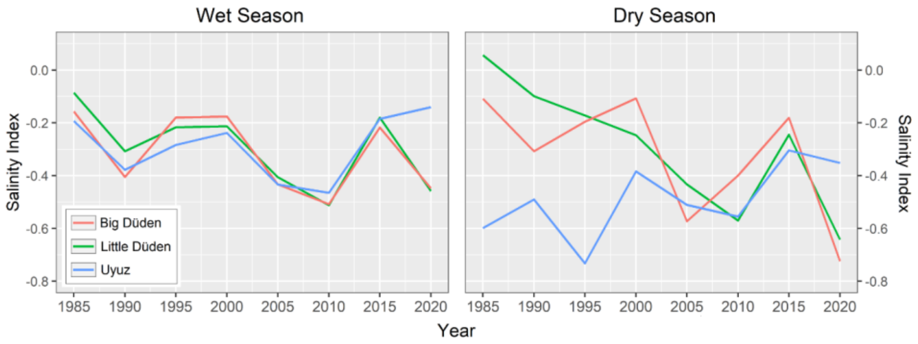

Figure 1-7 Changes in the salinity index for Lakes Düden, Little Düden and Uyuz from 1985 to 2020 with 5 years intervals in a) the wet season and b) the dry season.

Change in biota

The major changes in lake area and salinity in the KCB have led to major changes in the biota, including biodiversity, though the changes are not all well documented.

Here, we use waterbirds and fish to illustrate the threats that the biota have faced and are presently facing in the KCB.

Populations of globally threatened waterbird species

Common pochard had a small breeding population, albeit a very large migrating and wintering population in KCB (Fig. S1). During the late-90's and early-2000's, the common pochard breeding population in the basin peaked with >120 pairs, and it was found at several sites across KCB. However, in 2019, its breeding population was down to only 6 pairs. The highest recorded number of common pochard during migration was observed at Lake Düden in 1970 when 45,000 individuals were counted on a single day. During the last 20 years, no more than 200 migrating/molting individuals have been observed in the basin. The wintering population of the species in KCB used to be large; thus, more than 45,000 individuals wintered at Lake Düden and Lake Beyşehir in the 80's and 90's. During the last few years, however, the wintering populations have mostly been confined to Lake Beyşehir with only 2,000-3,000 individuals.

Marbled teals used to breed at several localities in the basin, all of which have either been totally lost or severely degraded, such as Ereğli and Hotamış Marshes (see Case 1). The highest recorded breeding population in the basin was 60 pairs in 1985 (Fig. 8). Migrating individuals have only been observed in the Ereğli Marshes and Lakes Düden, Samsam and Beyşehir, and since 1994 no migrating marbled teal has been observed in KCB (Fig. S1). The species has not been observed in the KCB since 2000 and not in the whole of Turkey since 2015 and, accordingly, the species is feared to be extinct.

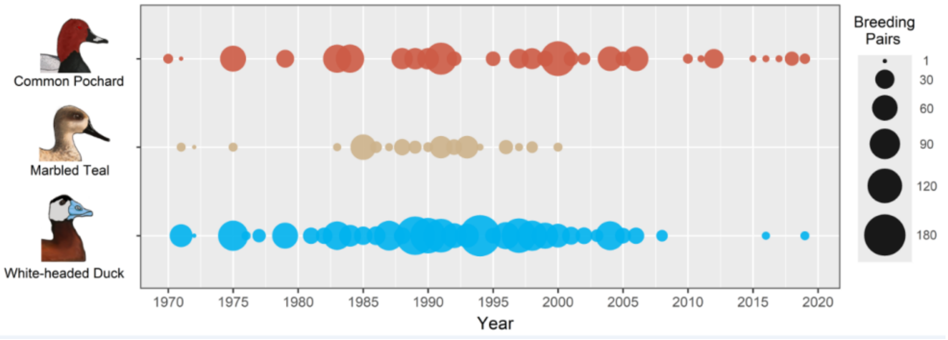

Figure 1-8 Changes in the sizes of breeding populations of the three globally threatened waterbird species common pochard, marbled teal and white-headed duck from 1970 to 2020 in the KCB.

White-headed duck populations in KCB have suffered significant losses over the last few decades (Fig. 8, Fig. S1). The breeding population size peaked in the late 80's with at least 152 breeding pairs distributed over several wetlands. The breeding population dropped to only a few pairs in the late 2010's and was confined to a single locality with 3-4 pairs in 2019 (Gürsoy-Ergen 2019), which might be an overestimation according to the latest fieldwork and sightings that reported no breeding pairs in the basin in 2019 and only a single pair in 2020 (Özgencil 2019; Ogün Aydın *pers. comm.*). More than 1,500 molting/migrating individuals were observed across the KCB in the 80's, whereas only 3 individuals were observed at a single locality in 2019. The wintering population of the species in the basin was higher than 500 individuals in the late 90's and early 2000's. Only a single individual has been sighted wintering in the region since 2005.

Both Slender-billed Curlew and Red-breasted Goose were rare visitors in the basin with <4 records during 1980-2000. All sightings of the two species were in wetlands that are currently either totally drained or severely degraded. The two species have not been observed in the basin for a long time, and the former is thought to be globally extinct (Buchanan et al. 2018).

Changes in breeding waterbird communities between 1998 and 2018

Our comparison of the two bird atlases indicated a widespread decline in the species richness of breeding waterbirds in the whole basin, with loss of 18 species over the last 20 years (Fig. 9). Total breeding waterbird richness has shrunk from 62 species to 48 species, and 76% of the species that no longer breed in KCB were red-listed at national scale in the assessment of 2004 (Kılıç and Eken 2004). Among these species were the iconic common crane (*Grus grus*), which used to breed around the former Eşmekaya Marshes, and the Dalmatian pelican (*Pelecanus crispus*), which used to breed in the former Ereğli Marshes, and some rare breeders such as the Caspian tern (*Hydroprogne caspia*) whose remaining populations are distributed over only a few sites in Turkey. During this time period, only four new species have (re)colonised the basin – cattle egret (*Bubulcus ibis*), great cormorant (*Phalacrocorax carbo*), white-tailed lapwing (*Vanellus leucurus*) and yellow-legged gull (*Larus michahellis*).

Compared with the situation 20 years ago, out of the 34 50x50 km grid squares, 21 had a lower species richness (mean change: -7.53) and 10 exhibited zero net change, while only 3 had a higher breeding waterbird species richness (Fig. 9). The biggest losses of breeding waterbird diversity have occurred in Ereğli, Hotamış and Eşmekaya Marshes with a loss of > 40 species in each.

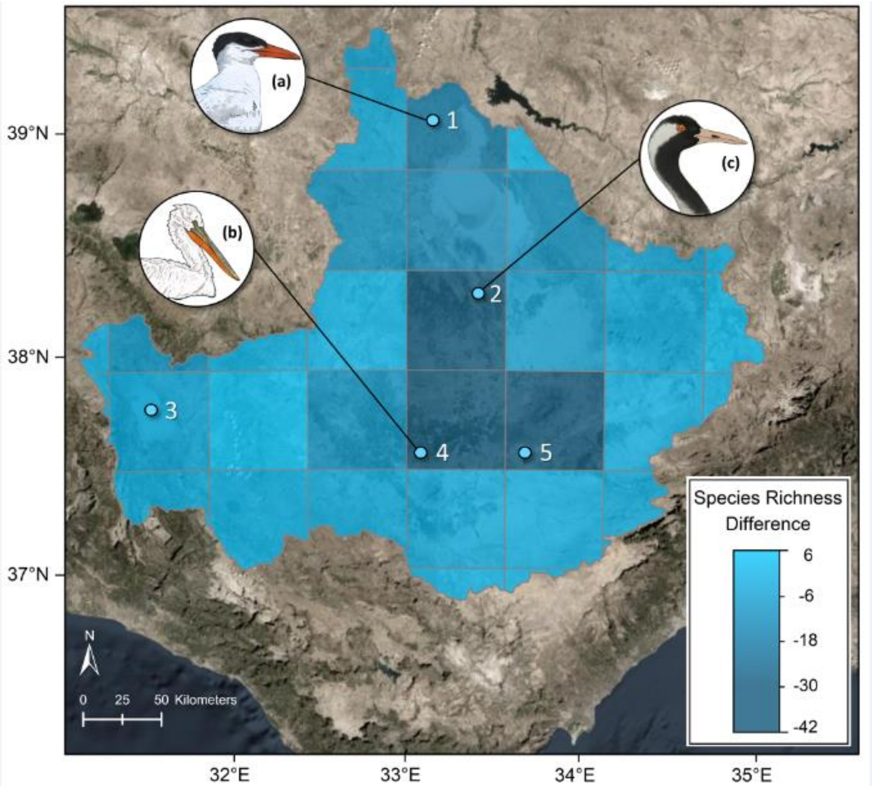

Figure 1-9 Map showing species richness loss of breeding waterbirds in the basin over the last 20 years. Some of the species that no longer breed in KCB are a) Caspian tern, b) Dalmatian pelican, and c) common crane. 1: Lake Düden, 2: Former Eşmekaya Marshes, 3: Lake Beyşehir, 4: Former Hotamış Marshes, 5: Former Ereğli Marshes. Satellite imagery source: Esri, DigitalGlobe, GeoEye, Earthstar, Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

Threat to fish species

KCB hosts 38 fish species of which 28 are endemic (74%). This extreme endemism ratio is 1.6 times higher than the average for the whole of Turkey, which is already a biodiversity hotspot for fishes (384 species of which 47.4% are endemic) (Çiçek et al. 2020). Of the endemic species in KCB, 61% are considered threatened or near threatened by IUCN (Supporting Material 3, Fig. S2), and the Beyşehir Bleak (*Alburnus akili*), endemic to Lake Beyşehir and its tributaries, has now gone extinct (Küçük 2012). Endemic fish populations in KCB have exhibited major reductions over the last few decades (Meke et al. 2012; Yeğen et al. 2015; Küçük et al. 2016), coinciding with habitats dry out, and the majority of, once widespread, fish species are now restricted to small refuges (Freyhof et al. 2020). The range contraction of these declining endemic fish populations bears witness of an ongoing extinction process (Pimm et al. 2014; Ceballos et al. 2015).

The already stressed native and mostly endemic fish fauna of the KCB (see Supporting Material 3, Table S1, for more information) is further threatened by non-native invasive species introductions that include pikeperch *(Sander lucioperca)*, tench (*Tinca tinca*) and Prussian carp (*Carassius gibelio)* (İnnal and Erk'akan 2006; Kuru et al. 2014; Tarkan et al. 2015). Moreover, *Atherina boyeri* was illegally dispersed by fishermen in the early 2000s due to its economic value (Gençoğlu and Ekmekçi 2016). Furthermore, *Gambusia holbrooki, Oncorhynchus mykiss* and *Pseudorasbora parva* were also introduced, and *Alburnus escherichii, Cyprinus carpio* and *Knipowitschia caucasica* were translocated to KCB (Tarkan et al. 2015). *Anatolichthys anatoliae* in the Central Anatolia region, *Anatolichthys iconii* in Lake Beyşehir and *Paraphanius similis in* Lake Akgöl have been dramatically affected by the exotic mosquitofish (*G. holbrooki*) (Yeğen et al. 2006; Kurtul and Sarı 2019).

CASE STUDIES

To illustrate the severity of the changes that the KCB lakes and wetlands have already faced and will expectedly face in the future, we present three case stories on the iconic marshes, Lake Meke Maar and Lake Beyşehir.

Case 1: The iconic marshes

Formerly, KCB had several large marshes of exceptional biological value, which contributed to biodiversity, fisheries and reed-cutting and the maintenance of a local mild climate (Fig. 1). Among these were the iconic Hotamış, Ereğli and Eşmekaya Marshes, which have almost or totally disappeared over the last four decades.

The Hotamış Marshes covered ca. 174 km^2 (33.050 E, 37.550 N) in the mid-80's, and at its deepest point the water depth was 3 m (Ertan et al. 1989; Magnin and Yarar 1997). The size of the marshland decreased over time, mainly due to diversion of its major inflows through construction of drainage channels and groundwater extraction and, to a lesser extent, reduced rainfall in the catchment (amounting to only 10% between 1965 and 1994). Before then, the marshes supported an extraordinary diversity and abundance of birds, making it an Important Bird Area (IBA) (Kılıç and Eken 2004) for breeding and non-breeding populations of globally threatened bird species, including white-headed duck and marbled teal. Once, the Hotamış Marshes, which were not easily accessible to humans, accommodated more than 110,000 birds in winter. However, following drainage in the 90s, the size of the wintering waterbird population size has decreased to only a few thousand.

The area of the Ereğli Marshes was even larger than that of the Hotamış Marshes (estimated total area: 215 km^2) and included Lake Akgöl with a surface area of 192 km^2 when its water level was highest in the early 20th century (Akkuş et al. 1991; Magnin and Yarar 1997). The main inflow of the marshes was the İvriz stream (providing 230 $hm^3\ y^{-1}$) up until 1984 when it was diverted to the İvriz dam for the purpose of irrigation (Fig. 10). Thereafter, the derivative channel Karaman Deliçay and sewage effluent from the nearest town, Ereğli, became the main inflow, drastically lowering the water input. In 1988, the former was also diverted to Gödet Dam, leaving the treated sewage effluent from Ereğli as the main inflow to the marshes. At one point, the Ereğli Marshes hosted five endemic fish species, including Anatolian gudgeon (*Gobio hettitorum*), Anatolian loach (*Oxynoemacheilus eregliensis*), Anatolian minnow (*Pseudophoxinus anatolicus*), Ereğli minnow (*Garra kemali*) and killifish (*Paraphanius similis*), but they have all disappeared. The marshes were also home to a huge variety of breeding, migrating and wintering waterbirds and designated as an IBA in the late 80's (Ertan et al. 1989). The large marshes supported populations of globally endangered waterbirds like white-headed duck and marbled teal and some nationally rare breeders like white pelican (*Pelecanus onocrotalus*), Dalmatian pelican and white-tailed lapwing (*Vanellus leucurus*) (Magnin and Yarar 1997). The marshes were also an important wintering ground for waterbirds, occurring in tens of thousands, before they dried out in the 90's (Fig. 10; DKMP 2019).

The Eşmekaya Marshes were the smallest of the three with a maximum surface area of 112.5 km^2 in the 80's (Magnin and Yarar 1997). A dam was planned for the area in the mid-90's; it never came into use, but the construction of diversion channel drained most of the area (Magnin and Yarar 1997). The marshes were home to important populations of two endemic freshwater fish species – spring minnow (*Pseudophoxinus iconii*) and killifish (*Anatolichthys anatoliae)* (Eken et al. 2006; Küçük et al. 2016). The marshes also accommodated rich bird communities making it an IBA (Magnin and Yarar 1997) where nationally rare breeders such as pallid harrier (*Circus macrourus*) and short-eared owl (*Asio flammeus*) were found (Eken and Magnin 2000; Eken et al. 2006). Furthermore, Eşmekaya hosted a few to several breeding pairs of the globally threatened common pochard and white-headed duck before it went dry (Karauz and Kıraç 1999; Kılıç and Eken 2004).

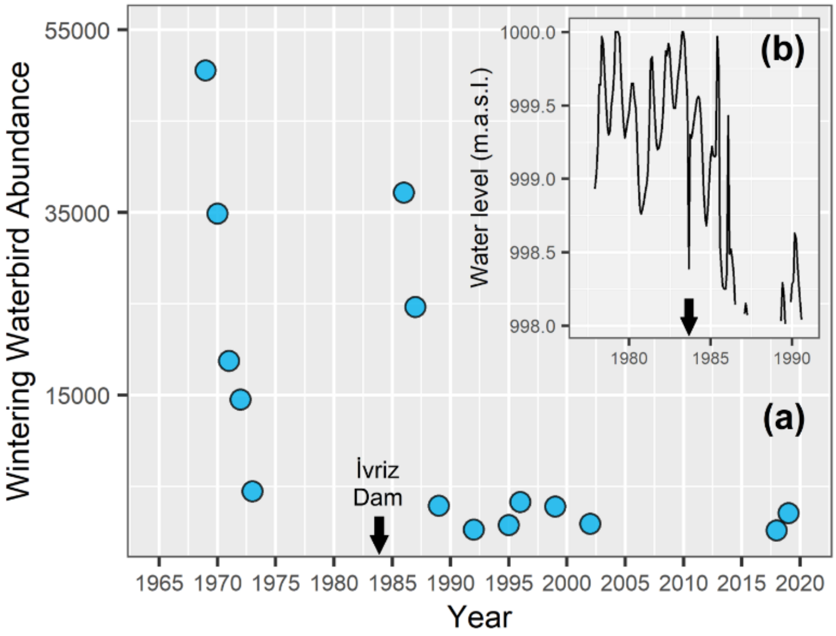

Figure 1-10 Changes in a) wintering waterbird abundances and b) water level (m.a.s.l) of Lake Akgöl in the Ereğli Marshes.

Case 2: Lake Meke Maar

The lake was formed by the flooding of the crater of an extinct volcano about 4 million years ago after an eruption. Around 9,000 years ago, a second eruption formed another volcanic cone inside the lake with a maar forming the ionic Lake Meke Maar. Lake Meke Maar was declared a first grade protected area in 1989 and registered as a natural monument in 1998, and in 2005 the lake and its surrounding area were declared a Ramsar site. Although the lake water cannot be used directly for agricultural purposes, water was pumped for irrigation from wells within the lake catchment. The lake was once 12 m deep (İnandık 1965), but the decreased groundwater levels had devastating effects, causing a shrinkage of surface area after 2005, and today the lake has dried out completely (Fig. 11a). The salinity index of the lake also decreased in accordance with the declining water levels, indicating rising salinity (Fig.11b,c). The shrinkage of lake surface area became particularly pronounced after 2000, especially during the dry season, with a subsequent increase in salinity.

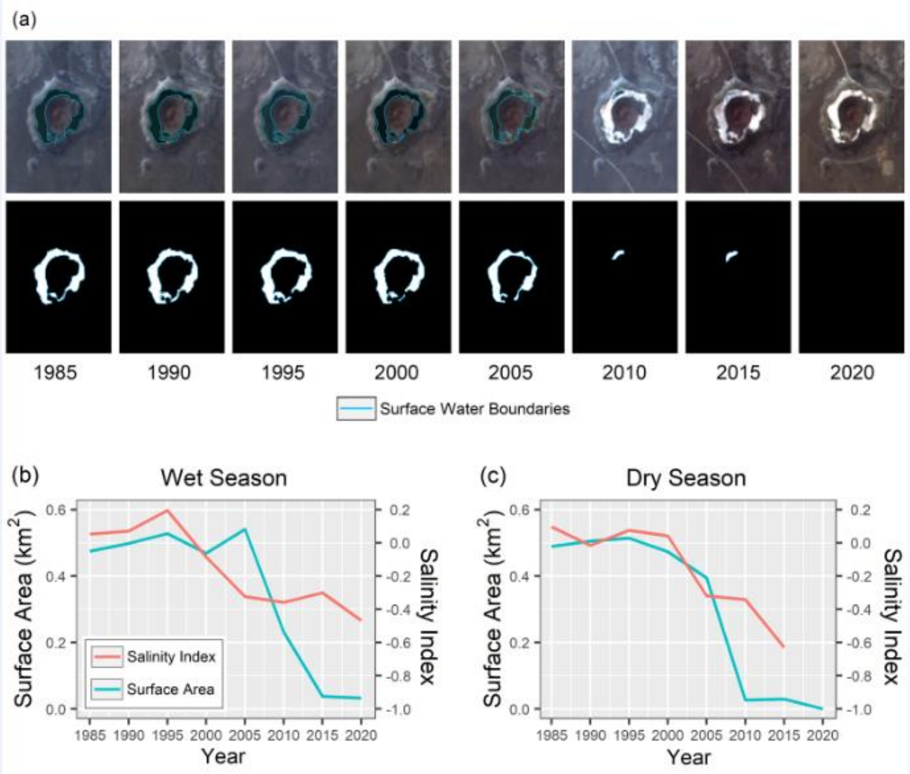

Figure 1-11 Landsat TM images of Lake Meke in the dry season (a), area and salinity index change in the lake for 1985-2020 in the wet season (May; (b)) and (c) in the dry season (August; (c)).

Although the lake did not accommodate significant numbers of birds, it did have breeding populations of several threatened species including Egyptian vulture (*Neophron percnopterus*) and saker falcon (*Falco cherrug*) (Ertan et al. 1989). At high water levels in the 90’s, the lake supported 600+ wintering waterbirds, including the threatened species white-headed duck and common pochard (DKMP 2019).

Case 3: Lake Beyşehir

Lake Beyşehir with a surface area of 650 km^{2}is the largest freshwater lake in Turkey and the whole Mediterranean Sea basin. The lake basin has existed since the Middle

Miocene (15.9–11.6 mill. years ago). The lake shows inter- and intra-annual water level fluctuations (Fig. 12) and has a maximum depth of 8-9 m depending on the season. The catchment area of the lake is 4,704 km^2 and it is positioned in an upstream area of the KCB. Nearly half the catchment (42.7%) is covered by range-brush and 25.5% by agricultural land, while forested areas (evergreen and deciduous forests) constitute 11.2%. The lake is primarily fed by waters from the Sultan and Anamas Mountains and springs from Mesozoic calcareous cracks, precipitation and snow melts, and it has one outlet. The lake is oligotrophic to mesotrophic, with low phytoplankton biomass and nutrient concentrations (Bucak et al. 2018).

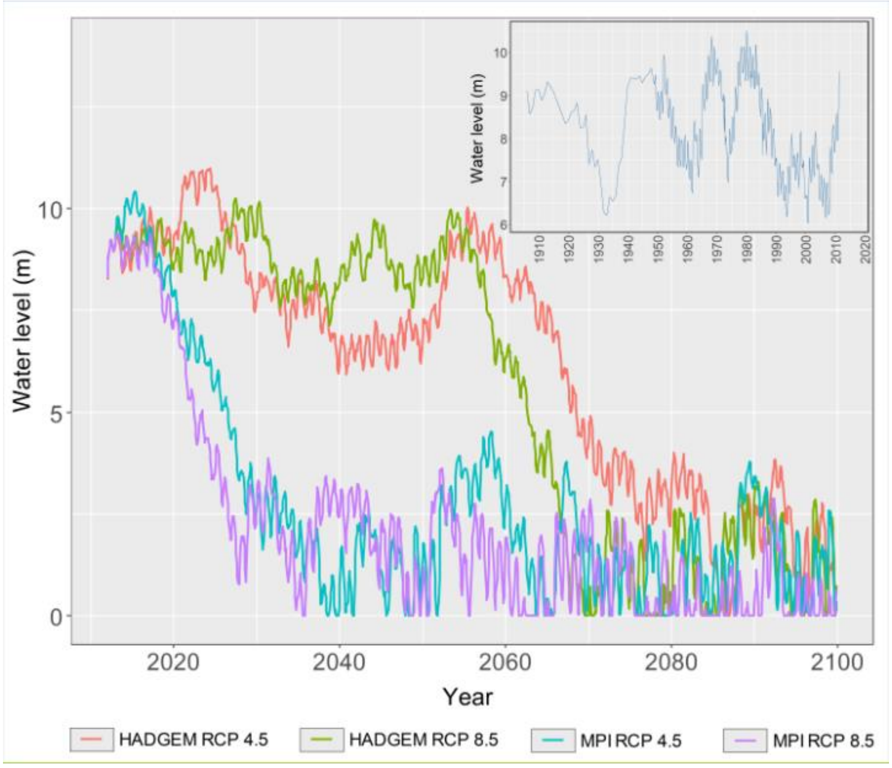

Figure 1-12 Changes in actual water level of Lake Beyşehir from 1910 to 2010 and under different climate change scenarios (HadGEM model, RCP 4.5 scenario, HadGEMmodel, RCP 8.5 scenario, MPImodel, RCP 4.5 scenario, MPImodel, RCP 8.5 scenario) (reproduced from Bucak et al. (2017)).

The first study of fish in the lake was carried out in 1958, revealing six fish species among which there were no predators (Numan 1958). A number of species have since then been introduced, pikeperch (*S. lucioperca)* in 1978, tench *(T. tinca)* in early 1990s, prussian carp (*C. gibelio*) in late 1990s, big-scale sand smelt (*A. boyeri*) in early 2000s, topmouth gudgeon (*P. parva*) in the early 2010s, with rapidly increasing populations (Balık 1997; Yeğen et al. 2006; Meke et al. 2012; Bayçelebi et al. 2020). This led to significant changes in the native fish fauna, causing a dramatic decline of the endemic fish species, and Beyşehir bleak *(A. akili*) extincted (Küçük 2012). Today, 15 fish species, native to the lake, are threatened with extinction, of which 7 are assessed as endangered and one as vulnerable according to IUCN (see Supporting Material 3, Table S1). The introductions also substantially affected the waterbird communities. The islands in the lake used to accommodate big colonies of wading, diving and scooping piscivorous birds such as black-crowned night heron (*Nycticorax nycticorax*), great cormorants (*Phalacrocorax carbo*) and Dalmatian pelicans (*Pelecanus crispus*), which have either disappeared totally or declined drastically in numbers following the stocking of the non-native fish (Ertan et al. 1989; Magnin and Yarar 1997; Bucak et al. 2018).

Historical and paleolimnological studies have shown that the water level fluctuations were critical for the lake's ecosystem structure and functioning (Beklioğlu et al. 2006; Zohary and Ostrovsky 2011; Levi et al. 2016). During the time period 1960-2012, the monthly average water input to the lake (including precipitation, inflows and groundwater) was 91 ± 72 hm^3, and surface evaporation was 83 ± 35 hm^3. However, the average monthly water abstraction for irrigation of the downstream basin was as high as 24 ± 27 hm^3 (Bucak et al. 2017). The future water level state of the lake looks gloomy. Bucak et al. (2017) conducted a simulation of the future water level changes relative to different land uses and climate change scenarios using the model SWAT with a Support Vector Regression model (ε-SVR). In all scenarios, the results revealed a major reduction in water level, and the most pessimistic climate and land use scenario predicts a potential dry out by the 2030s at the current outflow regime (Bucak et al. 2017). Outflow management scenarios were also run to reveal the reduction of water abstraction needed to maintain the water level of the lake, and the result showed that a 20-60% reduction of the outflow is required to save the lake from complete disappearance. Therefore, urgent and strict water resource planning and outflow management are clearly vital to sustain the lake ecosystem and its many services (Bucak et al. 2017).

DISCUSSION

The past

The surface waters (lakes and marshes) in the KCB have undergone drastic changes over the past 20,000 years, until recently mainly due to natural variations in climate. During the last glaciation, KCB hosted many wetlands and the large paleolake Lake Konya, which persisted, albeit with intermittent dry periods, as late as until the end of the last glacial where it dried up permanently in the early Holocene. Many of the current lakes and wetlands in the southern basin are the remnants of the ancient Lake Konya, and these lakes host many endemic (e.g. fish) species and play a critical role for the regional avifauna. Judged from the examples presented, drastic loss of lake surface area and salinisation have occurred during the past 40 years, not least during the last two decades, in part due to changes in climate, but largely as a result of water abstraction and landscape regulation to support an increasing agricultural production. These changes have had significant effects on the lakes and their biota as illustrated clearly by the three case studies.

Analyses of existing data from 13 meteorological stations in KCB indicated an increase in annual mean temperatures at most of the stations and a decrease in annual precipitation at some, but not all sites (Fig. 2). The changes have contributed to a deterioration of the already damaged water balance, water withdrawal for agriculture, however, being by far the key factor behind the substantial changes observed in the groundwater table (overall 1 m /year since 1980s) and the major reduction of lake and marsh surface areas. Thus, a major increase in crop production and a shift to water thirsty crops have shifted the land use to intensively irrigated crop farming at the expense of the animal farming and herding that historically characterised the farming in the region (England et al. 2008). Especially after 2000, crop production has increased dramatically (Fig. 3), in part due to the establishment and privatisation of sugar factories, stimulated by the new Sugar Law adopted in 2001 (Türkşeker, 2020). This major increase in crop farming is clearly mirrored by the major drop in the groundwater tables (Fig. 4). In 2013, the water potential of the basin was estimated to 4,679 $hm^3 year^{-1}$, but the annual amount used was 4,996 hm^3, of which 95% was applied for irrigation. The water deficit owing to irrigation has led to water import from neighbouring catchments (e.g. the Blue Tunnel Project involving transfer of water from the Göksu catchment to Konya Plain). Such compensatory import is well known from other arid regions (e.g. Zadereev et al., online) but has negative consequences for the lakes in the exporting catchments, a notable example being the iconic Aral Sea (Aladin et al. 2018). Moreover, mainly in the southern areas of the KCB, a large number of reservoirs have been constructed, in some cases at the expense of natural lakes and marshes by diverting their major inflows. Reservoir construction is a common practice in semi-arid and arid areas worldwide with the objective to provide water for irrigation and drinking, but it has led to redistribution of water and water loss with devastating effects on downstream aquatic ecosystems (Albert et al. 2020; Zadereev et al. online). So far, changes in land use and irrigation rather than climate change have had the most devastating effects in semi-arid and arid areas worldwide in recent decades (Wurtsbaugh et al. 2017; Zadereev, 2018; Albert et al. 2020; Zadereev et al. online).

In the KCB, the surface areas of lakes have decreased markedly (e.g. Lake Düden) and several lakes have even dried out (see Case Study 1 and 2). Moreover, many lakes have become more saline, of which Lake Düden is an illustrative example (Fig 7). Increasing salinity may lead to reduced biodiversity (Williams et al. 1990; Schallenberg et al. 2003; Flöder et al. 2004, Kipriyanova et al. 2007; Jeppesen et al. 2015, Anufriieva and Shadrin, 2018; Golubkov et al. 2018) and a consequent loss of ecosystem functioning. Often pronounced effects are seen when specific salinity tipping points are surpassed, for example a complete loss of fish at high salinities (Lin et al. 2017; Vidal et al. 2021). Accordingly, widespread drainage and deterioration of the wetlands in the KCB have resulted in dramatic declines in the populations of threatened waterbirds in KCB over the last 60 years, most dramatically after the early-2000's (coinciding with the intensification of agriculture production), and this was more intense than the global population trends of the species (IUCN 2017; IUCN 2019). Some species have actually become extinct from the region (Fig. 8), which we attribute to the loss of important wetlands such as the Hotamış, Eşmekaya and Ereğli Marshes (see Case Study 1) and the widespread degradation and deterioration of the lakes, for instance Lake Düden (Fig. 6). During the past 20 years, the species richness of breeding waterbird has dropped markedly, most conspicuously so in the areas with the former Hotamış, Ereğli and Eşmekaya Marshes, suggesting that the widespread habitat loss and deterioration in KCB are the greatest causes.

The fish fauna of the KCB, with a large component of endemic species, is subject to serious threat of extinction (Çiçek et al. 2018). Abstraction and diversion of freshwater to dams and reservoirs with agricultural purposes at the expense of natural lakes and wetlands poses the major threat to the freshwater biodiversity, as it causes habitat fragmentation, alteration of natural seasonal patterns (Albert et al. 2020). The disappearance of wetlands in KCB (including the Lake Hotamış, Ereğli and Eşmekaya Marshes) forced the native fish fauna to seek refuge in restricted spring-fed tributaries, making them extremely vulnerable to hydrological alterations (İnnal and Erk'akan 2006). Several groups of endemic fishes (e.g. killifish, Anatolian minnow and Ereğli minnow) depend on springs and small streams for survival and have narrow distribution ranges (see Supporting Material 3, Table S1). Therefore, even relatively low environmental stress on these small fish populations can lead to local extinction, which is reflected by the threatened status of 61% of these endemic species. Introduction of new non-native fish, mostly invasive, species have taken place and they now comprise 20% of the fish fauna. This has led to an additional pressure on the native fish fauna, resulting in extinction (*A. akili*) (Küçük 2012), with potential effects also on waterbird populations (see Case Study 3). Carps, for example, can compete with diving omnivorous ducks, such as the three duck species studied here, for benthic macroinvertebrate food sources and thereby enhance eutrophication in shallow lakes, both of which may disturb the habitats of diving omnivorous waterbirds (Maceda-Veiga et al. 2017; Özgencil et al. 2020).

The future

The trend analysis suggests that the temperature in the basin is increasing, while precipitation does not show a significant trend, pointing to that the water loss from the basin will increase due to enhanced evaporation and transpiration. This is clearly evidenced by the observed negative SPEI values (Fig. 6) indicating water stress after 2000 due to enhanced evapotranspiration. Increased evapotranspiration was historically critical for either shrinkage or complete loss of lakes in the basin (e.g. paleolake Lake Konya), and now it appears that history is unfortunately repeating itself. Using the global circulation models MPI-ESM-MR, HadGEM2-ES and GFDL-ESM2M, together with the regional climate models RCP 4.5 and RCP 8.5, Dolsar (2015) has predicted the water balance in KCB until 2050, showing a decrease in the water resources of the basin that can only be eliminated by additional inter-basin water transfer.

With the current agricultural policies, agricultural production in KCB will likely continue to increase in the same manner as in the last 20 years in order to satisfy the demand of an increasing human population. Left uncontrolled, the production of thirsty crops such as sugar beets will increase and so will the extent of irrigated areas and the amount of water used (EIA, 2019). To ensure effective use of the basin, this could in part be counteracted by switching to water-saving irrigation methods and planting of crops suitable for the climate and water potential of the area through regional level action (Albert et al. 2020). If the demand for water remains at the current level or increases to meet irrigation needs, the groundwater table will expectedly drop further and demand even more inter-basin transfer of water, which would surely inflict a disaster in the catchment whose water is taken.

The major changes in climate and continued water abstraction will continue to create environmental changes in lakes also in the future. This is clearly illustrated by the simulation of the future water level changes in the largest freshwater lake in Turkey, Lake Beyşehir (case study 3), showing that the lake might suffer from frequent episodes of dry out, under the current outflow regime, already by the 2030’s-2050’s (Bucak et al. 2017). Reduced water input to the lake will result in a lower nutrient loading from the catchment to the lake, which, as judged from modelling results, will only insignificantly affect the biomass of algae in this nutrient-poor lake (Bucak et al. 2018). However, as a result of the increasing fluctuations in the lake level, the abundance of potentially toxic cyanobacteria might increase in the future (Zohary and Ostrovsky 2011), which will threaten the ecosystem integrity and possibly limit the use of the lake as a drinking water supply. More eutrophic lakes in semi-arid climate may be even more affected by the climate change. A mass balance and modelling study of Lake Mogan (outside the KCB) revealed that, in dry periods, low inflow rates and high evaporation produced increased in-lake nutrient concentrations due to both the concentration of nutrients in less water and increased internal loading (Coppens et al. 2016, 2020). The algal biomass and the abundance of cyanobacteria were also much higher in the drier and warmer scenarios. Overall, the results show that lower hydraulic loads and reduced flushing rates as a result of drier and warmer conditions lead to lower water levels and higher in-lake nutrient concentrations unless the nutrient loading decreases. Such changes are also accompanied by salinisation where even a few years with a prolonged hydraulic residence time can shift lakes to brine conditions (Beklioğlu et al. 2018)

Apart from eutrophication, the expected salinity changes will severely affect the biodiversity and trophic dynamics of the KCB lakes (Brucet et al. 2011; Lin et al. 2017; Jeppesen et al. 2020; Zadereev et al. 2020; Vidal et al. this volume), and major shifts may occur when certain salinity thresholds are surpassed (Jeppesen et al. 2007; Lin et al. 2017).

Wetland habitat loss and degradation should be minimised to preserve the remaining waterbird populations in the region. Unless strict measures are taken to conserve the habitat quality of the remaining wetlands, the basin will soon no longer be able to support any of the threatened waterbirds. Yet, the return of thousands of waterbirds, including breeding white-headed ducks (Gürsoy-Ergen 2019), to the Sultan Marshes in Dereli Closed Basin, which was restored after years of water shortage and drainage, shows that it may not be too late to save some of the IBAs in the region. The intense pressure on the KCB aquatic habitats has already resulted in a dramatic decline in the populations and range size of many fish species (Küçük et al. 2012; Freyhof et al. 2020). Many endemic species have been restricted to isolated refuge habitats such as springs and spring-fed streams, causing extreme limitation of dispersal. Therefore, immediate protection of these refuge areas, effective mitigation of current pressures and restoration of native aquatic habitats in KCB are critically important for the endemic fish fauna of KCB. If these pressures continue with the current trajectory, local extinction of fish populations may be imminent. The already damaged aquatic ecosystems have further been threatened by invasive species with a documented extinction of endemic fish in the basin. Restoring healthy and resilient ecosystems and strict control of invasive species are a priority to maintain the fish fauna of KCB with its high endemism.

CONCLUSIONS

Anthropogenic impacts have already inflicted serious damage to the lake and wetland ecosystems of KCB in terms of significant declines of populations across many taxa and a dramatic loss of species richness, habitats and likely also ecosystem services. The profound changes the recent decades are mainly attributable to overexploitation of the water resources and changes in land use, but also the impact of climate change becomes increasingly more significant. Decades of unsustainable water use, ill-guided agriculture policies, shrinkage of wetlands and lakes, increases in salinity and invasive fish species introductions in KCB have resulted in decreased populations of red-listed waterbird species as well as species richness loss of breeding waterbirds, decimated fish populations and endemic fish species in danger of extinction due to habitat loss and changes in salinity and nutrient loading. Future projections with different land use and climate scenarios indicate that climate change will exacerbate this situation; for instance, the largest freshwater lake in Turkey, Lake Beyşehir, might permanently dry out within 50 years. Moreover, aridification and decreased runoff will augment the trend of salinisation and nutrient enrichment in the remaining water bodies, which will contribute to the deterioration of the ecological functioning of the lakes and likely a more serious threat to the sustainability of agricultural activities and give rise to water quality concerns. Sustaining the lake ecosystems and their many services requires urgent and strict water resource planning and outflow management at basin scale (Bucak et al. 2018). In order to reverse the ecosystem degradation or even preserve the current status, there is a need for a framework policy that aims to restrict the exploitation of water resources within sustainable limits while simultaneously promoting conservation efforts. This seems achievable only if the basin-wide legal regulation of water abstraction is combined with economic incentives of transition to climatically appropriate crop farming.

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SUPPORTING MATERIAL

S1 | Abundance Estimates for the Red-listed Species and Mid-winter Waterbird Censuses

We have used all available published and unpublished sources on populations of red-listed waterbird species in the Konya Closed Basin to evaluate the changes in their population sizes (Ornithological Society of Turkey, 1969; Ornithological Society of Turkey, 1972; Ornithological Society of Turkey, 1975; Ornithological Society of Turkey, 1978; Beaman, 1986; Kasparek, 1987; Ertan et al. 1989; Martins, 1989; Karauz Kıraç, 1993; Kirwan, 1994; Kirwan and Martins, 1994; Karauz Kiraç and Kiraç, 1996; Magnin and Yarar, 1997; Eken and Magnin, 2000; Kirwan and Martins, 2000; Kirwan, 2003; Richardson, 2003; Kılıç and Eken, 2004; Eken et al. 2006; Kirwan et al. 2008; Kirwan et al. 2010; Kirwan et al. 2014; Özgenci,l 2016; Boyla et al,. 2019; Özgencil, 2019; Gürsoy-Ergen, 2019). We have followed a standard set of rules to convert written accounts and range estimates (i.e. min-max) into numbers. First of all, estimates and eBird sightings that did not report abundance (i.e. “present”) were discarded. Records that reported abundances as “few”, “a few”, “several” and “some” were also not considered. We chose to treat intervals as single numbers, and we simply took the mean of the lower and upper limits and used it as the final estimate. Here, numbers ending with integers were rounded to the closest integer (e.g. 3.5 -> 4). Estimates and sightings termed “At least N individuals/pairs” were treated as N individuals/pairs.

We used mid-winter waterbird census results for the years between 1965 and 2019 (DKMP, 2019a) to investigate the change in abundances of wintering waterbirds at IBAs given in the case study boxes and abundances of the red-listed waterbirds in the basin. The censuses used point counts (Bibby et al. 2000) from a fixed set of points, and the teams covered the whole surfaces of the wetlands in a single day (Özgencil et al. 2020). The censuses were conducted by experts. The census years and the number of available census years were different for the study IBAs, and there were multiple gaps of no-count periods for most of these IBAs. Nevertheless, the available data was good enough to picture overall tendencies in the trends.

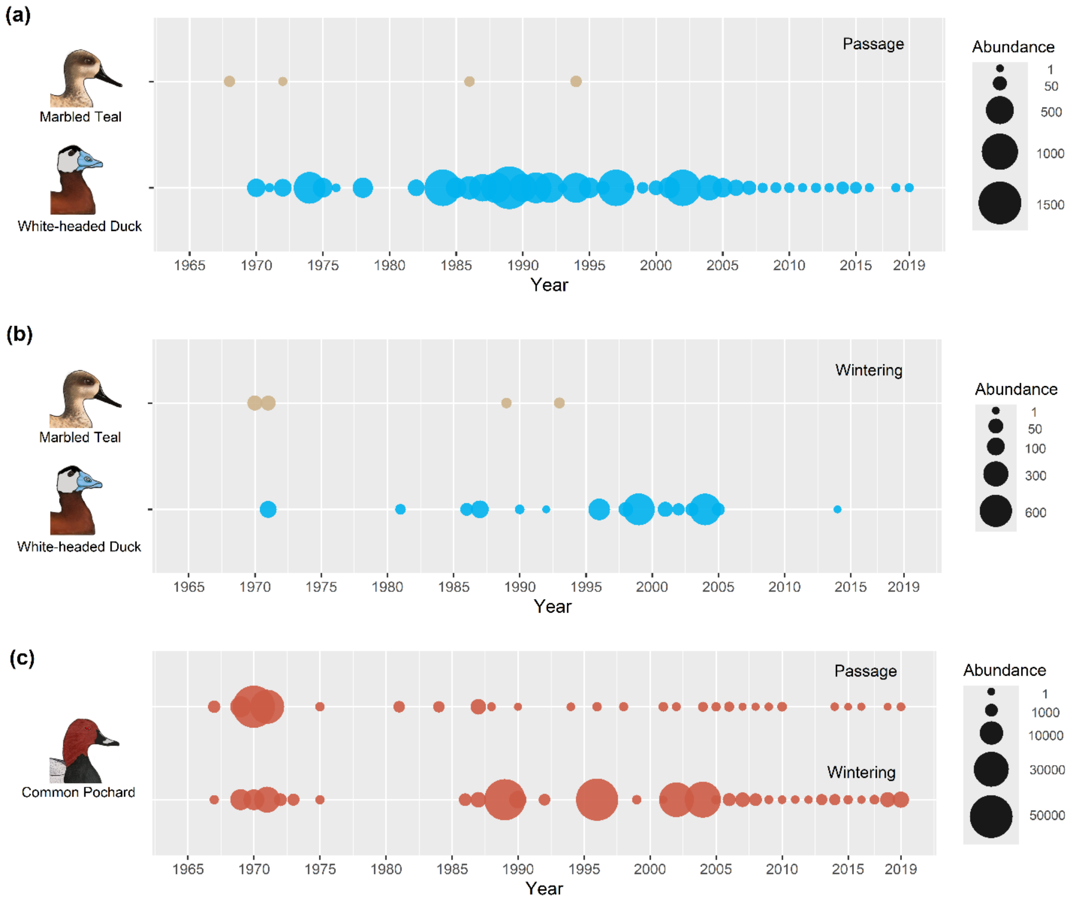

Fig. S1: Change in migrating (a and upper row in c - includes molting and post-breeding populations) and wintering (b and lower row in c) population sizes of the three globally threatened waterbird species in the basin.

S2 | The Breeding Bird Atlases

The 1998 breeding bird atlas was specific to the basin and was conducted in the breeding season between 9 May 1998 and 30 June 1998 (Eken and Magnin, 2000). The basin was divided into 10x10km UTM grid squares. The teams used point counts and line transects (Bibby et al. 2000) (while moving between the point count spots) to study the breeding birds of the basin. The atlas used the breeding codes given in Hagemeijer and Blair (1997). Two to eight point counts were conducted in each 10x10km square, and the points were chosen as to represent the full range of available habitats in the square. These spots were picked by using a detailed habitat map of the squares. The field teams were composed of expert ornithologists.

The 2014-2018 atlas was conducted at the national scale (Boyla et al. 2019). The breeding season for the study area was defined as the time frame between the beginning of April and he end of June, and it was divided into two periods: early breeding season and late breeding season. In each of the 50x50km UTM grid squares, two 10x10km squares were surveyed by teams made up by a mixture of experts and volunteers. These 10x10km squares were chosen so that they differ in terms of habitat type and represent the 50x50km habitat types well. The teams walked along two to four 1 km transects (not necessarily straight lines) for an hour in each 10x10km square and recorded every species that they saw or heard. The breeding codes in Hagemeijer and Blair (1997) were used. In addition to the line transects, the teams also gathered data while they were on the move between line transects. The teams conducted supplementary surveys in each 50x50 km habitat if some habitat types were thought to be missed.

For several reasons, we believe that the two atlases are comparable. First, the grid system used in the atlases overlap perfectly since exactly the same grids and squares were used in both. Second, also the breeding codes used were the same with the addition of a code for suspected non-breeders in the most recent atlas (Herrando et al. 2013). Third, the methods used in the atlases, point counts along fixed-radius point transects (Bibby et al. 2000) and line transects (Bibby et al. 2000), produce highly similar incidence (i.e. presence-absence) outputs (Sutherland et al. 2004; Buckland, 2006; Sutherland, 2006). For all these reasons, we believe that the incidence results of the atlases are compatible and comparable. Unfortunately, we could not use abundance data in our work, which would have provided a deeper insight into the changes that have taken place, simply because the 1998 atlas did not report abundances in its final report.

We chose to use the records with “probable” and “confirmed” breeding codes, as well as, “possible” breeding codes (Hagemeijer and Blair 1997) to make the most of the available data. For some shy species and species that breed in practically inaccessible habitats, it may be difficult to confirm the breeding. Considering the methodologies of the two atlases, it might not have been possible to get confirmed or probable breeding records for the species groups that require extra attention to assess accurately (Hagemeijer and Blair 1997), we chose to keep possible-coded records as well so as not to miss such species. We admit that this can potentially cause inclusion of some species that are oversummering or not truly breeding in the basin (more so for the first breeding atlas due to its temporally limited census design), but after getting some expert opinion, we found out that the number of such records seem to be no more than a few in the whole dataset.

S3 | Dataset of Freshwater Fish Fauna

A list of endemic freshwater fish species in KCB obtained from Kuru (2004), Innal and Erk’akan (2006), Geldiay and Balık (2007), Innal (2012), Kuru et al. (2014), Tarkan et al. (2015), Küçük et al. (2016), Çiçek et al. (2018), Freyhof et al. (2018), Çiçek et al. (2020), Freyhof et al. (2020) and Freyhof and Yoğurtçuoğlu (2020).

KCB with 28 endemic fish species is one of the important basin in Turkey, due to its high endemism rate. The current conservation status, based on the IUCN classification of the endemic fish species and distribution areas in the KCB is summarized in Table S1.

Table S1. The current conservation status and distribution areas of the endemic fish species of the KCB

Species	**Status**	**Distribution**
Alburnus akili Battalgil, 1942	EX	Lake Beyşehir
Anatolichthys anatoliae (Leidenfrost, 1912)	NT	Central Anatolia
Anatolichthys iconii (Akşiray, 1948)	NE	Lake Beyşehir, Lake Eğirdir, Lake Kovada and tributaries
Capoeta mauricii Küçük, Turan, Şahin and Gülle, 2009	EN	Lake Beyşehir and trıbutaries
Chondrostoma beysehirense Bogutskaya, 1997	EN	Lake Beyşehir and trıbutaries
Cobitis battalgili Băcescu, 1962	EN	Lake Beyşehir and Central Anatolia
Cobitis bilseli Battalgil, 1942	EN	Lake Beyşehir and trıbutaries
Garra kemali (Hankó, 1925)	EN	Lake Beyşehir and Central Anatolian lake tributaries
Gobio battalgilae Naseka, Erk'akan and Küçük, 2006	DD	Lake Beyşehir and trıbutaries
Gobio gymnostethus Ladiges, 1960	CR	Eastern Lake Tuz basin
Gobio hettitorum Ladiges, 1960	CR	Southern Lake Tuz basin,Karaman
Gobio insuyanus Ladiges, 1960	CR	Western Lake Tuz basin, Cihanbeyli
Gobio microlepidotus Battalgil, 1942	VU	Lake Beyşehir and Göksu River
Oxynoemacheilus angorae (Steindachner, 1897)	LC	Central and Northwestern Anatolia
Oxynoemacheilus atili Erk'akan, 2012	NT	Lake Beyşehir and tributaries
Oxynoemacheilus eregliensis (Bănărescu and Nalbant, 1978)	VU	Central Anatolian lake tributaries
Paraphanius similis (Akşiray, 1948)	NE	Lake Akgöl, Zengen spring-Niğde
Pseudophoxinus anatolicus (Hankó, 1925)	EN	Lake Akgöl and Lake Beyşehir
Pseudophoxinus battalgilae Bogutskaya, 1997	LC	Lake Beyşehir, Manavgat River

Pseudophoxinus caralis (Battalgil, 1942)	NE	Lake Beyşehir and tributaries
Pseudophoxinus crassus (Ladiges, 1960)	EN	Lake Tuz tributaries
Pseudophoxinus hittitorum Freyhof and Özuluğ, 2010	EN	Lake Beyşehir tributaries, Çumra stream
Pseudophoxinus iconii Küçük, Gülle and Güçlü, 2016	NE	Lake Tuz tributaries
Seminemacheilus dursunavsari Çiçek, 2020	NE	Goksu River drainage and Lake Beysehir tributaries
Seminemacheilus ekmekciae Yoğurtçuoğlu, Kaya, Geiger and Freyhof 2020	NE	Lake Tuz tributaries
Seminemacheilus lendlii (Hankó, 1925)	VU	Western central Anatolia
Squalius anatolicus (Bogutskaya, 1997)	LC	Lake Beyşehir, Lake Tuz and tributaries
Squalius cappadocicus Özuluğ and Freyhof, 2011	CR	Lake Tuz tributaries, Aksaray

EX, extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern; DD, data deficient; NE, not evaluated based on the IUCN Red List.

Among 28 endemic species of the KCB, 16 were categorised as threatened with extinction (Figure S2). Of these threatened species, four were classified as critically endangered, eight as endangered and three as vulnerable. Of the total number of endemic taxa assessed, two species were near threatened, three species were least concern and one species was extinct. Furthermore, one species was classified as data deficient due to insufficient knowledge and six species as not evaluated (IUCN 2020).

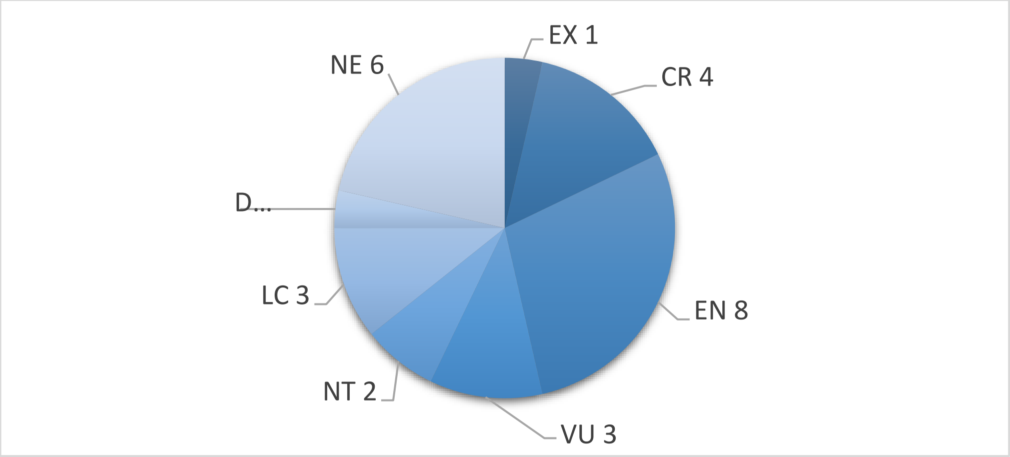

Fig. S2. The number of endemic freshwater fish species listed in IUCN Red List Category. CR; critically endangered, DD; data deficient, EN; endangered, EX; extinct, LC; least concern, NE; not evaluated, NT; near threatened and VU; vulnerable

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CHAPTER 2

CONTRASTING GREENHOUSE GAS EMISSIONS IN COASTAL AND INLAND MEDITERRANEAN SALINE LAKES

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ABSTRACT

Saline lakes and wetlands play a crucial role in global carbon and nitrogen cycles. However, our understanding of how salinity shapes GHG dynamics in saline lakes remains incomplete, particularly considering the potential variation between coastal and inland lake types. To address the variation in GHG dynamics across saline lake types, this study investigates GHG emissions and their environmental drivers in 33 inland and coastal saline lakes across western Anatolia, spanning a wide salinity range (0.4-260 ‰), during early summer. Diffusive fluxes of methane (CH_4), carbon dioxide (CO_2) and nitrous oxide (N_2O) varied considerably, ranging between 0 and 135, -44 and 2576 and 0 and 1.00 mmol m^{-2} d^{-1}, respectively. CH_4 emissions declined markedly above c. 5 ‰ salinity, while CO_2 and N_2O emissions showed weaker negative responses to salinity. Notably, dissolved organic carbon correlated with CH_4, whereas CO_2 and N_2O were linked to the NO_3^- availability. Coastal lakes differed from inland lakes, with most coastal systems showing no net emissions of CH_4 and N_2O and potentially acting as net sinks due to their lower nutrient and organic substrate levels. Conversely, inland lakes exhibited net positive CH_4 and N_2O emissions even at high salinities. Current findings suggest that projected salinization due to climate change in arid landscapes may result in a decrease in CH_4 emissions from shallow lake systems, whereas concurrent potential increase in higher nutrient loading may increase CO_2 and N_2O emissions.

Keywords: methane; carbon dioxide; nitrous oxide; carbon cycling; endorheic lakes; coastal lakes; salinization

INTRODUCTION

Shallow lakes and wetlands play a crucial role in the carbon (C) and nitrogen (N) cycles (Einsele *et al*., 2001; Murray *et al*., 2015; Rosentreter *et al*., 2021; Solomon *et al*., 2015) and despite their relatively small surface areas, they significantly contribute to the global greenhouse gases (GHGs) budget (Bastviken *et al*., 2011; DelSontro *et al*., 2018). They are key in the capture and burial of CO_2 via primary production and sedimentation while they can also emit large amounts of CO_2 through respiratory processes (Cole *et al.*, 1994; Duarte and Prairie, 2005). In addition, emissions from inland waters (including coastal wetlands, estuaries, reservoirs, streams, and rivers) constitute roughly half of the total global methane (CH_4) (~366 Tg y^{-1}) and 5% of the nitrous oxide (N_2O) (0.8 Tg y^{-1}) emissions (Ciais *et al*., 2014; Saunois *et al*., 2016, Tian *et al*.; 2020). Overall, they contribute *c.* 20 % of the total radiative forcing caused by GHGs (DelSontro *et al*., 2018b). Climate change and other anthropogenic impacts (*e.g.*, eutrophication) are expected to further increase GHG emissions (Ciais *et al*., 2014; DelSontro *et al*., 2018). Eutrophication (Beaulieu *et al*., 2019; Davidson *et al*., 2015; DelSontro *et al*., 2016; Meerhoff *et al*., 2022; Zhou *et al*., 2019) and temperature rise (Allen *et al*., 2005; Yvon-Durocher *et al*., 2014; 2017) promote increased CH_4 emission, while eutrophication and warming interact with potentially synergistic effects (DelSontro *et al*., 2016; 2018; Davidson *et al*, 2018; Meerhoff *et al*., 2022). N_2O, as another potent GHG gas, is also controlled by nutrient availability (Audet *et al.*, 2014; Wang *et al.*, 2009), temperature (Velthuis *et al*., 2022; Wang *et al*., 2023), and oxygen levels (Liikanen and Martikainen, 2003; Wang *et al*., 2009).

GHG emissions from saline ecosystems has been a growing research interest both in inland (Camacho *et al*., 2017; Soued *et al*., 2024) and coastal (Huertas *et al*., 2019; Zhou *et al*., 2022) environments due to the growing threat of salinization in inland waters (Cunillera-Montcusi *et al*., 2022) and due to the potential impact of salinity on CH_4 emissions in lentic environments. Sulfate (SO_4^{2-}) ion, abundant in natural saline waters, exerts a two-way control on CH_4 emissions by favoring sulfate-reducing bacteria (SRB) over methanogens, as SRB can utilize the same organic substrates but with a higher energy yield, and it directly promotes anaerobic oxidation of CH_4 through a coupled process involving SRB and archaea (Barnes and Goldberg, 1976; Bartlett *et al*., 1987; DeLaune *et al*., 1983; Wang, 1996; Hu *et al*., 2017). Recent research highlights the complex interaction between salinity, temperature (Chamberlain *et al*., 2020), and organic matter availability (Soued *et al*., 2024) in governing CH_4 dynamics in saline environments, as evidenced by the persistence of CH_4 production in industrial hypersaline ponds, due to halophilic archaea employing alternative metabolic pathways (Zhou *et al*., 2022). Early research suggests that N_2O emissions are lower in high salinity water bodies (Smith *et al*., 1983). However, studies of saline mangrove ecosystems have shown that they can act as sources or sinks of N_2O depending on factors such as temperature, pH, oxygen, NO_3 and organic matter availability, rather than salinity (Livesley and Andrusiak, 2012).

Overall, temperature, salinity, nutrient, and organic matter availability have interacting effects on lakes' GHG dynamics. Thus, analyzing the interactive effects of salinization, climate warming, water abstraction and eutrophication is crucial for predicting future lake responses and GHG emissions, especially in semi-arid regions where these effects are likely to be most pronounced (Beklioğlu *et al.,* 2018). Combined threats of climate change, increasing agricultural activity and groundwater abstraction for irrigation have already had grave impacts on the size, morphometry, salinity, ecosystem structure and functioning of shallow lake ecosystems (Jeppesen *et al*., 2020). Particularly, in arid and semi-arid regions such as the Mediterranean region, lower precipitation and increased water consumption are expected to exacerbate water level reductions; permanent or temporary lake dry-outs, salinization, and overall altered ecosystem functions (Beklioğlu *et al*., 2018; Çolak *et al*., 2022; Cunillera-Montcusi *et al*., 2022; Jeppesen *et al*., 2015), which may have implications for GHG dynamics while our limited knowledge on GHG dynamics across salinity and eutrophication gradients hinders accurate predictions.

Saline lakes display spatial a wide spatial heterogeneity dependent on their geographical context, which significantly influences their ecological and biogeochemical processes. Endorheic saline lakes, typically situated in arid and semi-arid regions with limited water exchange, have markedly longer residence times (Wang, 2020). Limited water exchange, coupled with high evaporation, concentrates dissolved materials within these lakes. Agricultural practices in the catchment can further enrich nutrients through runoff. Coastal lakes, on the other hand, maintain lower average nutrient concentrations due to constant dilution through regular (e.g., tidal) and irregular (e.g., storm surges) marine intrusions, resulting in lower nutrient concentrations and a dynamic hydrological regime (Scheffers and Kelletat, 2019). These contrasting conditions shape the biological interactions, biogeochemical processes, and the GHG dynamics of these two saline lake types.

In this study, we focused on a set of central Anatolian inland saline and brackish lakes, comparing them with coastal lakes in several estuarine lake systems on the Mediterranean coast of Anatolia. We hypothesized that salinity and nutrient availability interact to influence GHG dynamics in saline lakes, while contrasting nutrient conditions between inland and coastal lakes would further modulate their GHG emissions, being higher at more eutrophic conditions. Our goals were to i) document diffusive GHG emissions in central Anatolian saline lakes and southern Anatolian coastal lakes, ii) analyze the environmental drivers of GHG emissions and elucidate potential differences between the driving forces of GHG dynamics of coastal and inland saline lakes in this Mediterranean semiarid hot region, and iii) assess the possible future alterations in relation to salinity, lake morphology and eutrophic status changes.

STUDY SITE AND METHODOLOGY

Study Site

A total of 33 inland and coastal brackish to saline lakes in central and southern Türkiye were sampled in July 2021 and June 2022 (Fig. 1; Appendix A). All inland lakes (n=19) are located in KCB and BCB, except two, which were in adjacent basins with similar landscape and climate patterns. KCB is the largest closed basin (50 000 km^2) of Türkiye and covers 7 % of the country’s land area with an average altitude of about 900-1300 m. Having a cold semi-arid climate, the annual mean precipitation in the basin is 340 mm and the annual mean temperature of 11.9°C (Yılmaz *et al*., 2011). The smaller (6300 km^2) BCB features a similar altitude and climate profile, albeit moderately warmer and more humid with an annual average temperature and precipitation of 13.2°C and 413 mm, respectively (Çolak *et al*., 2022). Both basins are intensely cultivated, and irrigation relies heavily on surface- and groundwater abstraction, with major effects on lake water level surface area and salinity (Çolak *et al*., 2022; Yılmaz *et al*., 2021). Coastal lakes (n=14) are part of the several different estuarine systems in the southwestern and southeast Mediterranean coast of Türkiye, namely the Köyceğiz-Dalyan lagoon system (8 lakes), Göksu Delta (2 lakes) and Seyhan-Ceyhan rivers delta *i.e.*, Çukurova Delta (4 lakes). All these lagoon systems have a Mediterranean climate with a mean annual temperature of 18°C and average precipitation of 610-1200 mm (Bayarı *et al*., 1995; Seçkin *et al*., 2010). Köyceğiz-Dalyan system consists of Köyceğiz Lake discharging into the Mediterranean through a meandering stream network which connects several other coastal saline lakes. Göksu and Çukurova Delta plains are extensively cultivated with agricultural land occupying 50 and 32.5 % cover, respectively; their hydrology is heavily modified due to anthropogenic activities such as hydroelectric power plants, refineries, urban and wastewater discharges (Çakan *et al*., 2005; Çelekli *et al*., 2024). Both deltas support diverse ecosystems including saline and brackish lakes, salt marshes and sand dunes with a notable biodiversity (Seçkin *et al*., 2010).

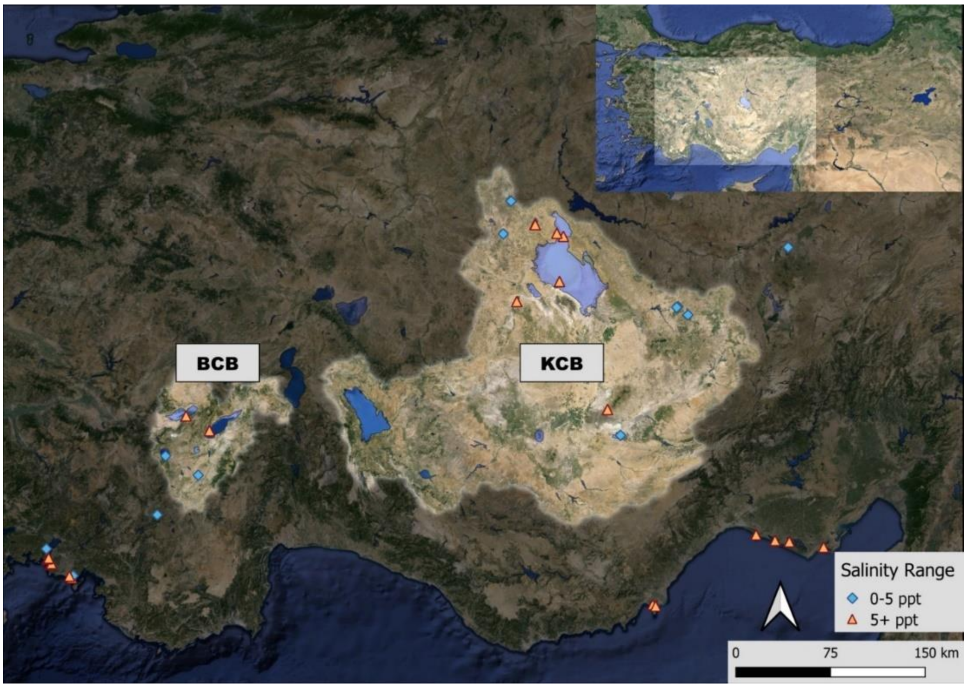

Figure 2-1 The study site and sampled lakes are overlaid with inland basin borders and coastal delta labels. BCB: Burdur Closed Basin, KCB: Konya Closed Basin.

Water Sampling

Water sampling was done at the deepest point of the lake or the subbasin. Physical parameters (water temperature, electrical conductivity, and dissolved oxygen (DO)) were measured on site with a YSI proDSS (YSI, USA) multimeter. The diffuse attenuation coefficient (K_d), a measure of light penetration, was determined using a spherical LI-250A (LI-COR, USA) lightmeter and the light extinction was calculated based on Kirk (1994). A depth integrated 40 L composite water sample was taken with a Ruttner sample, or with a HDPE pitcher in shallower lakes (<0.3 m). Water samples were taken in HDPE bottles for water chemistry analyses (unfiltered water for TN and TP, filtered for dissolved inorganic nutrients and dissolved organic carbon (DOC). For Chl-*a* analysis 100-1000 ml of water sample was filtered through 47 mm (Whatman GF/C) filters on site. Water and filter samples were preserved frozen at -20 °C until the analysis. Percent plant coverage (cov) and plant volume infested (PVI) at around the sampling site were estimated visually with a bathyscope where possible, or with the help of a plant rake to estimate the vegetation density.

GHG sampling

GHG samplings were done on a littoral site with a typical depth of 0.2-1.0 m in each lake (n=33). In 11 larger and deeper lakes, an additional pelagic site located on, or close to the deepest point of the lake, was sampled to investigate the spatial variability of GHG fluxes. In the statistical analyses, only the littoral sites were used for comparison with the rest of the shallow lakes, as stratification can alter GHG dynamics (Davidson *et al*., 2024). Fluxes of CO_2, CH_4, and N_2O were measured in the field using a floating chamber design adapted from Bastviken *et al.* (2015). The floating chambers were made from polypropylene tubs with a radius of 15 cm and 8 L volume. Chambers were equipped with floaters and coated completely with reflecting material to minimize solar heating. All gas measurements were done in the afternoon, typically between 2:00 and 6:00 pm, to standardize bias caused by diurnal variation across sites. Three floating chambers were deployed as triplicates to account for sampling variability. After being placed on the lake surface, the chambers were sampled with an airtight 25 ml polypropylene syringe, where 15 ml of gas sample was drawn from the chamber via the gas port equipped with a stopcock and then injected into 5.9 ml pre-vacuumed glass vial (Exetainer, LabCo). Every chamber was sampled 5 times (every 8-10 minutes) in approximately 40 minutes.

Laboratory analyses

All gas samples were analyzed for CO_2, CH_4, and N_2O concentrations within four weeks after sampling with gas chromatography (GC 8610, SRI Instruments, USA) coupled with a flame ionization detector (FID) equipped with a methanizer for CO_2 and CH_4, and an electron capture detector (ECD) for N_2O. The GC used two serially connected Haysep-D columns and a backflush system to eliminate water vapor and two serially connected for the analytical separation of the analyte gases. (Oven temperature: 50°C for 5.8 min, ECD temperature: 320°C, and methanizer temperature: 300°C during operation). High purity N_2 (99.999 %) was used as the carrier gas (flow rate: 10 mL min^{-1}) and hydrogen in methanizer (25 mL min^{-1}), while air was used as the cell gas for FID (250 mL min^{-1}) (see Ertürk Arı *et al.*, 2021).

The GC reads were calibrated using a multi-calibration curve approach where certified reference gases with several concentrations were analyzed and the whole concentration range were divided into several calibration sub-ranges aiming at achieving the best linear relationship within each range. CH_4, CO_2 and N_2O were diluted to 20 concentrations between 0-50000 ppm, 10 concentrations between 0-20000 ppm and 9 concentrations between 0-10 ppm, respectively. Six concentration sub-ranges for CH_4, two concentration sub-ranges for CO_2 and N_2O were chosen ($r^2>0.98$ for all) and raw area signals for each sample were calibrated using the corresponding sub-range to achieve best accuracy. The limit of quantification for CH_4, CO_2 and N_2O were 0.18, 53 and 0.09 ppm, respectively.

The fluxes were calculated from the increase rate of gas concentrations in the chambers with the following equation (Keller *et al.*, 2020; Ertürk Arı *et al.*, 2021).

$$F_{Gas} = \left(\frac{dp_{Gas}}{dt}\right) . \left(\frac{V}{RTS}\right)$$

Where, F_{Gas} is the flux of CH_4, CO_2 or N_2O (mmol m^{-2} d^{-1}), dp_{Gas}/dt is the rate of change of the partial pressure (concentration) of the gas in question, i.e., slope of the gas concentration plot (µatm d^{-1}), V is the volume of the sampler (m^3), R is the ideal gas constant (0.082 L atm K^{-1} mol^{-1}), T is the absolute temperature (K) and S is the area of the chamber (m^2). To estimate the total radiative forcing of GHGs, sustained global warming potential (SGWP) was calculated by multiplying the flux of CH_4 with 45 and N_2O with 270 to calculate their warming effect as the CO_2 equivalent over a 100-year period (Neubauer and Megonigal, 2015), or C_{eq}. SGWP was expressed as g CO_2 m^{-2} d^{-1}.

Lake water total phosphorus (TP) and soluble-reactive phosphorus (SRP) concentrations were determined using the ammonium molybdate and ascorbic acid reduction method (Mackereth *et al.*, 1978). Concentrations of nitrate (NO_3^--N) + nitrite (NO_2^--N) (denoted as NO_3 thereafter) and total nitrogen (TN) were determined using a Skalar autoanalyzer (Breda, Netherlands) with alkaline persulfate UV digestion at 90°C for TN (Kroon, 1993) in 2021; and a Seal Analytical (Norderstedt, Germany) AA3 autoanalyzer, with alkaline persulfate digestion at 115°C for 120 minutes for TN (Grasshoff *et al*. 1983) in 2022. Total dissolved silicate (Si) was determined through the reaction of silicic acid with sodium molybdate in an acid medium and spectrophotometric detection at 365 nm (Golterman *et al*. 1978). DOC samples were first filtered through pre-combusted (450°C for 4 h) Whatman GF/F filters and analyzed on a TOC-V CPN (Shimadzu, Tokyo, Japan) analyzer in NPOC mode at high temperature (680°C) after adding 10 µL 85% H_3PO_4 (Zhou *et al.*, 2019). Chlorophyll-a (Chl-*a*) concentrations were measured spectrophotometrically at 663 and 750 nm wavelength after ethanol extraction (Jespersen and Christoffersen, 1987).

Statistical Analyses

One-way ANOVA and Welch's two sample t-test were used to test the difference of environmental parameters between coastal and inland lakes and salinity ranges. Pairwise correlations between GHG fluxes (CO_2, CH_4, and N_2O) and environmental factors (temperature, salinity, nutrients, DOC, Chl-*a*) were first explored using Pearson's correlations. Afterwards, separate multiple regression analyses were carried out for each GHG as response variables, where salinity, NO_3, SRP, TN, TP, Si, DOC, Chl-*a*, PVI and basin type (coastal vs inland) were used as predictor variables. The predictor variables deviating from normal distribution were log transformed with minimum offset addition to avoid negative values in the dataset. The statistical model performance was checked using diagnostic plots for homoscedasticity. Extreme outliers for three data points (one in CO_2, TP, and SRP each) were excluded from the regression analyses; however, they were discussed in the results section. The analyses were conducted over all lakes combined as well as separately for each basin type (inland vs coastal) and salinity (<5 ‰ vs >5 ‰) subsets due to distinct ecological characteristics between coastal and inland lakes and significant reduction in CH_4 emissions at c. >5 ‰ salinity (Poffenbarger *et al*., 2011). All statistical analyses were performed in R version 4.3.0 (R core team, 2023) using R studio version 2023.09.1 (Posit team, 2023), *MASS* package (Venables and Ripley, 2002), *corrplot* (Wei and Simko, 2021) and *ggplot2* package for data visualization (Wickham, 2016).

RESULTS

3.1. Lake physical and chemical characteristics

Twenty-six of the lakes were shallow (maximum depth: 0.05-4.5 m, median: 0.7 m, mean: 1.3 m) and lacked thermal stratification while seven deeper lakes (median: 32 m, mean: 63 m, range: 14.5-160 m) exhibited summer stratification. The salinity of the lakes varied largely between 0.18 to 260 ‰ (median: 13.6 ‰) inland lakes and coastal lakes were 13.6 ‰ and 2.9 ‰, and 15.1 ‰, respectively. DOC, NO_3, SRP, TN, and TP in inland lakes were 1 to 2 orders of magnitude higher than that of in the coastal lakes (Table 1) (p=0.008, 0.02, 0.05, 0.03, respectively). Average *chl*-a was lower in the coastal lakes (12.0 µg L^{-1}) than that of in the inland lakes (25.4 µg L^{-1}), although the difference was not statistically significant (overall median: 6.2 µg L^{-1} and range: 0.20 -153 µg L^{-1}). NO_3 concentration correlated with TN (p=0.003), TP (p=0.053), and DOC (p=0.018) (Fig S3a). In addition, SRP also moderately correlated with TN (p=0.038), TP (p=0.001), Si (p=0.007), and DOC (p=0.02); however, there was no correlation between Chl-*a* and SRP. TN, TP, and DOC strongly correlated as indicators of organic matter abundance, and TN and TP showed moderate correlation with Chl-*a* concentration (r=0.43, p=0.018 and r=0.47, p=0.001, respectively).

Table 2-1 Means and standard deviations of physical and environmental variables (diffuse attenuation coefficient (K_d), water temperature (T_W), air temperature (T_A), dissolved oxygen saturation (DO), NO_3, soluble reactive phosphorus (SRP), Si, total nitrogen (TN), total phosphorus (TP), dissolved inorganic carbon (DOC), Chlorophyll-*a* (Chl-*a*), plant volume infested (PVI), and plant coverage (cov)) of the lakes sampled in 2021 and 2022.

Variable	Coastal (n=14)	Inland (n=19)	All (n=33)
Altitude (m)	0.6 (1.4)	1019 (138.5)	587 (521)
Lake max depth (m)	6.5 (10.9)	20.4 (45.5)	14.5 (35.5)
K_d (m^{-1})	0.8 (6)	4.3 (7)	2.9 (13)
T_w (°C)	27.5 (2.2)	25.2 (4.7)	26.2 (4)
T_A (°C)	29.3 (2.4)	28.2 (5.7)	28.7 (4.6)
Salinity ‰	18.6 (13.7)	57.7 (82.5)	41.1 (65.5)
DO (%)	116 (31.7)	107 (57.3)	111 (47.7)
NO_3 (µg/L)	14.5 (15.8)	495 (984)	291 (776)
SRP (µg/L)	9.1 (3.2)	608 (1814)	354 (1393)
Si (µg/L)	3555 (1935)	6984 (7239)	5530 (5828)
TN (µg/L)	767 (630)	4105 (5603)	2689 (4542)
TP (µg/L)	52.3 (94.7)	837 (2400)	504 (1844)
DOC (mg/L)	5.3 (2.6)	74 (140.4)	44.9 (110.8)
Chl-*a* (µg/L)	12.0 (22.4)	25.4 (38.2)	19.7 (32.7)
PVI (%)	24 (22)	13 (22)	18 (23)
cov (%)	56 (34)	35 (41)	44 (39)

3.2. Spatial variability of CH_4, CO_2 and N_2O fluxes among lakes

Overall CH_4, CO_2, N_2O fluxes and SGWP (interquartile range) for all lakes varied between 0.3–13.4, 12–101, 0–0.05 mmol m^{-2} d^{-1}, and 1.2-19.4 g CO_2 m^{-2} d^{-1}, respectively (Table 2). CH_4 fluxes were in the range of -0.1 to 135 mmol m^{-2} d^{-1} with a median of 2.3 mmol m^{-2} d^{-1}. Inland and coastal median CH_4 fluxes were significantly different (p=0.02) and were 6.0 and 0.4 mmol m^{-2} d^{-1}, respectively (Fig. 2a). The average CH_4 flux also significantly differed across salinity ranges (p=0.002) with the lower (0-5 ‰) and higher (>5 ‰) salinity range had a median of 27.1 and 0.3 mmol m^{-2} d^{-1}, respectively (Fig. 2a). Reliable CH_4 emissions could not be determined in 39 chambers in 14 sites (12 coastal and 2 inland) due to weak linear relationship ($R^2 < 0.7$). Furthermore, the maximum CH_4 concentration never exceeded 6 ppm (mean = 3 ppm) in these chambers, with background levels (1.9 ppm) accounting for 40-85 % of the measured values. This suggests these chambers likely received no net CH_4 emissions, with water column concentrations in equilibrium with the atmospheric CH_4 concentration. CO_2 fluxes were in the range of -44 to 2576 mmol m^{-2} d^{-1} with a median of 41 mmol m^{-2} d^{-1}. No significant difference in mean CO_2 fluxes was observed between coastal and inland or high- and low salinity lakes (Fig. 2b). N_2O fluxes were in the range of -0.01 to 1.00 mmol m^{-2} d^{-1}, with a median of 0.02 mmol m^{-2} d^{-1}. A total of 21 sites in 16 lakes (14 coastal, 2 inland lakes) showed minimal, negative or zero net emissions ($R^2<0.7$). Mean N_2O emissions significantly differed between coastal and inland lakes ($p=0.009$) and low and high salinity lakes ($p=0.04$) (Fig. 2c)

Table 2-2 Median and interquartile range (in parentheses) of diffusive CH_4, CO_2, N_2O fluxes, and sustained global warming potential of all sampled lakes and subgroups according to catchment type and salinity groups.

	All (n=33)	Coastal (n=14)	Inland (n=19)	Salinity: 0-5 ‰ (n=12)	Salinity: 5> ‰ (n=21)
CH_4 (mmol m^{-2} d^{-})	2.3 (0.3-13.4)	0.4 (0.1-0.6)	6.0 (2.5-21.3)	15.8 (5.2-32.9)	0.3 (0.2-1.6)
CO_2 (mmol m^{-2} d^{-})	41 (12-101)	13 (0-98)	53 (30-111)	70 (32-136)	29 (-1-56)
N_2O (mmol m^{-2} d^{-})	0.02 (0-0.05)	0 (0-0.01)	0.05 (0.03-0.1)	0.04 (0.02-0.1)	0 (0-0.04)
C_{eq} (g CO_2 m^{-2} d^{-})	5.0 (1.2-19.4)	0.0 (1.3-4.6)	10.1 (4.2-21.0)	19.7 (9.8-35.1)	2.5 (0.3-4.7)

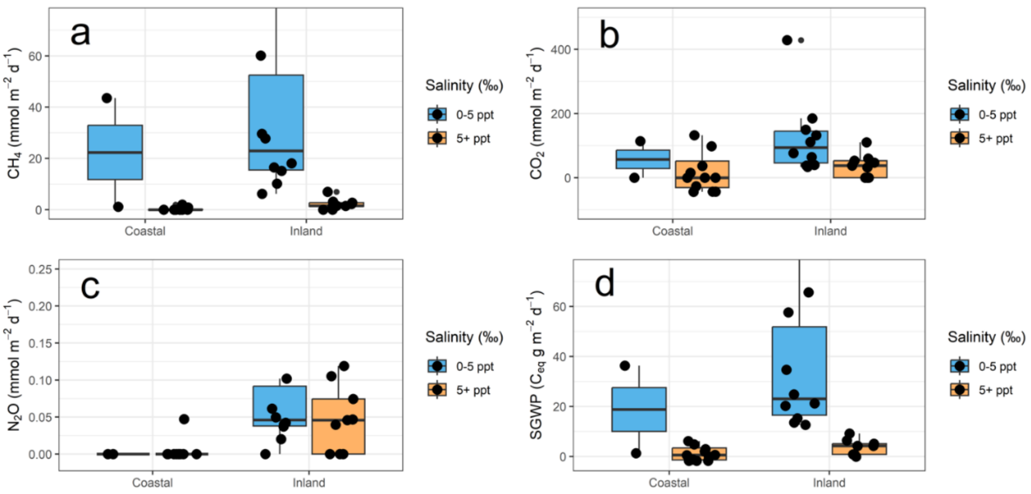

Figure 2-2 GHG emissions and their sustained global warming potential (SGWP) in coastal vs inland and low vs high salinity lakes. a, CH_4, b, CO_2, c, N_2O fluxes; d, SGWP.

The SGWP of lakes (interquartile range) ranged from 1.2 to 19.4 g CO_2 m^{-2} d^{-1} (median: 5.0 g CO_2 m^{-2} d^{-}) with similar levels between coastal and inland lakes (Fig. 2d), although contributions of CH_4, CO_2 and N_2O to total SGWP were different. In lakes with net positive emissions (n=27), SGWP was primarily driven by CH_4 emissions, (50 % of total SGWP on average), followed by CO_2 (42 %) and N_2O (7

%). In inland lakes, CH_4 emissions become more dominant (61%), followed by CO_2 (28 %) and N_2O (10 %). Conversely, in coastal lakes CO_2 dominated (71 %) SGWP with lower CH_4 (26 %) and N_2O (2 %) contributions. Lakes with net negative SGWP (n=6) were all coastal lakes except one, where their SGWP were driven by their CO_2 uptake with minimal N_2O and CH_4 emissions.

3.2.1 Spatial variability of CH_4, CO_2 and N_2O fluxes within deep lakes

Among the 11 deep or large lakes sampled in both nearshore and central zones, five exhibited thermal stratification. Littoral CH_4 fluxes were, on average, 1.8-3.5 times higher than central fluxes, with the greatest difference observed in stratified lakes (Fig. S2). CO_2 fluxes were 1.3 times higher in littoral compared to pelagic zones, while N_2O fluxes were 0.8 times lower in littoral compared to pelagic zones.

3.3. Drivers of GHG emissions

Pairwise correlations of CO_2, N_2O and CH_4 flux rates with physical (salinity, K_d), biogeochemical (NO_3, SRP, TN, TP, Chl-*a* and DOC) parameters and plant abundance (coverage, PVI) revealed significant correlations over the entire data (Fig.S3a) as well as within basin types (Fig. S3b,c), and salinity ranges (Fig. S3d,e). CH_4 flux had a moderate positive correlation with CO_2 ($r=0.54$, $p<0.001$) and N_2O ($r=0.54$, $p<0.001$). CO_2 and N_2O fluxes also positively correlated ($r=0.68$, $p<0.001$). All three GHGs was negatively correlated with salinity; however, the association and statistical significance of CH_4 and salinity ($r=-0.62$, $p<0.001$) were stronger than that of CO_2 ($r=-0.38$, $p<0.05$) and N_2O ($r=-0.36$, $p<0.1$). CH_4 correlated positively with TP and DOC (r=0.34 and 0.3, respectively, $p<0.1$) while CO_2 correlated positively with NO_3 and Si ($r=0.6$, $p<0.05$; and $r=0.36$, $p<0.1$, respectively). In addition, N_2O had positive correlations with NO_3 and SRP (r=0.54 and 0.36, respectively, $p<0.01$). Similar correlations were found within both coastal and inland lakes (Fig. S3b,c), including the negative association of CH_4 (both inland and coastal), CO_2 (inland)

and N_2O (inland) with salinity; positive correlation of CO_2 (coastal) and N_2O (inland) with NO_3. On the other hand, CH_4 correlated positively with PVI in inland lakes, and CO_2 negatively correlated with PVI in coastal lakes. In low salinity lakes, N_2O and CO_2 positively correlated with NO_3; however, CH_4 did not correlated with any of the measured variables (Fig. S3d). In high salinity lakes, all three GHGs had positive correlations with several nutrients and indicators of eutrophication (CH_4 with NO_3, TP and DOC; CO_2 with NO_3; N_2O with DOC), but negative correlations with plant abundance (PVI and cov, Fig. S3e).

The linear models were mostly concurrent with the observed correlations between GHGs and environmental variables in the whole dataset, and the subsets for salinity groups (Table 3). In whole dataset, CH_4 was linked positively with DOC but negatively with salinity and PVI (R^2-adj =0.77, $p<0.001$). CO_2 and N_2O emissions were associated negatively with salinity and positively with NO_3 (R^2-adj=0.45 and 0.47, respectively, $p<0.001$). Basin type (coastal vs inland) was not statistically significant in any of the three whole dataset models. Furthermore, linear models for the subsets of basin types revealed similar relationships, especially in inland lakes, where CH_4 emissions were associated with salinity and DOC but not PVI; CO_2 emissions were associated with salinity, NO_3 and Si; and N_2O emissions were with salinity, NO_3, DOC and TN (Table 3). In coastal lakes, CH_4 emissions were negatively linked with salinity and PVI, while CO_2 emissions were only associated with NO_3. No significant model could be fitted for the coastal lake N_2O emissions (Table 3). Similar patterns also emerged across salinity ranges. In the low salinity range, no statistically significant model predicting CH_4 could be developed. CO_2 was positively associated with NO_3 in both high and low salinity. N_2O was linked negatively with salinity and positively with NO_3 in low salinity lakes. In high salinity lakes, CH_4 was associated negatively with salinity, PVI and NO, and positively with DOC and SRP. N_2O appeared to be linked positively with DOC and negatively with TP.

Table 2-3Multiple linear regression models for CH_4, CO_2, and N_2O fluxes for the entire dataset (n=30), inland lakes only (n=19), coastal lakes only (n=11), 0-5 ‰ salinity (n=11), and >5 ‰ salinity (n=19). Resp[a]: response variable; sal[b]: salinity; Type[c]: basin type; Int[d]: intercept. *** $p<0.001$, ** $p<0.01$, * $p<0.05$, “” p<0.1. Nonsignificant ($p>0.1$) relationships were left blank

Data	Resp[a]	R^2-adj	sal[b]	DOC	NO_3	PVI	Type[c]	Int[d]
Entire	CH_4	0.77***	-0.91***	0.74*		-0.29		
n=30	CO_2	0.45***	-0.18*		0.25***			1.7***
	N_2O	0.48***	-0.27**		0.22*			-1.8***
Coast.	CH_4	0.67**	-1.37**			-0.45	-	3.5*
n=13	CO_2	0.35*			0.31*		-	2.5**
	N_2O	n.s.					-	
Inland	CH_4	0.73***	-0.71***	0.56*			-	0.7*
n=17	CO_2	0.61*	-0.14**		0.15**		-	1.3**
	N_2O	0.48**	-0.53**	0.92*	0.53**		-	
0-5 ‰	CH_4	n.s.					-	
n=11	CO_2	0.43*			0.17*		-	1.9***
	N_2O	0.73*	-0.66*		0.48**		-	-2.1***
>5 ‰	CH_4	0.81***	-0.76**	0.59**	-0.16	-0.81***	-	0.8*
n=19	CO_2	0.30**			0.23**		-	1.4***
	N_2O	0.31*		0.86**			-	-1.7***

DISCUSSION

Our snapshot study conducted in the East Mediterranean saline lakes indicated that salinity is the primary control of GHG emissions. However, coastal saline lakes and endorheic inland saline lakes had different emission patterns, reflecting their contrasting hydrology and nutrient concentrations. The magnitude of inhibitory effect of salinity on GHG emissions depended on nutrient availability (N, P, Si and C), leading to less efficient inhibition of GHG emissions in more nutrient rich inland lakes.

4.1 Response of greenhouse gas emissions to salinity and other ecological variables

4.1.1. Salinity

Salinity exerted the strongest negative control over CH_4 efflux, corroborating previous findings. A meta-analysis (Poffenbarger *et al*., 2011) based on diffusive CH_4 flux observations from numerous worldwide tidal and estuarine wetland studies across different salinity levels revealed that oligohaline (0.5-5 ‰ salinity) systems had the greatest variability of CH_4 emissions with a mean of 34.3±50.5 mmol m^{-2} d^{-1} while the polyhaline systems (<18 ‰ salinity) emit significantly lower CH_4 (0.23±0.46 mmol m^{-2} d^{-1}). Moreover, a recent study investigating the inland saline lakes in the Canadian Prairie revealed a similar case for the inland saline waters (Soued *et al*., 2024). Concurrent with these findings, we observed substantially higher emissions in low salinity lakes (mean CH_4 of 27.1 mmol m^{-2} d^{-1}) than that of in high salinity lakes (mean of 1.09 mmol m^{-2} d^{-1}) (Fig. 2a), likely reflecting the inhibitory effect of SO_4 over the methanogens through substrate competition (Bartlett *et al*., 1987; Wang *et al*., 1996). Salinity was negatively linked to CO_2 and N_2O emissions, but to a lesser extent. Salinity stress can result in lower productivity in saline systems (Jeppesen *et al*., 2007; 2015; Ollivier *et al*., 2019), which in turn, causes lower organic substrate availability, leading to positive, albeit low CO_2 emissions. The negative effect of salinity on N_2O emissions has also been observed (Smith *et al.* 1983), potentially due to inhibition of nitrifying bacteria, which limits the key substrate (NO_3) for denitrification (Craft, 2009), or direct inhibition of denitrification itself (Rysgaard *et al.*, 1999). However, salinity effects can vary depending on factors like microbial adaptation (Marks *et al.*, 2016) or other environmental conditions, e.g. temperature, nutrient, and oxygen levels (Livesley & Andrusiak, 2012; Welti et al., 2017).

4.1.2. Nutrients and organic matter

Organic substrate and nutrient availability positively correlated with all three GHGs albeit with large variability in the strength of relationship with different nutrients. Regression analyses revealed that DOC had a positive link with CH_4 (Table 3), which is in line with previous studies showing high emissions in nutrient or organic matter rich waters (Audet *et al.*, 2020; Beaulieu *et al.*, 2019; Ollivier *et al.*, 2019; Peacock *et al.*, 2019, 2021). Although high organic matter (in terms of DOC or TP) did not always lead to high emissions, lakes with the lowest organic content were usually associated with low or no positive emissions (Fig. S4a). Additionally, CH_4 flux was strongly associated with the DOC to salinity ratio (R^2-adj=0.67; $p<0.001$) (Fig. S4b), suggesting that high substrate availability can modulate the negative effect of salinity. High organic substrate availability likely reduces competition for resources, allowing both methanogenesis and sulfate reduction to co-occur, even under high sulfate concentrations, as outlined in Soued *et al.* (2024).

CO_2 emissions exhibited a positive correlation with NO_3 concentration, contrasting with some of the previous studies suggesting a negative link due to nutrient-driven CO_2 uptake (Balmer and Downing, 2011; Pacheco *et al.*, 2014). However, high nutrient loading in small, eutrophic lakes may lead to higher CO_2 emissions (Casper *et al.*, 2001; Ollivier *et al.*, 2019). The observed positive CO_2 emissions in our shallow, well-mixed lakes likely arose from the combined effect of nutrient-driven organic matter deposition and readily available oxygen reaching the sediment, which fuels CO_2 respiration (Ollivier *et al.*, 2019). However, this needs further investigation as we did not find an empirical relationship between CO_2 and DOC or other organic matter proxies such as TP. In addition, Si positively associated with

CO_2 in inland lakes, potentially reflecting influence of groundwater seepage, often enriched in both CO_2 and Si (Peacock *et al.*, 2019; Perkins *et al.*, 2015). Finally, Lake Küçükdalyan in the coastal Köyceğiz basin was an exception with remarkably high CO_2 emissions (2576 mmol^{-2} d^{-1}) despite having low nutrient concentrations overall. Geothermal activity, prevalent in the region (Avşar *et al.*, 2017; Bayarı *et al.*, 1995), may be responsible, as a study identified seven subaqueous hot springs within a 3 km radius (Avşar *et al.*, 2017) in the lake-channel system. While supporting benthic temperature data is lacking, geothermal outgassing is a likely explanation.

Regression analyses suggested that NO_3 concentration was the main driver of N_2O emissions. The positive association between NO_3 and N_2O suggests the dominance of the denitrification pathway in sedimentary production of N_2O (Burgos *et al.*, 2015; Kortelainen *et al.*, 2020; Tian *et al.*, 2018; Zheng *et al* 2022). Furthermore, high turbulence in shallow lakes likely promotes N_2O production through the resuspension of organic matter, which fuels mineralization including nitrification, and persistent oxygen availability favoring incomplete denitrification, a known pathway for N_2O formation (Zhu et al., 2021). Also of relevance is the fact that DOC may have stimulatory effect on N_2O flux in the inland lakes while coastal lakes did not exhibit this relationship (Table S1), possibly due to their minimal N_2O emissions. This is further supported by the lack of a statistically significant model in the coastal lake regression analysis due to the prevalence of zero N_2O values.

Overall, our findings suggest that difference of saline and brackish inland lakes and coastal estuarine wetlands act differently in terms of CH_4, CO_2 and N_2O emissions and their C_{eq} contributions reflects their different nutrient and organic substrate profiles. Inland saline lakes, acting as accumulation endpoints of endorheic basins, have 10-1000 times higher nutrient and organic substrate concentrations than coastal lakes (Table 1) potentially leading to sustained GHG emissions even in hypersaline condition. Furthermore, basin type did not significantly influence GHG emissions in any of the models, supporting a consistent underlying mechanism across lake types.

4.1.3. Macrophyte Abundance

Our findings suggest an overall inhibitory effect of macrophyte abundance on CH_4 emissions (Table 3) while Chl-*a* did not show any relationship with any of the three GHGs, contrasting with numerous earlier studies, where TP and Chl-*a* had a clear positive effect (Beaulieu *et al*., 2019; 2020; Deemer and Holgerson, 2021). Potential mechanisms involved could be the enhanced CH_4 oxidation and plant impact on organic carbon cycling. High submerged plant coverage is known to inhibit CH_4 emission as they provide surface for CH_4 oxidizing bacteria and change redox conditions in the sediment by supplying oxygen (Bastviken *et al*., 2023; Davidson *et al*. 2018; Esposito *et al*., 2023). Furthermore, our findings suggest the macrophyte abundance may be negatively correlated to the water column organic matter levels (see Fig. S3a, S3e), thereby weakening the predictive power of Chl-*a* for CH_4 emissions.

4.2. Limitations of the study

Our study provides the first snapshot survey of GHG fluxes from inland and coastal saline lakes in central and western Anatolia. However, the GHG emissions derived from this limited snap-shot survey should be considered with caution due to several reasons. Firstly, the limited sample size prevented us from making robust GHG budgets, in fact, they only enabled us to analyze main spatial patterns and drivers. Furthermore, our findings do not account for ebullition, a crucial emission pathway (Bastviken *et al.* 2004), which could underestimate CH_4 flux and bias our findings towards factors affecting diffusional pathways. Secondly, depending solely on short-term, daytime, early summer measurements might miss important spatial and temporal variability in CH_4 emissions, as seasonal patterns, such as stratification can remarkably alter emission patterns (Davidson *et al*., 2024). Moreover, limited summer observations restrict conclusions to this specific period, neglecting seasonality of temperature, DOC, and other relevant factors such as nutrient levels and growing season. Additionally, daytime measurements overlook potential nighttime variations, especially in CO_2 emissions driven by metabolic activity (e.g., respiration and photosynthesis). Furthermore, the contrast between coastal and inland lakes may be underestimated due to methodological constraints. Flux chambers are prone to underestimate negative GHG fluxes, particularly of CH_4 and N_2O, due to their low ambient concentrations. In cases where the water surface acts as a sink of CH_4 or N_2O, the maximum rate of gas uptake that is quantifiable is limited to initial chamber concentration, i.e., atmospheric concentration of these gases, which may lead to underestimate lake's capacity as sink. The dominance of zero or negative net emissions for CH_4 and N_2O in coastal lakes highlights the potential underestimation bias inherent in flux chambers for these low-concentration gases. This implies that coastal lakes might function as even more significant carbon and nitrogen sinks than our measurements suggest. This aligns with recent research highlighting the carbon sequestration potential of saline vegetated coastal wetlands (Brown *et al*., 2016; Fourqurean *et al*., 2012; Serrano *et al*., 2021; Ward *et al*., 2021). Consequently, the contribution of these coastal ecosystems to total SGWP in our study might be slightly overestimated, potentially reducing the observed contrast between inland and coastal lakes. However, a key takeaway is the confirmation of our hypothesis – inland shallow saline lakes tend to be net sources, while coastal lakes potentially tend to be sinks, rather than sources.

4.3. Sustained global warming potential of the lakes and future implications

The hydrology, size, morphometry and salinity of the lakes in the Central-Western Anatolia have already been subject to dramatic changes due to increased evaporation and groundwater abstraction and these effects are predicted to exacerbate (Yılmaz *et al*., 2021; Çolak *et al*., 2022). While our study suggests a general trend of reduced GHG emissions, especially CH_4, with increasing salinity, interactions between salinization and other expected future changes, including i) temperature rise, ii) internal loading of nutrients and organic matter due to changes in lake size and morphology, and iii) increase of catchment nutrient load and other anthropogenic pressures leading to eutrophication may complicate future predictions.

Although in our study effect of water temperature was not a significant driver of observed GHG fluxes, sedimentary CH_4 production rate is known to be quite temperature dependent across diverse climatic regions (Aben *et al.*, 2020; DelSontro *et al.*, 2016; Wik *et al.*, 2014) and 4°C change may cause more than 50 % rise in CH_4 emissions, especially through ebullition (Aben *et al.*, 2020). A recent study (Chamberlain *et al.*, 2020) revealed that a drought induced salinization event in a wetland increased temperature dependence of CH_4 productivity, dampening the expected decline in CH_4 emission as a response to salinization and lowered productivity. Our dataset suggests that dissolved matter concentrations are negatively associated with lake depth (Fig. S3a-d), implying shallower lakes tend to contain higher levels of nutrients and DOC. Thus, particularly in the inland lakes, the loss of lake area and depth will likely increase internal loading of nutrients, which, combined with temperature may lead to a rise in N_2O and CO_2 emissions. While loss of lake area and size is less of a problem in coastal areas because of sea and river connectivity, increasing water regulation on the rivers, coupled with intensification of agriculture in the catchment areas, can lead to elevated water residence times and higher dissolved matter concentrations. This can also stimulate GHG emissions in the lakes that are currently showing low or no net emissions, reduce their potential capacity as carbon sinks, or convert them into net sources. Thus, possible reduction in C_{eq} due to salinization will likely be reduced by increasing CO_2 and N_2O emissions. Our findings (although preliminary) suggest that a conservative 20 % rise in the average inland NO_3 and DOC concentrations could negate up to 70 % of the total SGWP reduction caused by a 1 ‰ salinity increase at the lower end of the salinity range, where GHG emissions are most sensitive to salinity (Fig. S1d).

CONCLUSION

The GHG emissions in Mediterranean inland and coastal shallow lakes revealed the primary control of salinity on the GHG emissions, which was further modulated by nutrient and organic matter availability. The difference in nutrient levels between coastal and inland saline lakes resulted in a large difference in GHG emissions in these ecosystems within similar salinity levels. Despite contrasting emissions between coastal and inland saline lakes, our study revealed a common set of mechanisms governing these processes. Further studies covering higher spatial and temporal resolution, different emission pathways (e.g. ebullition) and ecosystem complexities (e.g., stratification) are needed to better characterize the GHG dynamics and the carbon sink potential of saline lakes.

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CRediT authorship contribution statement

GY: Conceptualization, investigation, data curation, formal analysis, original draft; PEA, CAA, MK, JPP, YZ, LZ: investigation; TAD, JA, NK: conceptualization, supervision; MB, EJ, KO: conceptualization, supervision, funding acquisition, project administration. The manuscript was reviewed/edited through the contributions of all authors. All authors have approved the final version of the manuscript.

Declaration of competing interest

The authors declare no conflict of interest.

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SUPPLEMENTARY MATERIAL

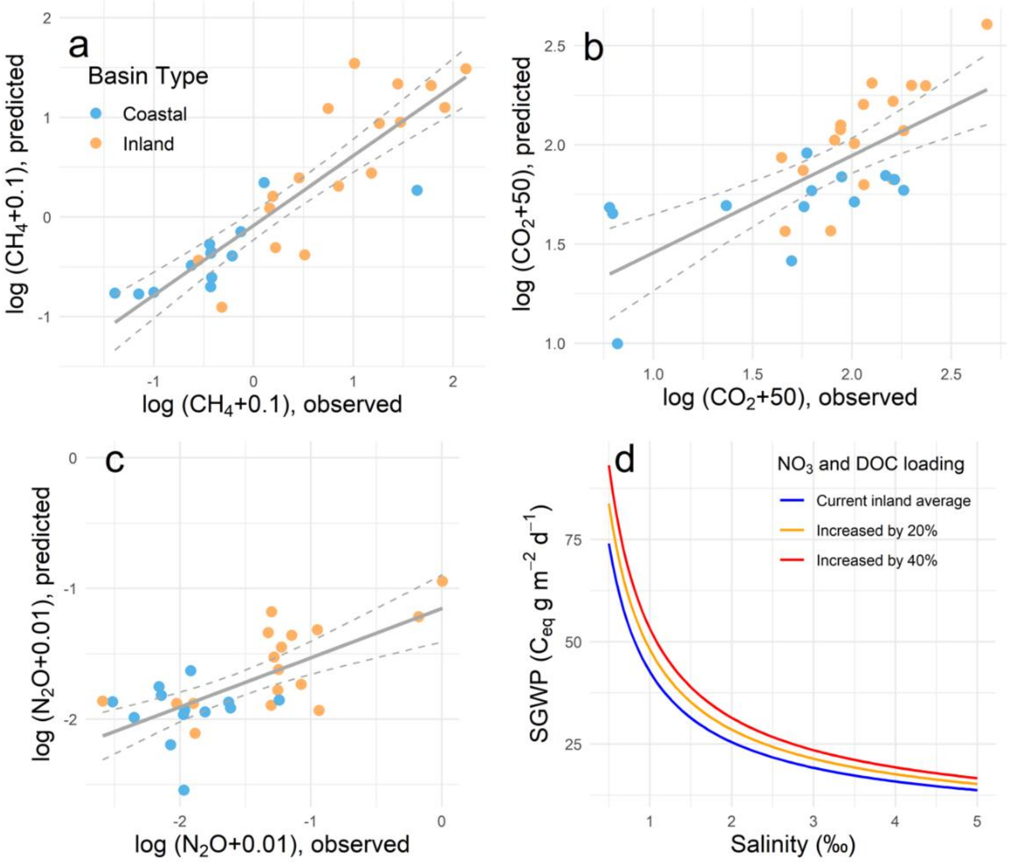


Figure S1. Relationship between CH_4, CO_2, and N_2O predicted by the multiple regression and all data measured. a, Log CH_4 predicted by the multiple-regression model (log (CH_4+0.1) = -0.91 log sal + 0.74 log DOC – 0.29 log PVI). b, Log CO_2 predicted by the multiple-regression model (log (CO_2+50) = -0.18 log sal + 0.25 log NO_3 + 1.7). c, Log N_2O predicted by the multiple-regression model (log (N_2O+0.01) = -0.27 log sal + 0.22 log NO_3 - 1.8). d, the modeled response of SGWP to variations in salinity, NO_3 concentration, and dissolved organic carbon (DOC) concentration. Current inland average of DOC and NO_3 (blue), current inland average of DOC and NO_3 increased by 20 % (orange), increased by 40 % (red).

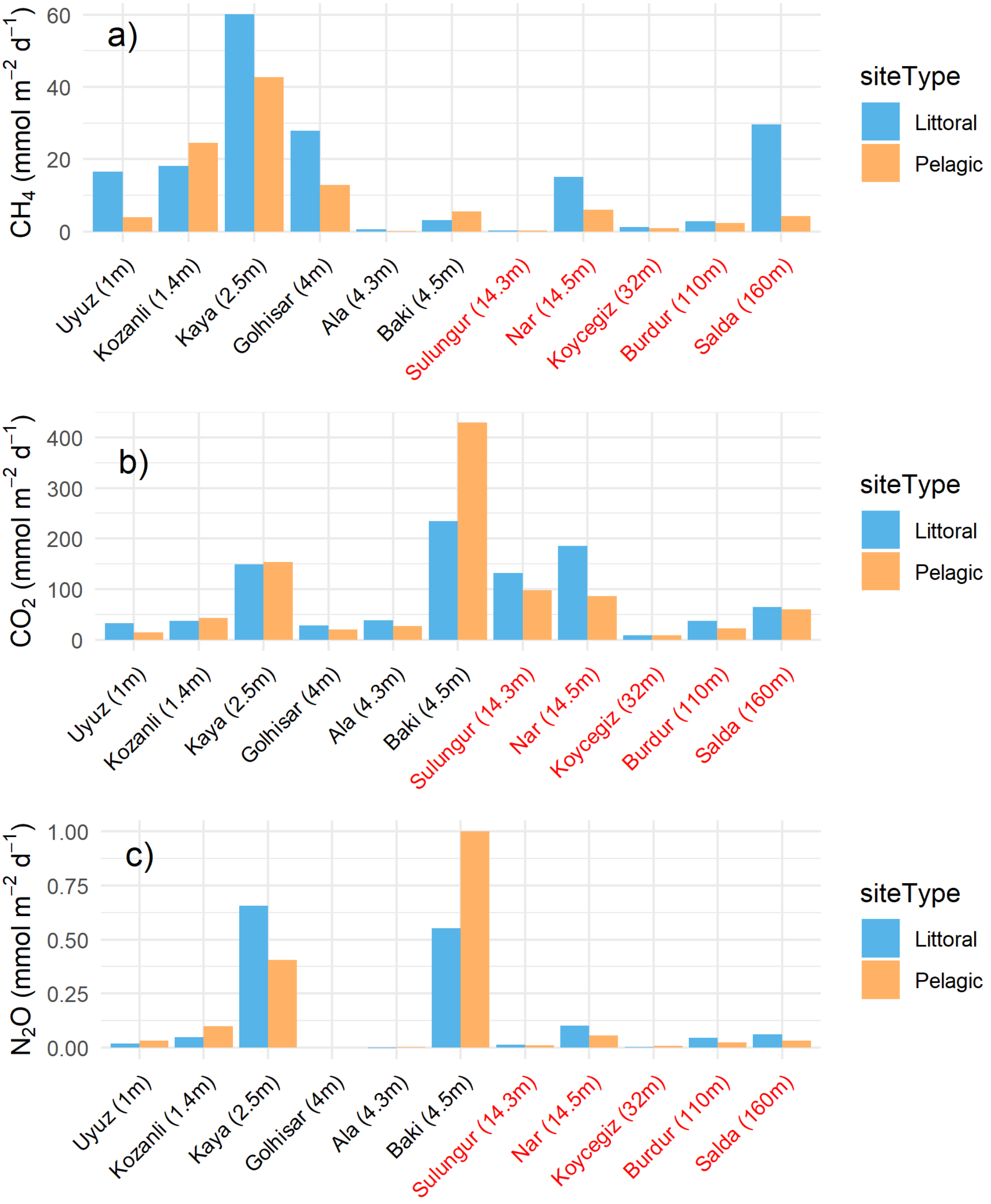
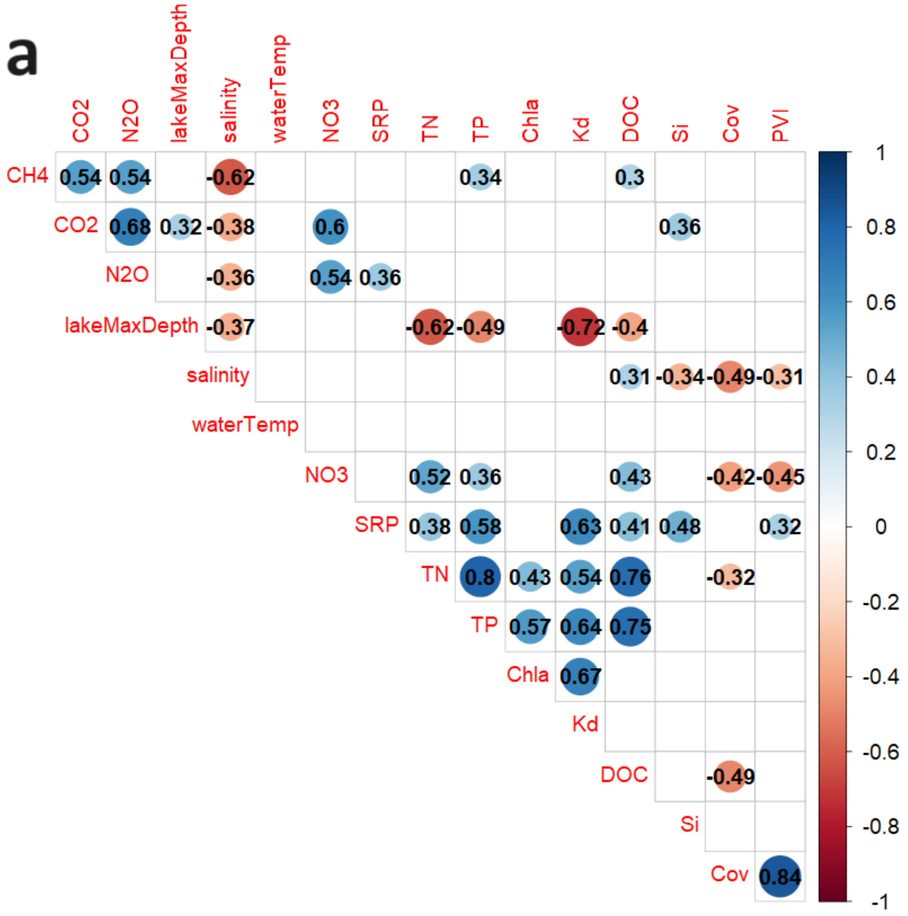
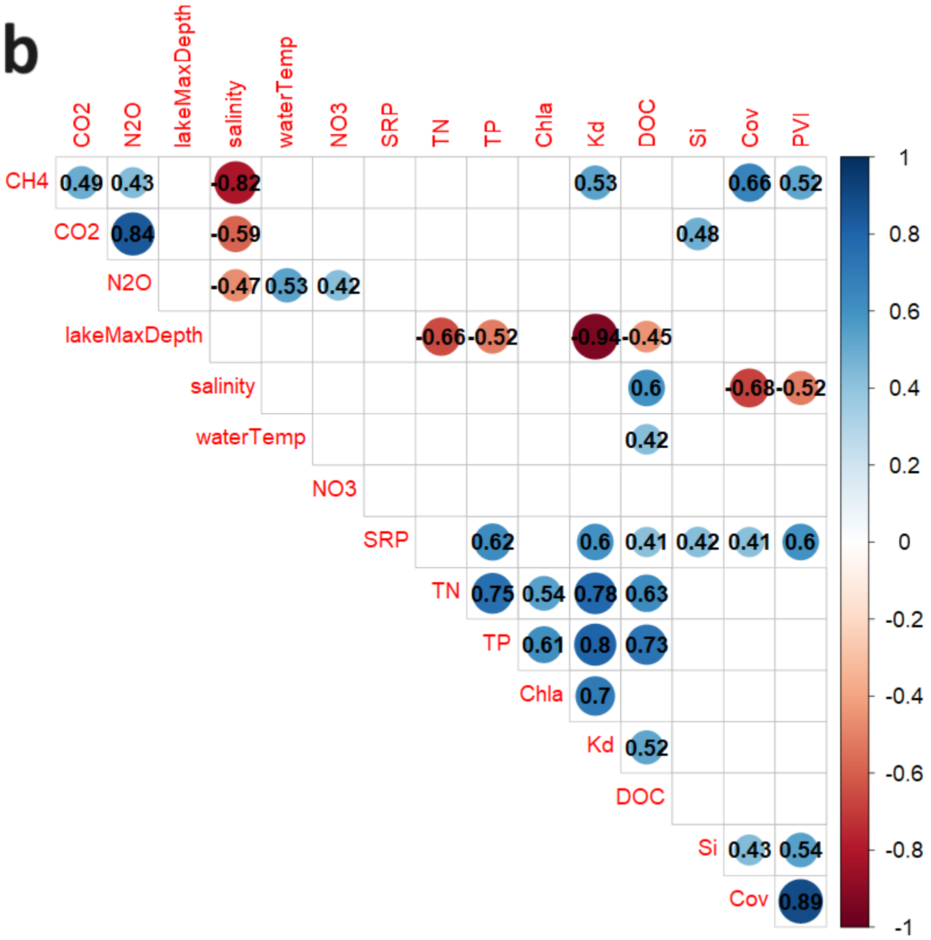


Figure S2. Comparison of diffusive a) CH_4, b) CO_2, and c) N_2O fluxes in 11 lakes with paired (littoral vs pelagic) sites. The maximum depth of each lake is indicated in parentheses. In each lake the littoral site was sampled at a depth of (0.1-1 m) and the pelagic site around the deepest point of lake or the subbasin. The lakes with thermal stratification are indicated in red.

Figure S3. (Below): Pearson's correlations for different lake categories: (a) whole dataset (n=30); (b) inland (n=19), (c) coastal (n=11), (d) low salinity (0-5 ‰, n=11), and (e) high salinity (5+ ‰, n=19). Circle size indicates significance level, with larger circles representing lower *p*-values (more significant correlations). Correlations with *p*> 0.1 are excluded.




b
CO2
N2O
lakeMaxDepth
salinity
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NO3
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Chla
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PVI
CH4
0.49
0.43
-0.82
0.53
0.66
0.52
CO2
0.84
-0.59
0.48
N2O
-0.47
0.53
0.42
lakeMaxDepth
-0.66
-0.52
-0.94
-0.45
salinity
0.6
-0.68
-0.52
waterTemp
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NO3
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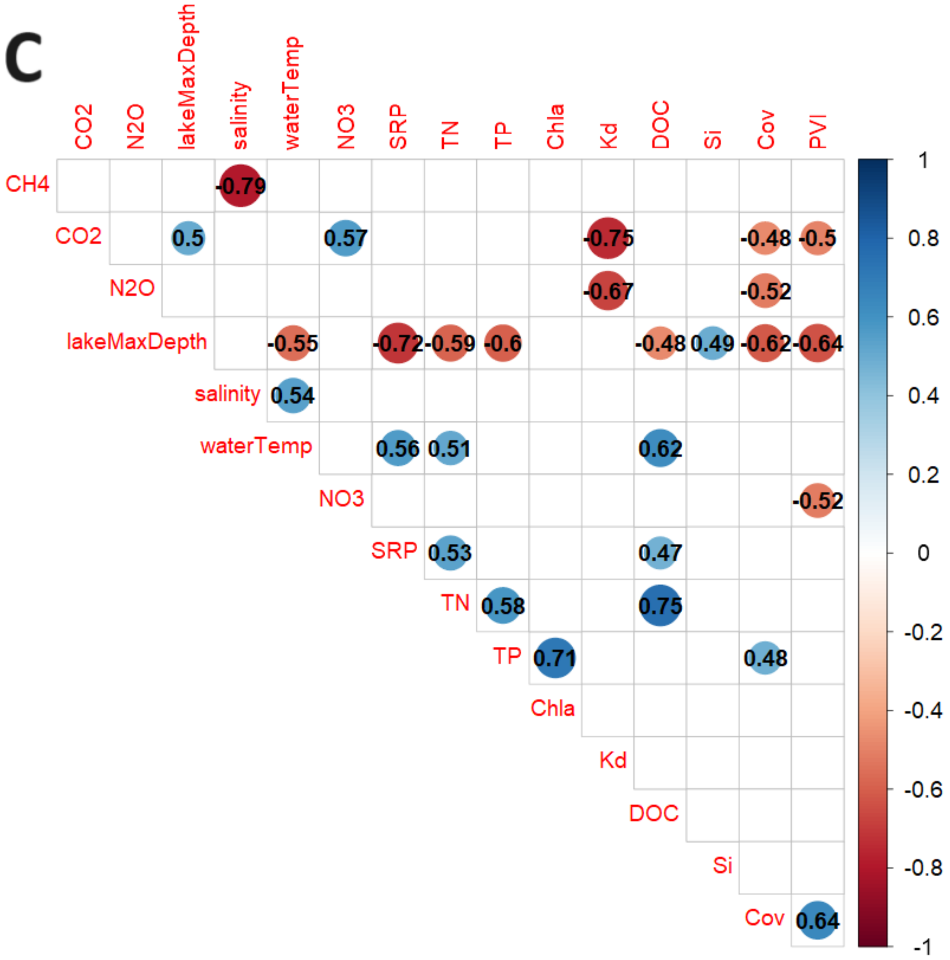
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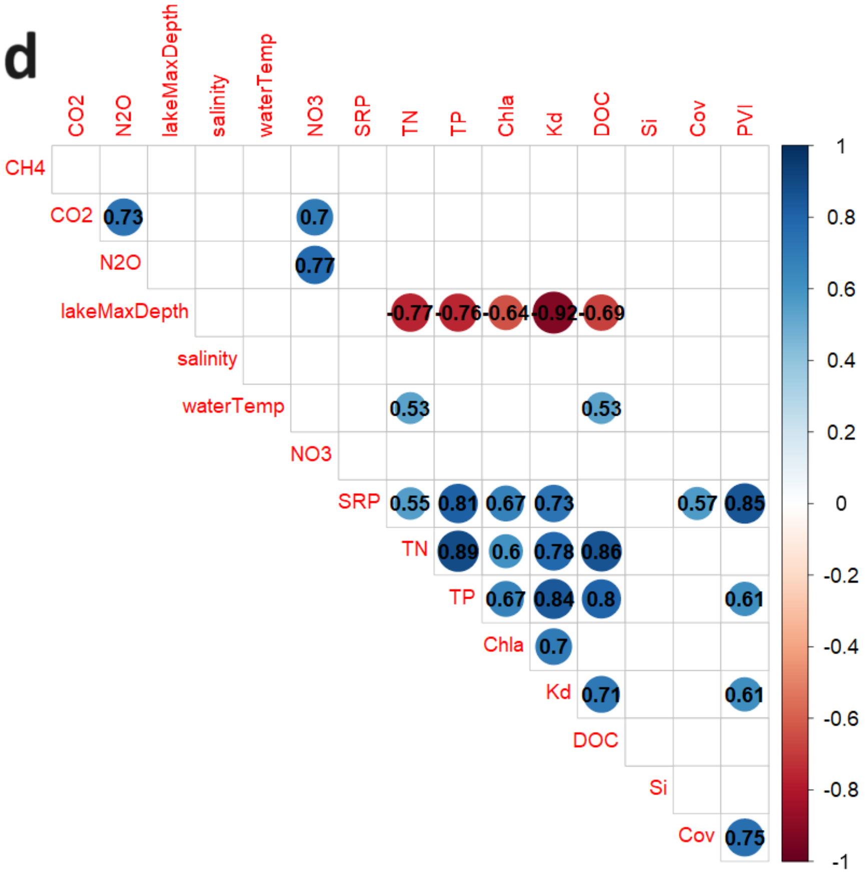
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N2O 0.77
lakeMaxDepth -0.77 -0.76 -0.64 -0.92 -0.69
salinity
waterTemp 0.53 0.53
NO3
SRP 0.55 0.81 0.67 0.73 0.57 0.85
TN 0.89 0.6 0.78 0.86
TP 0.67 0.84 0.8 0.61
Chla 0.7
Kd 0.71 0.61
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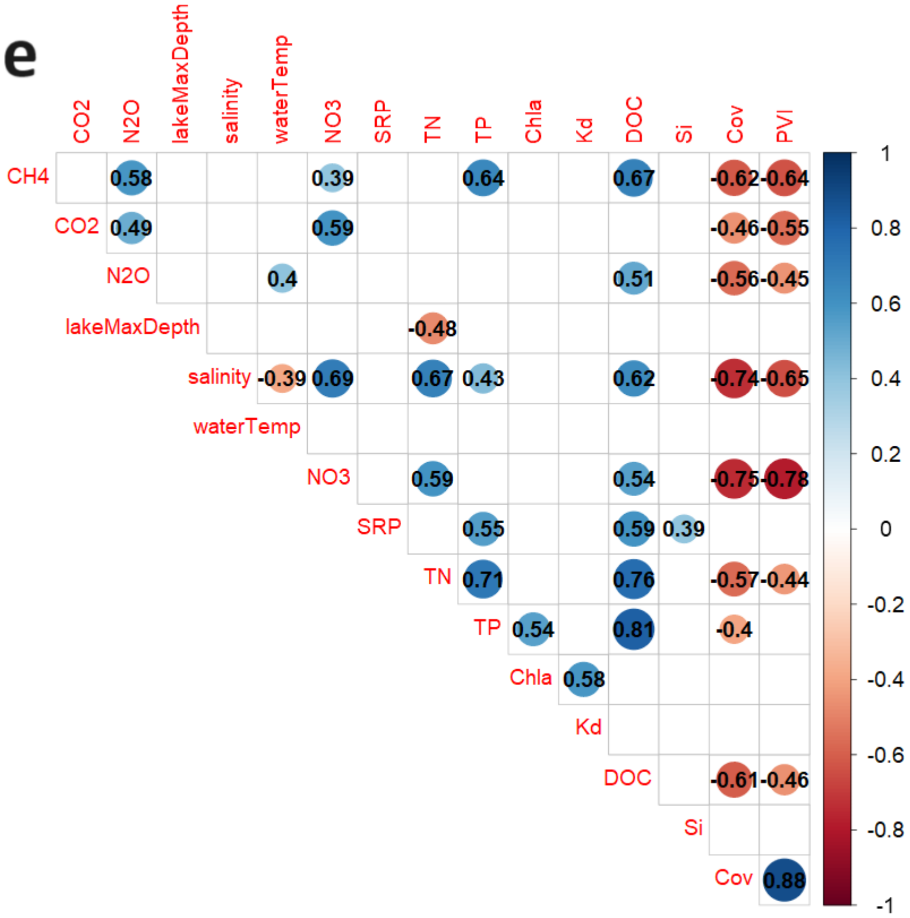
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CO2 0.49 0.59 -0.46 -0.55
N2O 0.4 0.51 -0.56 -0.45
lakeMaxDepth -0.48
salinity -0.39 0.69 0.67 0.43 0.62 -0.74 -0.65
waterTemp
NO3 0.59 0.54 -0.75 -0.78
SRP 0.55 0.59 0.39
TN 0.71 0.76 -0.57 -0.44
TP 0.54 0.81 -0.4
Chla 0.58
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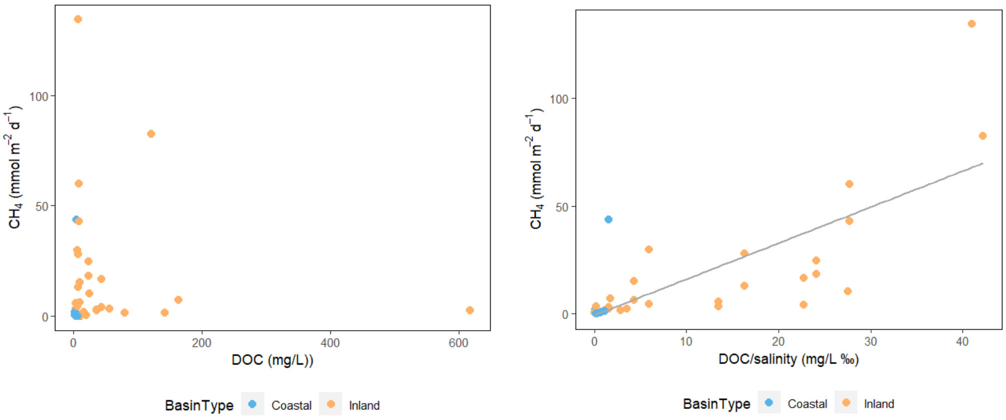

Figure S4. a: DOC vs CH_4 fluxes, b: DOC/Salinity vs CH_4 fluxes ($p << 0.001$, R^2-adj = 0.67)

Table S1. Coordinates, altitude, maximum depth and salinity of lakes with measured CH_4, CO_2, and N_2O emissions and associated standard deviations. Abbreviations: 1 C.: Coastal, I.: Inland; 2 Basin: BCB: Burdur Closed Basin, KCB: Konya Closed Basin, KDL: Köyceğiz-Dalaman Lagoon System, GD: Göksu Delta, CD: Çukurova Delta., 3 L.: Littoral, p: pelagic.

Basin Type[1]	Basin[2]	Lake Name	Site Type[3]	Alt (m)	Depth (m)	salinity	CH_4	CO_2	N_2O
C.	CD	Akyatan	L	0	0.8	16.2	0.14	7	0.01
C.	CD	Akyayan	L	0	0.75	43.1	-0.06	-27	-0.01
C.	CD	Dipsiz	L	0	0.45	13.9	0.26	13	-0.01
C.	CD	Tuzla Adana	L	0	0.4	43.5	-0.03	98	0.05
C.	GD	Akgol	L	0	0.7	11.3	0.28	-44	0.00
C.	GD	Kugu	L	0	0.5	13.3	0.27	-43	0.00
C.	KDL	Ala	L	0	4.3	18.4	0.51	39	0.00
C.	KDL	Ala	P	0	4.3	18.4	0.09	27	0.00
C.	KDL	Baldimaz	L	5	1.8	3.6	43.5	114	0.00
C.	KDL	Koca	L	1	29.4	5.3	0.65	53	0.01
C.	KDL	Koycegiz	L	2	32	3.3	1.18	9	0.00
C.	KDL	Koycegiz	P	2	32	3.3	0.86	9	0.01
C.	KDL	Kucuk dalyan	L	1	3.8	16.2	1.59	2576	-0.01
C.	KDL	Suluklu	L	0	0.4	13.1	0.27	-44	0.00
C.	KDL	Sulungur	L	0	14.3	39.6	0.28	132	0.01
C.	KDL	Sulungur	P	0	14.3	39.6	0.25	98	0.01
C.	KDL	Ortaca	L	0	1.5	20.1	0.00	0	0.00
I.	BCB	Acigol Denizli	L	838	0.2	68.5	1.46	53	0.07
I.	BCB	Burdur	L	846	110	22.5	2.76	38	0.05
I.	BCB	Burdur	P	846	110	22.5	2.26	23	0.02
I.	BCB	Golhisar	L	947	4	0.5	27.8	28	0.00
I.	BCB	Golhisar	P	947	4	0.5	12.8	21	0.00
I.	BCB	Karatas	L	1056	0.2	0.9	10.2	111	0.04

I.	BCB	Salda	L	1141	160	1.1	29.6	64	0.06
I.	BCB	Salda	P	1141	160	1.1	4.17	60	0.03
I.	KCB	Acigol Konya	L	987	85	68.8	1.56	110	0.04
I.	KCB	Akgol Konya	L	1002	0.2	2.9	82.45	132	0.04
I.	KCB	Baki	L	1185	4.5	0.3	5.51	429	1.00
I.	KCB	Baki	P	1185	4.5	0.3	3.11	235	0.55
I.	KCB	Bolluk	L	942	1.2	95.0	7.00	65	0.11
I.	KCB	Duden	L	967	0.2	175.7	2.28	47	0.12
I.	KCB	Kaya	L	1188	2.5	0.3	60.09	150	0.66
I.	KCB	Kaya	P	1188	2.5	0.3	42.70	154	0.41
I.	KCB	Kozanli	L	983	1.4	1.0	18.12	38	0.05
I.	KCB	Kozanli	P	983	1.4	1.0	24.56	43	0.10
I.	KCB	Little Duden	L	966	0.19	49.8	1.35	-4	0.00
I.	KCB	LittleTuz	L	911	0.05	116.9	0.18	7	0.00
I.	KCB	Nar	L	1371	14.5	2.4	15.14	185	0.10
I.	KCB	Nar	P	1371	14.5	2.4	6.02	87	0.06
I.	KCB	Seker	L	1040	1.2	0.2	134.62	76	0.04
I.	KCB	Tuz South	L	906	0.2	228.0	3.16	32	0.05
I.	KCB	Tuz North	L	906	0.2	260.0	0.38	-6	-0.01
I.	KCB	Uyuz	L	1191	1	1.9	16.50	33	0.02
I.	KCB	Uyuz	P	1191	1	1.9	3.85	15	0.03

CHAPTER 3

TEMPERATURE ASSOCIATED WITH MINOR METHANE AND NITROUS OXIDE EBULLITION IN SHALLOW SALINE LAKES: A SYNCHRONIZED MESOCOSM EXPERIMENT IN CONTRASTING CLIMATES

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Abstract

Saline lakes and ponds play a critical role in global carbon and nitrogen cycling. However, our understanding of how carbon and nitrogen exchange mechanisms respond to salinity variations within aquatic ecosystems remains limited. In order to address this knowledge gap, we conducted a mesocosm experiment to investigate the influence of salinity on greenhouse gas (GHG) emissions in shallow lake

ecosystems. The experiment was conducted in two sites (Ankara and Mersin, Türkiye) with contrasting climates synchronously, featured a gradient design with 16 salinity levels ranging from 0.4 to 50 g/L, in each site (total 32 mesocosms) and lasted 8 weeks, between October and December 2021. We focused on methane (CH_4), carbon dioxide (CO_2) and nitrous oxide (N_2O) emissions, considering both diffusive and ebullitive fluxes. Results indicate that temperature was the primary driver of CH_4 emissions, with a more pronounced effect of temperature on the ebullition in the warmer site mesocosms. While we did not observe a significant empirical effect of salinity on CH_4 emissions, the emissions were notably lower than in freshwater lakes. This suggests that salinity may have been influencing emissions, but its effect was masked by the high salinity levels in our experiment. While salinity was possibly inhibitory for both emission pathways, a minor yet significant ebullition, on average 3-50 times higher than diffusive fluxes was observed in the warmer site. CO_2 emissions were consistently negative in all mesocosms and controlled by temperature, salinity and organic matter availability. However, in both sites, tanks with high macrophyte coverage were significantly more undersaturated with CO_2, reflecting the critical role of macrophytes in carbon burial. Notably, N_2O emissions exhibited a more complex pattern; diffusive fluxes were cosistently negative and near baseline values across salinity levels, with the exception of high salinity mesocosms (>23 ppt), which were even more undersaturated with N_2O. On the other hand, ebullition, often considered negligible for N_2O, emerged as a minor but consistent contributor to N_2O emissions across salinities and sites. This study highlights the importance of considering both diffusive and ebullitive fluxes when assessing GHG emissions from saline aquatic ecosystems. Understanding the interactive effects of salinity, temperature, and other environmental factors on GHG dynamics is crucial for accurate predictions.

Introduction

Lake ecosystems play a critical role in the biogeochemical cycling of carbon (C) and nitrogen (N), serving as significant sources and/or sinks for potent greenhouse gases (GHGs) such as methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (N_2O) (IPCC, 2014). Freshwater salinization, a growing environmental challenge (Jeppesen et al., 2020; Cunillera-Montcusi et al., 2022), particularly in arid and semi-arid regions including Mediterranean Basin (IPCC 2007, 2014), significantly influences GHG dynamics within these ecosystems (Duarte et al 2008, Soued et al. 2024), especially inland lakes in the endorheic basins are especially vulnerable to salinization (Jeppesen et al. 2015). Given their global impacts, GHG emissions from lentic ecosystems and how they are interacting with climate change, eutrophication and salinization can have profound implications for global C and N budgets and atmosphere, as salinity is a key parameter for the ecosystem structure and functioning and in turn, biogeochemical functioning of the lake ecosystems. Therefore, understanding the effects of salinity and salinization over various biogeochemical processes is crucial for strategizing against the threats posed by climate change.

Lentic ecosystems can act as both carbon sinks and sources, depending on the environmental factors such as primary production, temperature, nutrient loading. While coastal lakes and wetlands are responsible for storing significant amounts of carbon as macrophyte biomass (i.e., “blue carbon”), (Brown *et al*., 2016; Ward *et al*., 2021) inland waters generally are considered net sources (Cole et al., 1994) of CO_2 and primary natural sources of CH_4 (IPCC, 2014). Temperature rise due to climate change accelerate ecosystem respiration and methanogenesis (Aben et al., 2017), the microbial production of methane (CH_4) in sediments, leading to increased CO_2 and CH_4 emissions from lakes. Eutrophication through nutrient enrichment also stimulates primary production, increasing organic matter production, which subsequently decomposes, enhancing CO_2 and CH_4 fluxes (Engel et al., 2014; Li et al., 2021). Furthermore, nutrient enrichment and climate warming often interact synergistically, exacerbating the individual impacts of warming and nutrient enrichment on lake ecosystems (Davidson et al., 2018; DelSontro et al., 2018). Salinity is also a primary driver governing many biological processes and exerting both direct and indirect influences on biogeochemical cycles of aquatic ecosystems. It has significant effects on the diversity and abundance of microbial communities such as methanogens and methanotrophs (Zhou et al., 202), which are directly responsible for CH_4 exchange mechanisms (Deng et al., 2014; Yang et al., 2016; Zang et al., 2023). Many studies have revealed that increase in salinity, especially as sulfate (SO_4^{2-}) ion, promote sulfur-reducing bacteria which outcompetes methanogens and inhibits CH_4 emissions in aquatic ecosystems (Bartlett et al., 1985; Pennock et al., 2010; Poffenbarger et al., 2011. In contrast, inhibitory effect of salinity is subject to modulation by organic matter availability (Soued et al., 2024), and temperature (Chamberlain et al., 2020) Salinity can also impact lake's trophic state and ecosystem respiration. Salinity stress, particularly in the context of salinization, can hinder primary production by plankton communities adapted to lower salinity conditions (REF), potentially altering CO_2 dynamics. Similarly, temperature rise and eutrophication can also influence nitrogen cycling processes of aquatic ecosystems. N_2O is produced as a byproduct of nitrification and an intermediate during incomplete denitrification in aquatic environments (Burgin et al., 2007; Liang et al., 2022). Studies suggest that N_2O emissions from lakes are primarily driven by nitrate (NO_3) (Liikanen et al., 2003; Kortelainen et al., 2019) and organic substrate availability (Myrstener et al.,2016). Other factors like pH, oxygen availability, and temperature also play a role (Butterbach-Bahl, et al., 2013), while the effect of salinity on N_2O emissions remains even less clear and dependent on other factors (Livesley and Andrusiak, REF).

While the inhibitory effect of salinity on diffusive CH_4 fluxes has been relatively well-studied, the impact on ebullition, the intermittent, episodic release of CH_4 from sediments, remains largely unexplored in saline systems, despite it is recognized as the major CH_4 emission pathway in freshwater ecosystems (Bastviken et al., 2004). Emerging evidence suggests that salinity may even more strongly inhibit ebullition than diffusion (Soued et al. 2024). However, fluctuations in salinity can significantly alter ebullition rates (Camacho et al., 2017) which may be especially important in eutrophic systems with dynamic salinity fluctuations, where the combined effects of salinity and other factors on the ebullitive fluxes are poorly understood. While often underestimated due to its episodic nature and the challenges associated with continuous monitoring, ebullition in saline systems can represent a potentially minor yet significant pathway of CH_4 emissions compared to freshwater systems. Predicting how ebullition responds to varying salinity gradients is further complicated by the sporadic and unpredictable nature of these event and requires longer, continuous monitoring efforts. These underscore the need for a comprehensive understanding of the dynamics across a range of salinity levels in saline lentic environments, especially given their dynamic nature and susceptibility to environmental change. Accurate assessments of GHG emissions from these systems are essential for refining carbon budgets, anticipating future ecological conditions, and their potential contribution to climate change.

To gain a better understanding of the effect of salinity on GHG dynamics (CH_4, CO_2, and N_2O) in shallow saline lakes, we conducted a synchronized mesocosm experiment in two identical mesocosm sites with contrasting climates. Our investigation aimed to address several key questions regarding GHG dynamics in shallow saline lakes, we hypothesize that (i) alternative emission pathways, such as ebullition, may override salinity thresholds in shallow saline lakes and ponds, even where SO_4 availability suppress diffusive CH_4 emissions. CH_4 can accumulate in sediments where SO_4 penetration is limited and then be released episodically through ebullition. We further hypothesize that (ii) salinization in shallow lakes and ponds by can elevate CO_2 emissions by imposing salinity stress and potentially inhibiting autotrophic processes relative to heterotrophic processes. (iii) Ebullition is an overlooked pathway in terms of N_2O emissions, especially in shallow, eutrophic systems that can be important in N_2O emission.

Methodology

Mesocosms are controlled environments that mimic natural ecosystems but allow for manipulation of specific factors. In this study, we established 32 mesocosms in two sites, replicating key features of shallow lakes and created a salinity gradient ranging from freshwater (0.5 ppt) to hypersaline (50 ppt) with 16 levels, each site. All other conditions, such as natural air temperature fluctuations and constant nutrient loading, were kept uniform across the mesocosms. This controlled setting enabled us to isolate the effect of salinity, climate and temperature on GHG production and emission within these simplified lake ecosystems.

Study site

GHG sampling was carried out as a part of a larger salinity gradient experiment conducted at two coordinated mesocosm sites with identical setups, one in Mersin (Mediterranean climate, 18.3°C, 600 mm precipitation) and the other in Ankara (semi-arid cold climate, 10°C, 380 mm precipitation), Türkiye, between 9th September 2021 and 13 May 2022. The aim of the experiment was to establish the ecological threshold salinity levels that effect GHG emissions in shallow lakes in differing semiarid and Mediterranean landscapes. The GHG emissions measurements took place between 9 October – 8 December 2021. Details of the broader experiment and related samplings were described elsewhere (see “Experiment 1” section in Özkan et al., 2023).

Experimental setup

We adopted a gradient approach with 16 mesocosms in each mesocosm site (32 mesocosms total) to investigate the influence of salinity across a wide gradient. Each mesocosm is a cylindrical high-density polyethylene (HDPE) tank (diameter: 2 m, height: 1.60 m, volume: 5.0 m3) with a water column height of 1.25 meters, and a sediment height of 0.3 m, resulting in a volume of approximately 3.9 m^3. The sediment in mesocosms was a 1:1 mixture of natural lake sediment taken from a brackish lake (c. 2 ppt) and chemically inert, washed silicate sand. Sediment mixture was added to a depth of 30 cm to each mesocosm prior to the experiment, to create biogeochemically realistic sediment-water column interactions for accurate representation of GHG dynamics. A salinity gradient was established across mesocosms ranging from 0 to 50 ppt, with each mesocosm representing a specific salinity level: 0.4, 2, 4, 6, 8, 10, 12, 14, 17, 20, 23, 26, 30, 35, 40, and 50 ppt. Tanks were filled with groundwater and adjusted to target salinities using NaCl and Na_2SO_4, emulating the seawater sulfate to chlorine ratio for a realistic, generalized and comparable representation of natural saline ecosystems. The salinity adjustments were done gradually, adding 1/30th of final salinity in the first 30 days of the experiment in the first phase (salinization). After attaining target levels at 30th day, salinity was stable at the targeted salinity levels and kept constant with biweekly water or salt (NaCl + Na_2SO_4) additions by adding salt when the salinity drops 5% below the target level. Eutrophic conditions were maintained in mesocosms by weekly additions of NO_3, NH_4 and PO_4 (75 µg/l of total phosphorus and 1500 µg/l of total nitrogen, assuming a TN:TP molar ratio of 20) assuming % 20 weekly loss throughout all experiment duration. The water and air temperature reflect the natural seasonal variation. Contrasting temperatures of Ankara and Erdemli allowed us to account for the effect of temperature, serving as an additional climate zone treatment.

GHG sampling and analyses

GHG sampling started in 5 October 2021, marking the start of stable salinity phase. The sampling was carried out weekly, covering an eight-week period where both diffusive and total fluxes were determined in 9 sampling occasions for diffusive flux and 8 sampling occasions for total flux, except in the penultimate week (1 December 2021) the sampling was not carried out in Ankara site due to ice cover. Diffusional fluxes were calculated from the water concentration using a headspace equilibration method, where 40 ml surface water from mesocosms were taken carefully into a 60 ml syringe not to disturb the diffusive gas, closed underwater using a 3-way stopcock. Afterwards, a 15 ml air sample in the syringe was taken into syringe, and then syringe is shaken vigorously for 1 minute to equilibrate the air with the water sample. The air samples in the syringe were then injected in 5.9 ml pre vacumed glass vials (Exetainer, LabCo, UK), which were kept in dark and analyzed in GC within two weeks. Air samples were also taken in every sampling occasion to account for the background values of the gases.

For total fluxes (including diffusion and ebullition) a floating chamber method was adapted from Bastviken et al. (2015). The floating devices were built from polypropylene tubs with a diameter of 30 cm and a volume of 8 L. Chambers, equipped with floaters, were covered entirely with reflective material to minimize heating. The chambers remained on the mesocosms for six-day intervals per week.After weekly water sampling, chambers were redeployed for the subsequent week. Chamber contents were sampled weekly using polypropylene syringes (15 ml air to 5.9 ml vials).

Gas samples were analyzed for CO_2, CH_4, and N_2O concentrations using gas chromatography (GC 8610, SRI, USA) equipped with flame ionization (FID) and electron capture (ECD) detectors, a dual-column setup with backflush to separate and quantify the target gases. For further details on the GC operating conditions, please refer to Ertürk Arı et al. (2021). A multi-point calibration using certified reference gases at various concentrations (0-50000 ppm for CH_4, 0-20000 ppm for CO_2, 0-10 ppm for N_2O) was employed. We divided the entire concentration range into sub-ranges with the best linear fit for each gas (CH_4, CO_2, N_2O). The raw data from samples was then calibrated within the corresponding sub-range for optimal accuracy. The LOQs for CH_4, CO_2 and N_2O were 0.18, 53 and 0.09 ppm, respectively.

Diffusional fluxes of GHG species were calculated according to Henry's law:

$$F_{gas}=k_{\mathrm{gas}}(C_{wat}-C_{\mathrm{eq}})$$

where F_{Gas} is the flux of CH_4, k_{Gas} (m h^{-1}) is the piston velocity and $Cwat-Ceq$ is the difference of concentration of gas dissolved in the water and the concentration of gas the water would have at equilibrium with the atmosphere. Cwat is back calculated from the headspace concentrations, and k_{gas} reported on Davidson et al. (2018) was chosen for the calculation of flux, with the assumption that the mesocosms sampled in this study were similar to those in the cited study in terms of depth, mixing properties and being sheltered against wind. Although this introduces uncertainty on calculating the actual fluxes, it allowed us to compare between mesocosms.

Total GHG fluxes were calculated from the increase rate of gas concentrations in the chambers with the following equation (Keller *et al*., 2020; Ertürk Arı *et al*., 2021).

$$F_{Gas} = \left(\frac{dp_{Gas}}{dt}\right).\left(\frac{V}{RTS}\right)$$

Where, F_{Gas} is the flux of CH_4, CO_2 or N_2O (mmol m^{-2} d^{-1}), dp_{Gas}/dt is the rate of change of the partial pressure (concentration) of the gas in question, i.e., difference between the measured concentration minus atmospheric background, V is the volume of the sampler (m^3), R is the ideal gas constant (0.082 L atm K^{-1} mol^{-1}), T is the absolute temperature (K) and S is the area of the chamber (m^2).

Physico-chemical parameters

Throughout the period of GHG sampling, a suite of physical, chemical, and biological parameters was also measured weekly. Temperature, specific conductance, dissolved oxygen (DO) and pH were measured with a handheld probe (YSI ProDSS, USA). Water transparency was measured with a Secchi disc. For water chemistry and biology, depth-integrated water samples were collected from each mesocosm using a tube sampler. These samples were stored in polyethylene bottles and were used to determine chlorophyll-*a* (Chl-*a*) concentration, total suspended solids (TSS), alkalinity, and nutrient levels. Chl-*a* concentration was determined spectrophotometrically at 663 and 750 nm wavelengths following the filtration of 50-500 ml sample with GF/C (Whatman) filters and subsequent ethanol extraction (Jespersen & Christoffersen, 1987). TSS was quantified by filtering 50-500 ml sample through a pre-weighed GF/C filter. The filter was then oven-dried at 105°C for 12 hours. The difference between the final and initial filter weights provided the TSS concentration (mg/L). Alkalinity was determined via a titration method (APHA, 1996), where unfiltered water samples were titrated with 0.01 N HCl, after consequential additions of phenolphthalein and BDH 4.5 indicator to determine carbonate and bicarbonate concentrations, respectively. Nitrate (NO_3) + nitrite (NO2) and total nitrogen (TN) concentrations were assessed using an automated Skalar N (Breda, Netherlands) autoanalyzer (Grasshoff et al., 1983). For TN analysis, samples were digested with an alkaline persulfate solution at 90 °C, following the method described in Kroon (1993). Total phosphorus (TP) and soluble-reactive phosphorus (SRP) were analyzed using the ammonium molybdate and ascorbic acid reduction methods (Mackereth et al.,1978). Dissolved silicate (Si) was measured using sodium molybdate reaction followed by spectrophotometric determination at 365 nm wavelength (Golterman et al. 1978). Water color was estimated as the direct measurement of absorbance at 420 nm after filtration through a glass microfiber filter (Grade GF/C, Whatman) and measured as triplicates for each sample (Blindow et al., 2002).

Statistical methods

ANOVA methods were used to test the difference of GHG fluxes between sites and salinity levels. Pairwise correlations between GHG fluxes (CO_2, CH_4, and N_2O) and environmental variables (temperature, salinity, nutrients, Chl-a, pH, alkalinity, total suspended solids) were first explored using Pearson's correlation. To achieve normality, variables were log transformed with minimum offset addition. To further explore general trends in the data, detect collinearities among variables and clusters, PCA was performed prior to model building. Data was then used to build linear mixed effect model for each response variable. In addition to response variables, i.e., diffusive fluxes (fCO_2, fCH_4, fN_2O) and total fluxes ($totCO_2$, $totCH_4$, $totN_2O$), the dataset includes salinity, temperature, nutrients (NO_3, SRP, TP, TN) and chl-a as continuous predictor variables; sampling occasions (date) were used as random effect (9 and 8 occasions for diffusive and total fluxes, respectively), and mesocosm site (Ankara vs Mersin) as categorical variable. To investigate the effects of potential climate impact over the individual response variables, in addition to whole dataset model, site specific models were also tested separately. The model was fitted using the *lmer* function from the *lme4* package in R (version 4.4.1). Restricted maximum likelihood (REML) estimation was used to fit the model. Model comparison was conducted using likelihood ratio tests with models fitted using maximum likelihood (ML). The significance of additional predictors was assessed by comparing nested models using the *anova* function. Collinearity was checked using variance inflation factors (VIFs) calculated with the *car* package. Effect sizes were assessed using the marginal R2 and conditional R2 values, which were calculated using the performance package.

Results

Diffusive fluxes of CH_4 (fCH_4) were generally low and close to baseline values across the sites and salinities (Table 1, fig 1A, D). The average fCH_4 flux was 0.25 and 0.13 mg C m^{-2} d^{-} for Ankara and Mersin, respectively. The fCH_4 ranged from -0.05 to 3.54 mg C m^{-2} d^{-} in Ankara and -0.05 to 0.65 mg C m^{-2} d^{-} in Mersin. Total fluxes of CH_4 ($totCH_4$) varied across salinity levels and sites. (Table 1). The average of $totCH_4$ was 0.50 and 2.20 mg C m^{-2} d^{-} for Ankara and Mersin. $totCH_4$ ranged between 0.03 – 2.60 and 0.03-29.9 mg C m^{-2} d^{-} for Ankara and Mersin, respectively, with Mersin significantly higher than in Ankara. The contribution of fCH_4 to the $totCH_4$ differed significantly between the sites. In Ankara, average diffusive to total flux ratio (dCH_4 / $totCH_4$) ranged between 0.10 to 1 (albeit with a few data points where fCH_4 was higher than $totCH_4$ at very low concentrations), suggesting diffusive fluxes comprise a dominant (50 % on average) fraction of total CH_4 emissions. In the Mersin this ratio was between 0.01 – 0.48, (17 % on average) indicating that diffusion account 17 % of the total fluxes on average, and ebullitive fluxes was 2.5 – 100 times higher than the diffusive fluxes. The fCH_4 and $totCH_4$ showed significant variability across salinity and sites albeit with no interaction between factors (Fig. 2).

Table 3-1 Diffusive and total CH_4 fluxes (mg C m^{-2} d^{-}) (median and interquantile range) and their relative ratios across salinities and experimental sites.

	Ankara		
Sal (ppt)	Diff	Tot	dCH_4 / $totCH_4$
0.4	0.27 (0.11-0.54)	0.24 (0.12-0.3)	2.63
2	0.16 (0.03-0.23)	0.15 (0.11-0.25)	0.91
4	0.39 (0.34-0.5)	0.65 (0.49-0.8)	0.60
6	0.25 (0.21-0.3)	0.52 (0.36-0.73)	0.54
8	0.32 (0.26-0.39)	0.66 (0.63-0.71)	0.57
10	0.16 (0.04-0.31)	0.33 (0.22-0.61)	0.52
12	0.2 (0.14-0.26)	0.48 (0.46-0.59)	0.35
14	0.13 (0.05-0.22)	0.25 (0.21-0.29)	0.56
17	0.22 (0.19-0.25)	0.16 (0.11-0.23)	1.30
20	0.3 (0.21-0.41)	0.67 (0.59-0.85)	0.40
23	0.09 (0.02-0.19)	0.1 (0.06-0.51)	0.20
26	0.15 (0.07-0.25)	0.24 (0.23-0.25)	0.64
30	0.2 (0.11-0.27)	0.11 (0.1-0.19)	1.14
35	0.1 (0.09-0.26)	1.78 (1.04-1.96)	0.10
40	0.13 (0.04-0.22)	0.24 (0.17-0.38)	0.46
50	0.13 (0.1-0.18)	0.16 (0.14-0.6)	0.36

Table 3-1 cont.

	Mersin		
0.3	Diff	Tot	dCH_4 / totCH_4
0.4	0.17 (0.08-0.33)	0.59 (0.21-0.73)	0.48
2	0.09 (0-0.12)	0.97 (0.34-2.57)	0.02
4	0.19 (0.12-0.27)	0.86 (0.41-1.36)	0.21
6	0.27 (0.13-0.48)	1.79 (0.53-2.44)	0.06
8	0.12 (0.02-0.18)	1.12 (0.12-2.66)	0.05
10	0.16 (0.07-0.18)	0.52 (0.48-0.65)	0.25
12	0.14 (0.07-0.15)	0.51 (0.29-0.87)	0.16
14	0.15 (0.04-0.16)	2.36 (0.25-12.57)	0.01
17	0.02 (-0.03-0.08)	0.12 (0.09-0.27)	0.45
20	0.1 (0-0.1)	0.36 (0.19-0.59)	0.16
23	0.18 (0.04-0.19)	0.7 (0.49-1.19)	0.12
26	0.13 (0.02-0.21)	2.29 (0.86-5.09)	0.04
30	0.09 (0.01-0.17)	0.24 (0.1-0.42)	0.31
35	0.07 (0.01-0.09)	0.43 (0.25-0.68)	0.09
40	0.14 (0.03-0.19)	2.71 (1.62-8.33)	0.01
50	0.07 (0.02-0.17)	0.16 (0.08-0.33)	0.26

Diffusive and total CO_2 flux (fCO_2 and totCO_2, respectively) patterns were quite different than of CH_4. The fluxes derived from chamber concentrations (totCO_2) showed minimal fluxes of CO_2, averaging 1.30 and 2.62 mg C m^{-2} d^{-} for Ankara and Mersin, respectively (Table 2). Diffusive CO_2 fluxes (fCO_2), calculated from dissolved CO_2 concentrations, were consistently negative in all mesocosms (except for the initial weeks in the 0, 4, and 6 ppt Mersin mesocosms), indicating that these systems were undersaturated with CO_2 and taking up CO_2 from the atmosphere at the sampling time (Fig 1B, E). Both mean fCO_2 and totCO_2 were significantly different with a significant interaction between factors, indicating differences between mesocosms with identical salinity levels at two sites.

Table 3-2 Diffusive and total CO_2 fluxes (mg C m^{-2} d^{-}) (median and interquantile range) across salinities and experimental sites (Fig. 3)

	Ankara		Mersin	
Sal (ppt)	Diff	Tot	Diff	Tot
0	-28.1 (-39--8.1)	3.82 (3.01-4.17)	-13.2 (-25.6-27)	5.93 (3.37-6.98)
2	-18.2 (-30.9-3.8)	3.59 (2.87-4.35)	-31.6 (-39.4--26.7)	3.23 (2.19-4.63)
4	-51.2 (-58.2--39.9)	0.06 (-0.06-0.81)	-20.9 (-31.7-5.1)	2.39 (1.53-3.61)
6	-42.8 (-44--39.3)	0.37 (0.27-0.45)	-13.9 (-19.7--2.4)	3.59 (2.95-4.88)
8	-51.1 (-53.1--43.4)	0.3 (-0.05-1.39)	-14.3 (-30.7--9.7)	2.83 (1.78-5)
10	-46.4 (-51--41.4)	0.77 (0.12-1.05)	-42 (-49.1--28.9)	0.67 (0.34-3.64)
12	-48 (-54--38.5)	0.4 (0.21-0.75)	-45 (-45.1--40.1)	0.38 (-0.03-1.34)
14	-50 (-52.5--44.9)	0.35 (-0.07-0.96)	-36.5 (-38.6--35.4)	1.3 (0.71-1.6)
17	-44.9 (-52--44.6)	0 (-0.17-0.5)	-37.4 (-40--36.5)	1.29 (0.6-1.66)
20	-43.9 (-50.6--41.1)	0.55 (0.01-1.65)	-41.6 (-44.6--40.8)	1.21 (0.53-2.12)
23	-44.9 (-48.8--38.6)	1.04 (0.61-1.68)	-40.1 (-42.4--32.5)	0.12 (0.05-0.32)
26	-40 (-45.7--37.6)	0.34 (0.1-0.46)	-36 (-38.3--32.5)	0.84 (0.36-1.82)
30	-41 (-45.2--35.5)	0.83 (0.2-1.19)	-33.4 (-37.4--30.6)	0.77 (0.54-1.05)
35	-41.1 (-47.7--38.9)	-0.05 (-0.15-0.21)	-35.1 (-38.4--25.7)	1.35 (1.13-1.72)
40	-36.4 (-39.4--34.8)	0.2 (0.04-0.9)	-36.5 (-37.5--30.8)	0.44 (0.27-0.72)
50	-36.1 (-39.6--34.5)	0.04 (-0.19-0.34)	-34.9 (-36.3--30.9)	0.63 (0.13-0.85)

Diffusive and total N_2O fluxes (fN_2O and $totN_2O$, respectively) exhibited a distinct pattern, with the difference between the two mirroring that observed for CH_4 fluxes, interestingly. The mean fN_2O in Ankara and Mersin were negative but close to zero, -0.02 and -0.07 mg N m^{-2} d^{-}, respectively, impliying dissolved N_2O concentrations were close to equilibrium with the atmosphere in both sites. However, fluxes derived from chambers ($totN_2O$) Ankara and Mersin were 5.7 and 12.7 mg N m^{-2} d^{-}, respectively. The mean fN_2O results were not significantly different between the two sites, but only different between salinity levels, while mean $totN_2O$ was significantly different between sites, salinities with a significant interaction between site and salinity level (fig. 4)

Table 3-3 Diffusive and total N_2O fluxes (μg N m^{-2} d^{-}) (median and interquantile range) across salinities and experimental sites (Fig. 3)

	Ankara		Mersin	
Sal (ppt)	Diff	Tot	Diff	Tot
0	-24 (-44-22)	5 (2.66-6.95)	40 (14-207)	20.18 (15.6-33.31)
2	-12 (-34-33)	3.08 (2-3.22)	-18 (-32--8)	8.03 (5.78-9.84)
4	-36 (-44--25)	4.6 (3.79-6.2)	103 (34-117)	17.13 (10.26-22.93)
6	-40 (-103--21)	3.35 (2.45-4.25)	33 (29-81)	17.72 (11.28-24.17)
8	-47 (-59--28)	3.95 (2.68-5.91)	95 (62-149)	22.16 (17.9-30.77)
10	-56 (-102-8)	5.31 (3.85-6.13)	23 (-8-51)	11.25 (7.61-13.71)
12	-48 (-107-1)	2.89 (1.99-4.96)	2 (-11-57)	8.74 (7.14-10.76)
14	-61 (-141-31)	4.13 (3.05-5.74)	47 (2-91)	15.05 (8.72-17.45)
17	-34 (-70-23)	4.92 (4.86-5.11)	-93 (-122--41)	8.3 (6.94-10.74)
20	-96 (-149--16)	4.61 (2.14-6.11)	-89 (-128--2)	8.08 (5.22-9.22)
23	-178 (-279--9)	5.78 (3.91-7.17)	9 (-5-45)	10.69 (9.26-12.97)
26	-57 (-238-394)	2.78 (1.85-3.35)	-76 (-223--62)	6.13 (3.74-8.22)
30	-6 (-240-194)	6.14 (5.8-7.19)	10 (-197-306)	12.18 (10.54-14.93)
35	498 (353-633)	10.05 (6.37-11.07)	-202 (-542-37)	12.06 (8.76-13.54)
40	95 (-337-981)	12.74 (8.46-16.96)	-679 (-823--167)	8.65 (6.21-10.4)
50	-550 (-1182--75)	7.82 (6.41-9.26)	-997 (-1484--245)	6.96 (5.17-8.91)

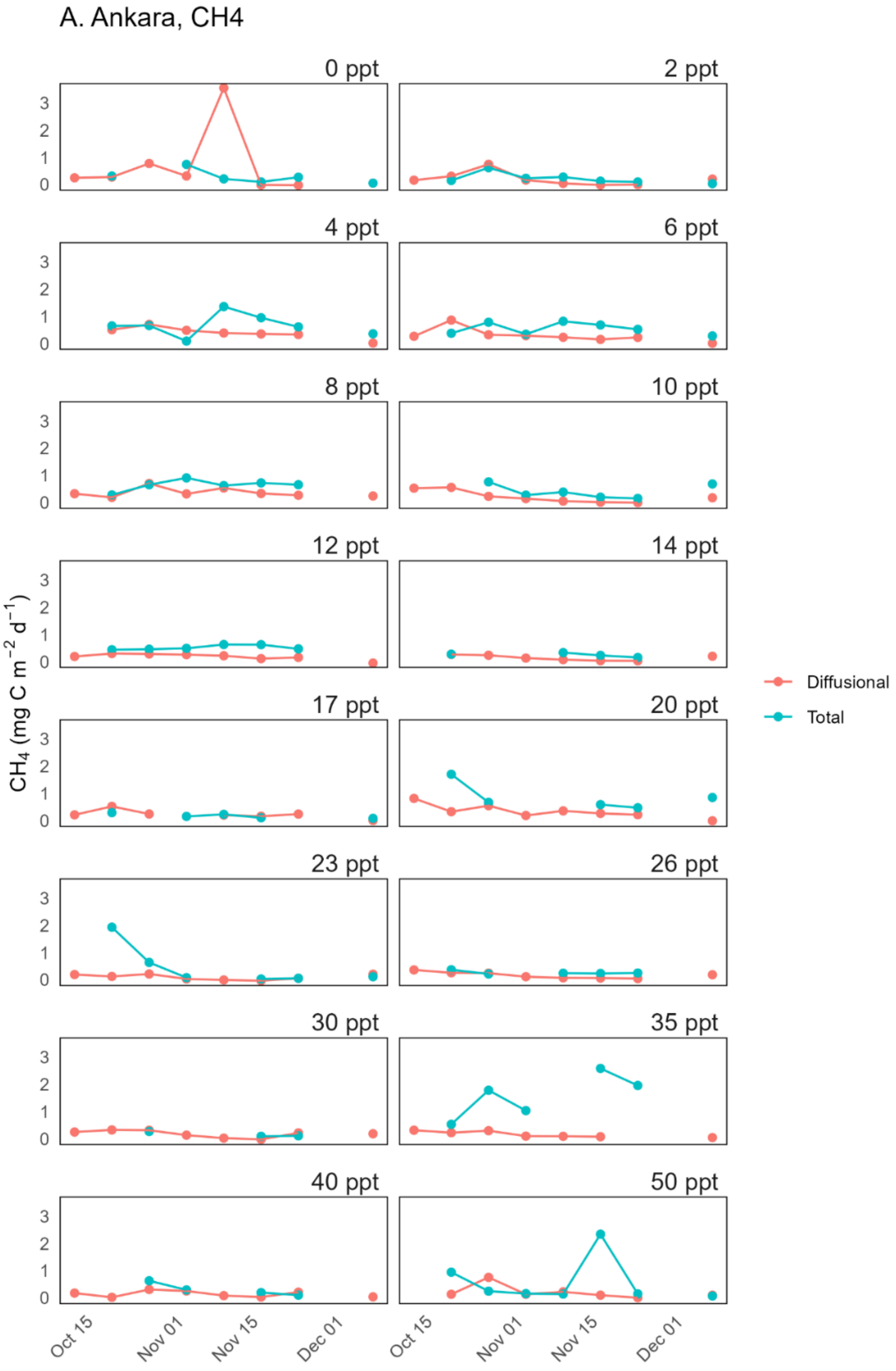


Figure 3-1 Diffusive and total fluxes of CH_4, CO_2 and N_2O throughout the sampling period across salinities (A. CH_4, B. CO_2 Ankara, C. N_2O fluxes at Ankara; D. CH_4, E. CO_2 and F. N_2O at Mersin mesocosms)

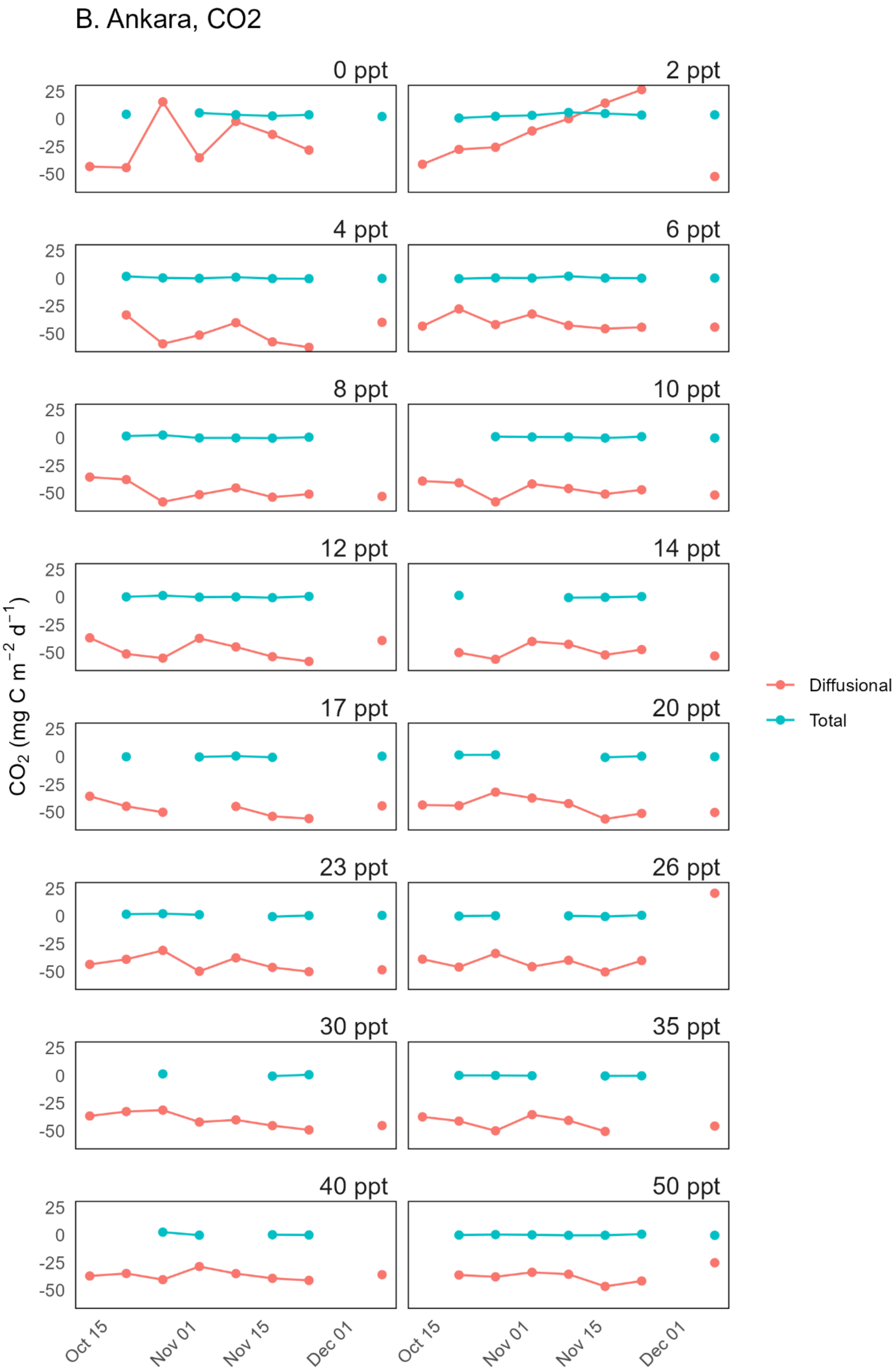

B. Ankara, CO2
0 ppt
2 ppt
4 ppt
6 ppt
8 ppt
10 ppt
12 ppt
14 ppt
17 ppt
20 ppt
23 ppt
26 ppt
30 ppt
35 ppt
40 ppt
50 ppt
25
0
-25
-50
CO$_2$ (mg C m^{-2} d^{-1})
Oct 15
Nov 01
Nov 15
Dec 01
Diffusional
Total

Fig.1. cont.

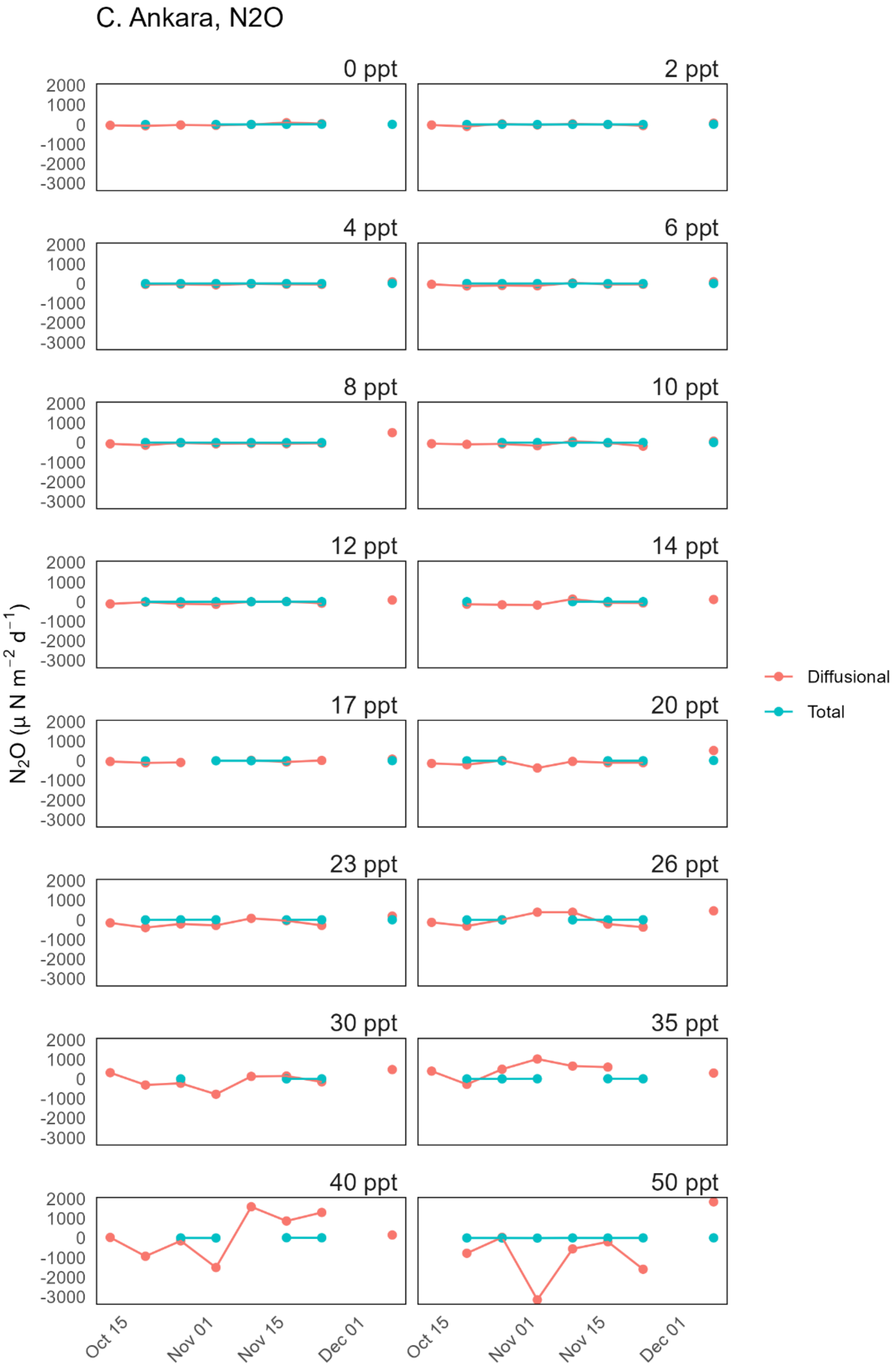

C. Ankara, N2O
0 ppt
2 ppt
4 ppt
6 ppt
8 ppt
10 ppt
12 ppt
14 ppt
17 ppt
20 ppt
23 ppt
26 ppt
30 ppt
35 ppt
40 ppt
50 ppt
2000
1000
0
-1000
-2000
-3000
N_2O (μ N m^{-2} d^{-1})
Oct 15
Nov 01
Nov 15
Dec 01
Diffusional
Total

Fig.1. cont.

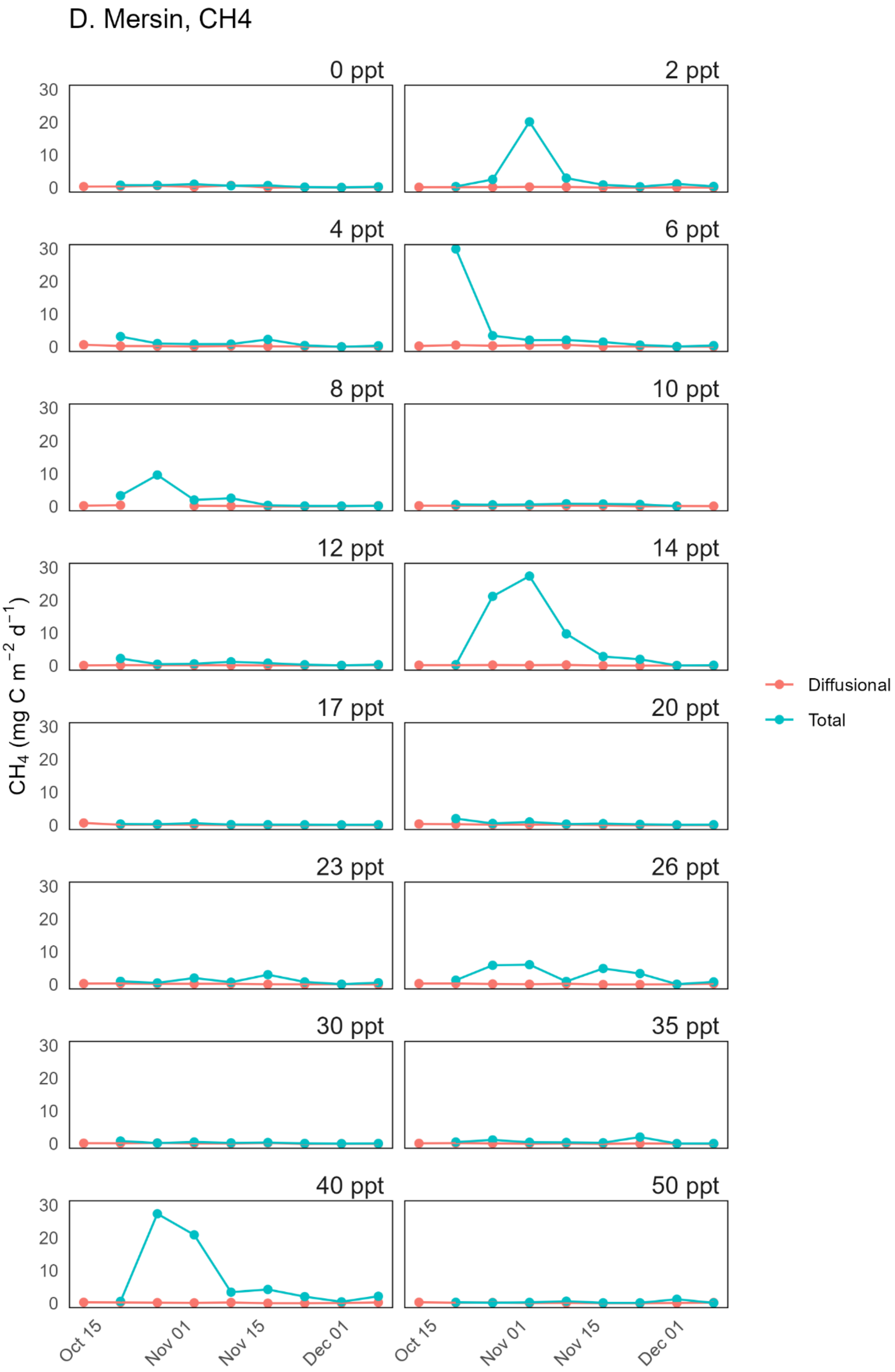

D. Mersin, CH4
0 ppt
2 ppt
4 ppt
6 ppt
8 ppt
10 ppt
12 ppt
14 ppt
17 ppt
20 ppt
23 ppt
26 ppt
30 ppt
35 ppt
40 ppt
50 ppt
30
20
10
0
CH$_4$ (mg C m^{-2} d^{-1})
Oct 15
Nov 01
Nov 15
Dec 01
Diffusional
Total

Fig.1. cont.

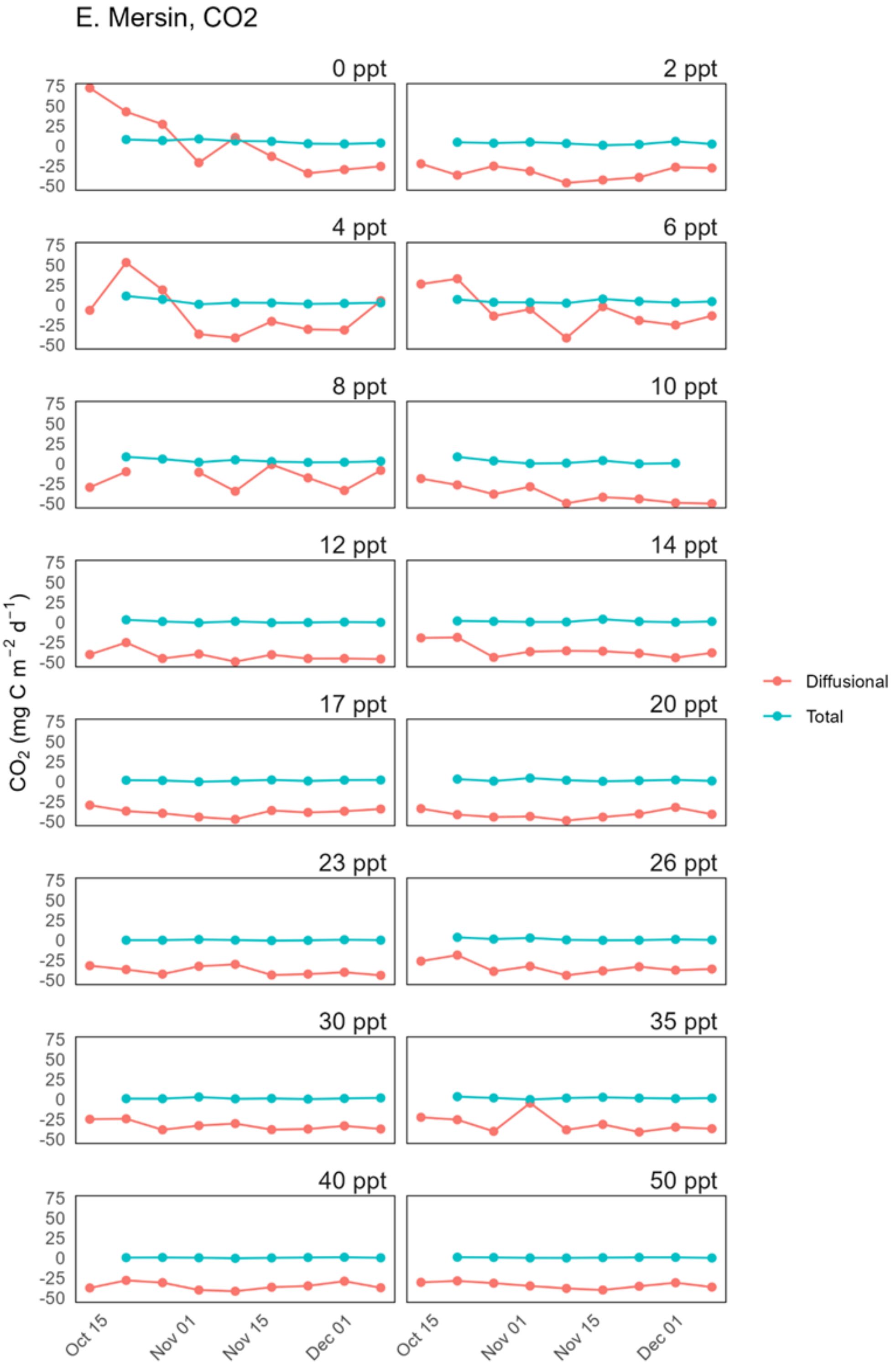

E. Mersin, CO2
0 ppt
2 ppt
4 ppt
6 ppt
8 ppt
10 ppt
12 ppt
14 ppt
17 ppt
20 ppt
23 ppt
26 ppt
30 ppt
35 ppt
40 ppt
50 ppt
75
50
25
0
-25
-50
CO2 (mg C m-2 d-1)
Oct 15
Nov 01
Nov 15
Dec 01
Diffusional
Total

Fig.1. cont.

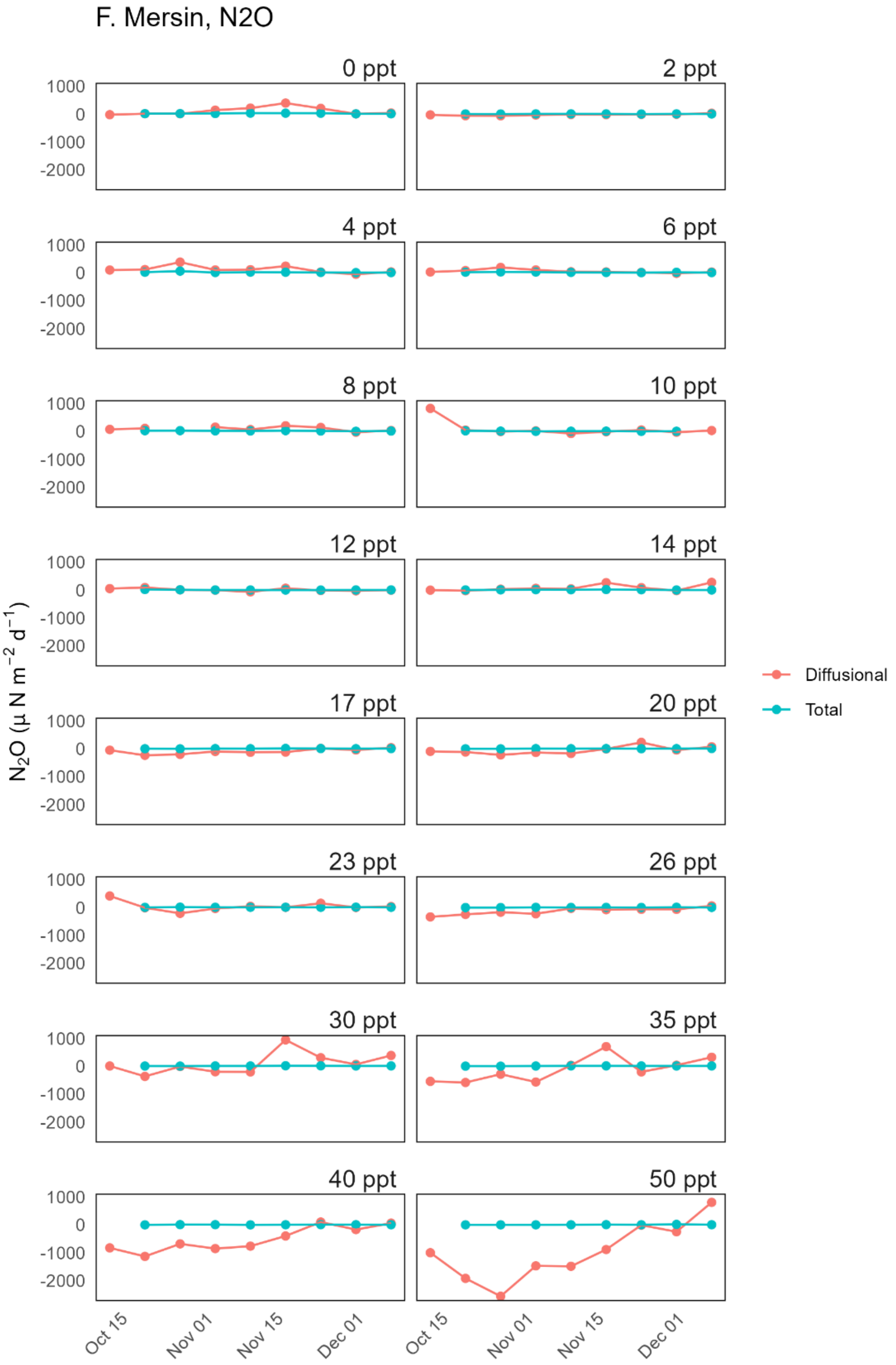

F. Mersin, N2O
0 ppt
2 ppt
4 ppt
6 ppt
8 ppt
10 ppt
12 ppt
14 ppt
17 ppt
20 ppt
23 ppt
26 ppt
30 ppt
35 ppt
40 ppt
50 ppt
1000
0
-1000
-2000
N2O (µ N m-2 d-1)
Oct 15
Nov 01
Nov 15
Dec 01
Diffusional
Total

Fig.1. cont.

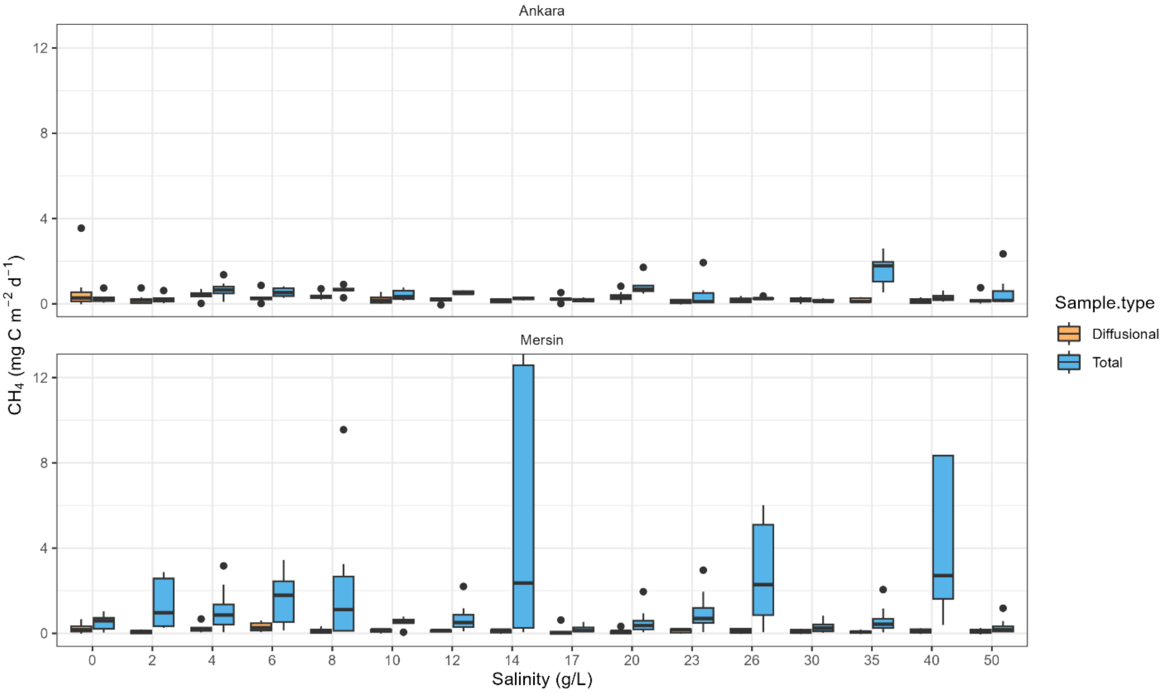


Figure 3-2 Average diffusional and total CH_4 fluxes across sites and salinity levels.

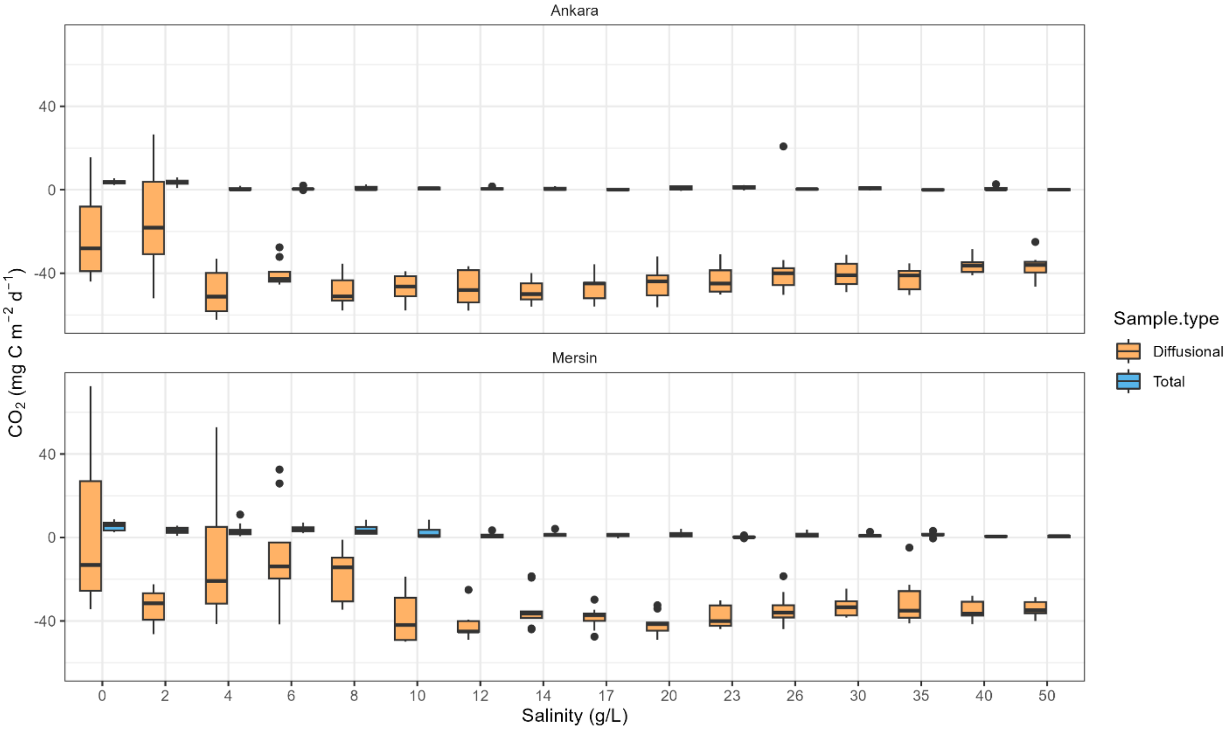


Figure 3-3 Average diffusional and total CO_2 fluxes across sites and salinity levels.

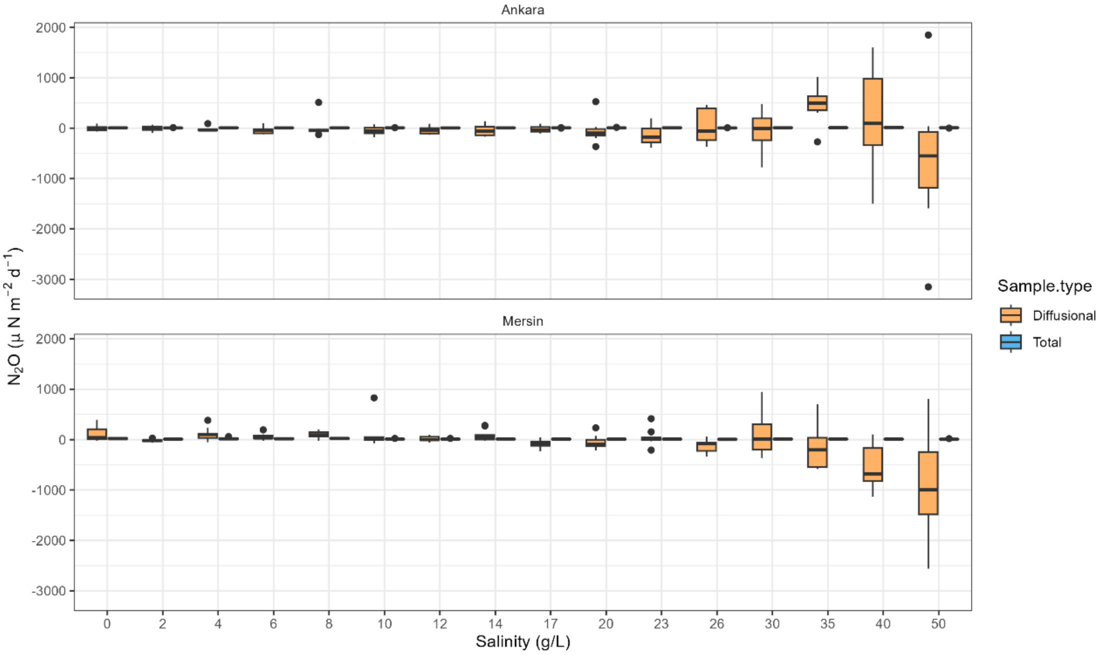


Figure 3-4 Average diffusional and total N_2O fluxes across sites and salinity levels.

Ankara and Mersin mesocosms displayed distinct environmental and biological responses across varying salinity levels. In Ankara, Secchi depth generally increased with salinity, peaking at mid-salinities (4, 8, 14, 17, 20 ppt), before declining at higher salinity levels, with a minimum of 48 cm observed at 50 ppt. In contrast,chl-a followed an opposite pattern, increasing significantly at higher salinities, reaching a maximum of 86 µg/L at 40 ppt and 153 µg/L at 50 ppt. Similarly, TSS, increased as salinity rose, peaking at 85 mg/L at 50 ppt. pH values in Ankara ranged from 8.37 to 9.53, with the highest pH observed at lower to mid salinities. Additionally, alkalinity steadily increased with salinity, with a maximum of 5.52 at 50 ppt, indicating greater buffering capacity at higher salinities. In the Mersin mesocosms, Secchi depth also followed an increasing trend with salinity, peaking at 101 cm at 17 ppt but dropping sharply at higher salinity levels, reaching 53 cm at 40-50 ppt. Chl-a similarly increased at higher salinities, with substantial peaks at 109 µg/L at 40 ppt and 230 µg/L at 50 ppt, following the same trend observed in Ankara. The pH in Mersin was generally lower than in Ankara, ranging from 7.74 to 8.35, with the highest value recorded at 10 ppt. Alkalinity was also lower in Mersin, ranging from

0.48 to 2.2, with a maximum observed at 50 ppt. In both sites, consistently high Secchi depth, pH, alkalinity and low chl-a and TSS reflected the macrophyte dominance of the mid salinity mesocosms.

Nutrient concentrations exhibited distinctive patterns. SRP increased as salinity rose, peaking at 50 ppt, in both sites, while NO_3) levels were highest at at 0 ppt and declined as salinity increased. TP and TN followed similar trends, with both peaking at 50 ppt in both sites. Overall, both mesocosms exhibited similar responses to increasing salinity. However, pH and alkalinity levels were notably higher in Ankara, while Mersin exhibited higher peaks for nutrient concentrations, especially at lower salinities.

Table 3-4 Average Secchi transparency (cm), chl-a concentration, total suspended solids (TSS), pH, alkalinity, soluble reactive phosphorus (SRP), NO_3 concentration, total phosphorus (TP) and total nitrogen (TN) across mesocosm sites and salinity levels.

Ankara mesocosms

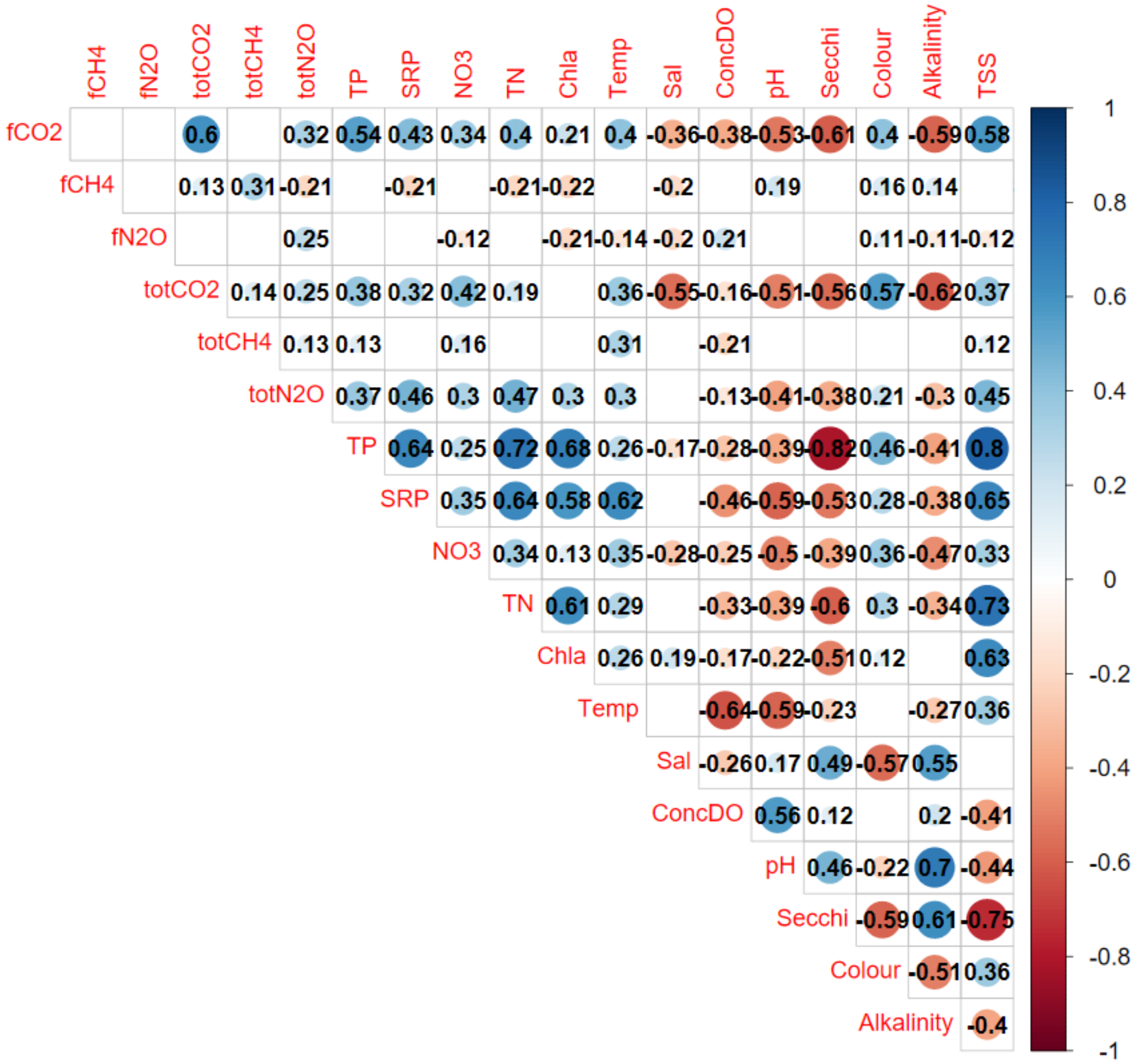
Salinity ppt	Secchi cm	Chl-a μg L	TSS mg L	pH	Alkalinity	SRP μg L	NO_3 μg L	TP μg L	TN μg L
0	30	18	32	8.37	0.99	9.3	204	96	879
2	48	16	40	8.49	1.52	7.7	102	89	951
4	120	5	9	9.53	4.52	4	42	27	549
6	76	11	16	9.04	3	3.9	88	37	632
8	118	13	11	9.34	3.88	3.5	10	30	414
10	115	7	12	9.12	3.47	3.7	10	28	445
12	100	15	19	9.34	4.63	3.3	5	37	543
14	120	11	16	9.1	3.65	3.5	9	28	586
17	118	8	18	9.14	4.06	3.3	22	22	478
20	120	8	21	9.41	4.46	3.4	11	34	572
23	112	20	25	9.2	4.24	5.5	19	50	709
26	120	3	26	9.03	3.18	3.6	17	22	497
30	96	33	49	9.19	4.18	6.4	36	37	863
35	83	42	47	9.31	4.16	8.8	116	60	1105
40	93	86	69	9.17	3.57	9.1	29	85	1436
50	48	153	85	9.43	5.52	11.3	39	99	1495

Mersin mesocosms

Salinity ppt	Secchi cm	Chl-a μg L	TSS Mg L	pH	Alkalinity	SRP μg L	NO_3 μg L	TP μg L	TN μg L
0	23	25	138	8.06	0.48	14.1	1138	108	1407

2	41	20	44	8.18	1.05	8.5	512	59	1064
4	42	31	49	7.87	0.9	11.9	451	73	948
6	20	81	164	7.81	0.85	14.6	304	169	934
8	31	21	70	7.74	0.83	11.5	845	77	1319
10	78	17	26	8.35	2.03	11.4	730	46	1325
12	92	23	24	8.34	1.8	11.7	167	51	842
14	93	20	24	8.13	1.69	11.8	23	62	747
17	101	19	23	8.18	1.67	10.6	32	34	586
20	96	21	26	8.22	2.1	11.7	21	36	709
23	83	42	33	8.3	2.32	10.6	102	45	917
26	82	32	37	7.96	1.48	11.5	17	45	880
30	82	38	41	8.01	1.75	12	57	53	1117
35	86	43	45	7.9	1.91	14.7	174	52	1122
40	53	109	69	8.11	2.05	13.9	73	90	1484
50	53	230	86	8.04	2.2	22.7	114	120	1618

Pearson's pairwise correlation analysis revealed many significant associations between the emissions and environmental parameters (Fig. 5). $TotCO_2$ and fCO_2 both had significant ($p<0.1$) pairwise correlations with, $totN_2O$, they were moderately correlated with nutrients, NO_3, SRP, TN and TP, and Chl-*a*, and also physical parameters including temperature, water color, and TSS. Significant negative associations were with salinity, DO, pH, water column transparency (Secchi), and alkalinity for fCO_2 and $totCO_2$. Conversely, fCH_4 exhibited weak negative associations with SRP, TN, Chl-*a*, and salinity, and positive association with water color, alkalinity and pH. $TotCH_4$ was positively associated with TP, NO_3, temperature, and TSS, while its correlation with salinity is negative. fN_2O, showed significant negative correlations with NO_3, Chl-a, temperature, salinity, alkalinity and TSS, possibly reflecting its low variance and minimal values. On the other hand, $totN_2O$ exhibited medium to strong correlation with NO_3, SRP, TN, TP, temperature, TSS and water color while it was negatively associated with water transparency (Secchi), pH, DO, and alkalinity.



	fCH4	fN2O	totCO2	totCH4	totN2O	TP	SRP	NO3	TN	Chla	Temp	Sal	ConcDO	pH	Secchi	Colour	Alkalinity	TSS
fCO2			0.6		0.32	0.54	0.43	0.34	0.4	0.21	0.4	-0.36	-0.38	-0.53	-0.61	0.4	-0.59	0.58
fCH4			0.13	0.31	-0.21		-0.21		-0.21	-0.22		-0.2		0.19		0.16	0.14	
fN2O					0.25			-0.12		-0.21	-0.14	-0.2	0.21			0.11	-0.11	-0.12
totCO2				0.14	0.25	0.38	0.32	0.42	0.19		0.36	-0.55	-0.16	-0.51	-0.56	0.57	-0.62	0.37
totCH4					0.13	0.13		0.16			0.31		-0.21					0.12
totN2O						0.37	0.46	0.3	0.47	0.3	0.3		-0.13	-0.41	-0.38	0.21	-0.3	0.45
TP							0.64	0.25	0.72	0.68	0.26	-0.17	-0.28	-0.39	-0.82	0.46	-0.41	0.8
SRP								0.35	0.64	0.58	0.62		-0.46	-0.59	-0.53	0.28	-0.38	0.65
NO3									0.34	0.13	0.35	-0.28	-0.25	-0.5	-0.39	0.36	-0.47	0.33
TN										0.61	0.29		-0.33	-0.39	-0.6	0.3	-0.34	0.73
Chla											0.26	0.19	-0.17	-0.22	-0.51	0.12		0.63
Temp													-0.64	-0.59	-0.23		-0.27	0.36
Sal													-0.26	0.17	0.49	-0.57	0.55	
ConcDO														0.56	0.12		0.2	-0.41
pH															0.46	-0.22	0.7	-0.44
Secchi																-0.59	0.61	-0.75
Colour																	-0.51	0.36
Alkalinity																		-0.4

Figure 3-5 Pearson's correlations between diffusive (fCH_4, fCO_2, and fN_2O) and total ($totCH_4$, $totCO_2$, and $totN_2O$) GHG emissions and limnological variables. Temp: temperature (°C), Sal: salinity (ppt), ConcDO: dissolved oxygen (mg/L), Secchi (cm), colour (abs), TSS: total suspended solids (mg/L). Circle size indicates significance level, with larger circles representing lower *p*-values (more significant correlations). Correlations with $p > 0.1$ are not shown on the table.

Pearson’s correlations between diffusive (fCH_4, fCO_2, and fN_2O) and total ($totCH_4$, $totCO_2$, and $totN_2O$) GHG emissions and limnological variables. Temp: temperature (°C), Sal: salinity (ppt), ConcDO: dissolved oxygen (mg/L), Secchi (cm), colour (abs), TSS: total suspended solids (mg/L). Circle size indicates significance level, with larger circles representing lower *p*-values (more significant correlations). Correlations with $p > 0.1$ are not shown on the table.

The PCA analysis corroborated the pairwise correlations and highlighted similar associations between variables (Fig. 6). According to the results, the first principal component (PC1) was positively associated with pH and Secchi transparency. Conversely, PC1 showed strong negative associations with TSS, TP, TN, SRP, temperature, Chl-*a*, fCO_2, $totN_2O$, and with $totCH_4$, albeit to a lesser degree. Although not included quantitatively in the PCA analysis, macrophyte dominance trend in the mesocosms were superimposed on the figure in relation to pH, Secchi transparency, and alkalinity, as mid-salinity mesocosms (10-23 ppt in Mersin and 8-40 ppt in Ankara) consistently covered with macrophytes *(Stuckenia pectinate)* were also displaying high pH, alkalinity and lower turbidity (Özkan et al., 2023). This indicates that higher pH and more transparent waters tend to have lower levels of nutrients and organic matter proxies (TSS, TN, TP). Conversely, higher temperature mesocosms are linked to increased turbidity, higher organic matter proxies, and elevated levels of fCO_2, $totN_2O$ and $totCH_4$. This suggests that these conditions are associated with organic matter availability, temperature, and NO_3 concentration. On the other hand, the second principal component (PC2) was predominantly associated with salinity. Salinity had a strong negative association with fCH_4, indicating that higher salinity is linked to lower fCH_4 levels. Overall, PC1 likely captures the variance related to nutrient and organic matter dynamics and PC2 the influence of salinity.

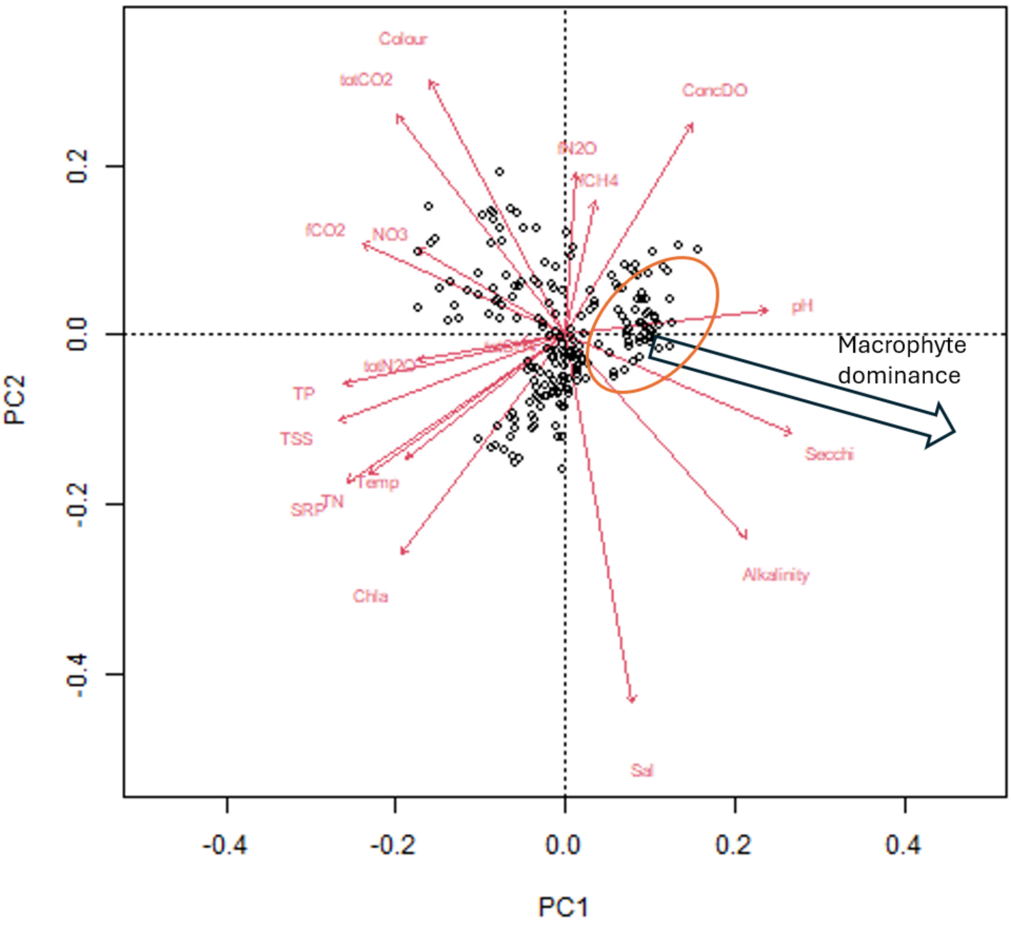


Figure 3-6 PCA of the variables and general trend of macrophyte dominance.

Linear mixed effects models for the diffusive and total fluxes of CH_4, CO_2, and N_2O as response variables concur with the PCA and correlations results (Table 4). The model for fCH_4 (whole dataset) revealed the primary driving effect of temperature, TP, and site, with an additional interaction between site and temperature, while TN and SRP was negatively associated (R^2-marginal=0.25). In both Ankara and Mersin sites, temperature was positively associated with fCH_4; while salinity emerged as a negative effect only in Ankara dataset. In addition, different nutrients were negatively linked to fCH_4 (TP in Ankara and TN in Mersin).

$TotCH_4$ was chiefly driven by temperature and TP, a proxy for organic matter, and the effect of salinity was insignificant (R^2-marginal=0.19). In Ankara, $totCH_4$ model revealed a negative link with TN, but with a very low effect size (R^2-marg= 0.03), reflecting the scarce ebullition events and overall low totCH_4 in Ankara. On the other hand, Mersin model concurred greatly with the whole dataset, revealing a positive link of totCH_4 with temperature and TP, and a negative link with SRP (R^2-marg= 0.29).

Model for fCO_2 revealed that temperature and TP were the main drivers across sites, while salinity imposed a relatively minor but significant negative effect (R^2-marginal=0.48, 0.35, 0.5 for whole data, Ankara and Mersin, respectively.) The model for totCO_2 was not reported due to the challenging nature of CO_2 measurements with the flux chambers (see Discussion). The fN_2O model revealed the most prominent driver as temperature, with site category also being significant and interacting with the temperature (R^2-marginal=0.33). The totN_2O models exhibited mixed results with various effect sizes (R^2-marg= 0.15, 0.06 and 0.2 for whole data, Ankara, and Mersin, respectively). The most significant variable with the highest coefficient was the intercept for all three models, likely reflecting minimal fN_2O values. On the other hand, in totN_2O models, temperature was the most prominent negative association across all data and subsets of Mersin and Ankara. In the whole data site also emerged as a significant factor (but not the interaction of temperature:siteMersin). In addition, TN was a positive driver in whole data and Ankara, while TP and NO_3 were positively associated with totN_2O in Mersin dataset.

Table 3-5 The mixed effects model results for diffusive and total fluxes of CH_4, CO_2, and N_2O, coefficient and P value and effect size R^2-marginal were given for every significant parameter in the model. int: intercept, Sal: salinity, Temp: temperature, R^2-marg: R^2-marginal.

	Diffusive			Total		
	Predictor	Coefficient	*p*-value	Predictor	Coefficient	*p*-value
CH_4	Temp	0.54	0.007	int	-2.67	0.008
Whole	TP	0.24	0.006	Temp	1.15	0.12
	TN	-0.30	0.004	TP	0.54	0.005

	SRP	-0.18	0.04	SRP	-0.56	0.005
	NO_3	0.04	0.0003	siteMersin	-3.85	0.03
	siteMersin	-1.26	0.05	Temp:siteMersin	3.26	0.015
	siteMersin:Temp	0.80	0.08			
	R^2-marg= 0.24, n=265			R^2-marg=0.19, n=216		
CH_4	Int	-1.01	0.009	Int	0.59	0.34
Ankara	Sal	-0.11	0.009	TN	-0.38	0.08
	Temp	0.89	0.02			
	TP	-0.19	0.03			
	R^2-marg= 0.24, n=122			R^2-marg= 0.03, n=89		
CH_4	Int	-2.58	0.007	Int	-7.85	0.02
Mersin	Temp	1.90	0.01	Temp	5.96	0.03
	TN	-0.42	0.0007	TP	0.96	0.0003
	NO_3	0.08	<0.0001	SRP	-1.36	0.0008
	R^2-marg= 0.45, n=143			R^2-marg= 0.29, n=127		
CO_2	int	1.36	<0.0001			
Whole	Sal	-0.05	<0.0001			
	Temp	0.14	0.005			
	TP	0.21	<0.0001			
	Chla	-0.03	0.025			
	siteMersin	-0.43	0.004			
	Temp:siteMersin	0.35	0.004			
	R^2-marg= 0.48, n=264					
CO_2	Int	1.05	<0.0001			
Ankara	Sal	-0.04	0.010			
	Temp	0.16	0.002			
	TN	0.14	0.016			
	TP	0.15	0.006			
	Chla	-0.04	0.020			
	R^2-marg= 0.35, n=122					
CO_2	Int	0.85	0.003			
Mersin	Sal	-0.07	<0.0001			
	Temp	0.58	0.008			
	TP	0.18	<0.0001			

	R^2-marg= 0.50, n=143					
N_2O	int	0.69	<0.0001	int	-0.17	0.67
Whole	Sal	-0.02	0.001	Temp	-0.88	<0.0001
	Temp	-0.05	0.21	TN	0.62	<0.0001
	TN	0.035	0.06	Chla	-0.08	0.09
	NO_3	-0.006	0.02	siteMersin	0.54	<0.0001
	Chla	-0.027	<0.0001			
	siteMersin	0.21	0.035			
	Temp:siteMersin	-0.15	0.06			
	R^2-marg= 0.15, n=264			R^2-marg=0.41, n=215		
N_2O	Int	0.71	<0.0001	Int	0.18	0.74
Ankara	Chla	-0.02	0.003	Sal	0.18	0.001
				Temp	-0.99	0.05
				TN	0.45	0.002
	R^2-marg= 0.06, n=122			R^2-marg= 0.33, n=89		
N_2O	Int	1	<0.0001	Int	2.31	0.0001
Mersin	Sal	-0.02	0.0007	Temp	-1.75	0.0002
	Temp	-0.24	<0.0001	TP	0.56	<0.0001
	Chla	-0.023	0.008	NO_3	0.08	0.0002
				Chla	-0.16	0.020
	R^2-marg= 0.20, n=142			R^2-marg= 0.27, n=126		

Discussion

The distinction between diffusive and total fluxes (where we assume it is diffusive + ebullitive flux) is particularly important in the case of CH_4 as ebullition is often the major release pathway. For CO_2 and N_2O ebullition is generally less pronounced due to their higher solubility in water. Especially CO_2 undergoes repeated cycling through biological processes and its uptake and release in a day is far less straightforward compared to CH_4, making its direct measurement via chamber methods challenging or misleading due to these diurnal fluctuations. Thus, we focus on diffusive CO_2 flux, fCO_2, for the discussion. In the case of N_2O, while ebullition is typically a minor contributor to N_2O emissions (Gao et al., 2013), our results indicate a minor albeit significant contribution of N_2O. Therefore, both diffusive and total N_2O fluxes were discussed.

Methane

Diffusive CH_4 fluxes (fCH_4) were in the lower end of the previously reported values for shallow (freshwater) lakes and wetlands (Dummyreff et al. 2020) but aligning more closely with values reported with natural saline lakes (Camacho et al., 2017: 0.1-3 mg C m^{-2} d^{-}; Chapter 2: 1.2-20 mg C m^{-2} d). This is likely due to the inhibitory effect of salinity on CH_4 emissions, which is a well-established phenomenon in aquatic ecosystems (e.g., see Barnes and Goldberg, 1976; Wang, 1996). Paradoxically, regression analyses revealed a more complex relationship between fCH_4 and salinity. While a negative relationship was present in Ankara mesocosms, this relationship was not observed in the overall or Mersin mesocosm datasets. Two potential explanations can account for these observations. Firstly, above a certain salinity level (c. 4-5 ppt), CH_4 emissions sharply decline (Poffenbarger et al., 2011), which may be obscuring the overall effects of salinity, as most mesocosms in our study exceeds far beyond this threshold level, rendering the effect of salinity on fCH_4 undetectable. Secondly, the greater variability and overall higher fCH_4 fluxes compared to Mersin mesocosms, where fCH_4 is close to baseline, non-emitting levels, may have made the impact of salinity more detectable, leading to a significant negative effect only in Ankara mesocosms.

Temperature was the primary driver of fCH_4, in the overall, Ankara, and Mersin mesocosms, ubiquitously stimulating CH_4 emissions, consistent with the well-established relationship of temperature with CH_4 emissions (Aben et al., 2017; Davidson et al., 2018; Yvon-Durocher et al., 2014). In addition, the site as categorical variable was significant, with Mersin having a negative effect, reflecting the average lower fluxes in Mersin. However, the Mersin site, characterized by warmer average temperatures (c. 10 ºC), showed a more significant relationship between temperature and fCH_4. Furthermore, significant interaction between temperature and Mersin site suggests the effect of temperature is much stronger in Mersin, where the temperature-driven increase in CH_4 production was amplified in the warmer conditions. In other words, although Mersin had a lower average fCH_4 (as also indicated by the negative siteMersin coefficient), the positive interaction term implies that the effect of temperature on fCH_4 was stronger at this site. Thus, the higher temperatures at Mersin mesocosms led to a greater increase in fCH_4 than the same increase in temperature would at Ankara mesocosms. These differences (e.g., higher temperature dependence with lower emissions in Mersin mesocosms) may be plausibly attributed to the complex and stochastic outcomes of the secondary effects caused by temperature, such as elevated respiration, CH_4 oxidation, and transfer rates (Chamberlain et al., 2020).

Temperature emerged as the primary driver of ebullition, with thewith Mersin mesocosms exhibiting significantly higher $totCH_4$, where on average it was 3 to 100 times higher than fCH_4, indicating frequent ebullition events. On the other side, $totCH_4$ in Ankara mesocosms was consistently lower and comparable to fCH_4, suggesting that ebullition was a rarer occurrence. TP, a proxy for organic matter, was positively associated with $totCH_4$ in overall and Mersin models, aligning with previous studies that shows organic matter availability fueling CH_4 ebullition (Beaulieu et al., 2019; DelSontro et al., 2016). The interaction between site category and temperature followed a similar pattern as in the fCH_4, showing a greater temperature dependence in the warmer Mersin site. However, the Ankara model showed a poor fit (R^2-marg=0.03), likely due to consistently and invariably low $totCH_4$, obscuring any potential temperature effect.

Salinity was not significant in any of the model fits, likely reflecting the effect of high salinity range, similar to fCH_4 results. However, both in Ankara and Mersin sites, ebullitive fluxes were quite low (average 0.5 and 2.3 mg C m^{-2} d^{-}, respectively), compared to globally reported values. For instance, Aben et al., (2017) reported a mean ebullitive flux of 84 mg C m^{-2} d^{-} in a mesotrophic mesocosm experiment, while even this is a relatively low emission compared to more eutrophic freshwater systems in the temperate and subtropical regions, where 100-1000 mg C m^{-2} d^{-} is not uncommon (Aben et al., 2017). This suggests the overall inhibitory effect of salinity on the totCH$_4$.

The co-occurrence of near-zero or negative diffusive CH$_4$ fluxes with net positive, albeit low, ebullitive CH$_4$ emissions in the warmer Mersin site represents an intriguing finding of our study. This observation underscores the complexity of CH$_4$ dynamics in saline lentic environments, and highlights ebullition as a potentially significant yet overlooked pathway, especially in the subtropical, typically warmer regions. A plausible conceptual mechanism for this observed discrepancy involves organic matter degradation, CH$_4$ transport and sedimentary microbial processes (Fig. 7). Organic matter is produced in the water column and exported to the sediment, where it is being remineralized by microbial activity, first by the oxygen, as it produces the highest energy yield. On the top layer of the sediment after oxygen depletion, alternative electron acceptors (NO$_3$, Fe(III), Mn(IV)) take over the remineralization process, following the "thermodynamic ladder of geomicrobiology" (Bethke et al 2011), before sulfate reducing bacteria (SRB) takes over. SO$_4$, abundant in natural saline systems (also in our mesocosms), creates favorable conditions for SRB, which outcompete methanogens, which often leads to low or negligible CH$_4$ production in the first place.

However, under specific conditions, such that organic matter export rate to the sediment is high enough, or limited SO$_4$ availability at depth, methanogenesis, the last step of organic matter remineralization in "the ladder", can persist. (Also of relevance here is the fact that high organic matter availability weakens the substrate competition between SRB and methanogens (Soued et al, 2024; Chapter 2), favoring their co-occurrence. CH$_4$ produced in this lower sediment diffuses upper layers, where it is effectively oxidized aerobically and anaerobically through various coupled processes (e.g., AOM/SRB) at the redox transient zone (Bastviken et al., 2002; Reeburgh, 2007; Su et al., 2020), leading to low, even undersaturated CH$_4$ above the transient zone. However, if the CH$_4$ production rate is higher than the diffusion and oxidation, the layer can accumulate CH$_4$, which in turn is released to the atmosphere as bubbles after a critical threshold or by a physical trigger, bypassing oxidative processes in the upper layers. This may explain why almost zero fCH_4 and net positive totCH_4 can occur at the same time. This mechanism could explain the occurrence of simultaneous net positive ebullition and near zero diffusive CH_4 fluxes in our mesocosms.

Nevertheless, however plausible seeming, this speculative mechanism needs to be formulized into a set of testable hypotheses and needs to be proven with future work focusing sedimentary processes, including (i) estimating organic matter export to the sediment, (ii) calculating oxidation rates vs sediment depth, (iii) determining the involved chemical species across the sediment including H2S peak and SO_4 depletion, (iv) documenting the CH_4 accumulation underneath.

Overall, we showed that under specific conditions ebullition can be a minor but non-negligible source of CH_4 emissions. However, salinity, although was not represented in models, imposed a primary control over the sedimentary production of CH_4, inhibiting emissions from any pathway. In this context, our first hypothesis regarding the ebullition might be overriding salinity thresholds did not hold true; as salinity directly limits the CH_4 production, and therefore limiting any emission pathway.

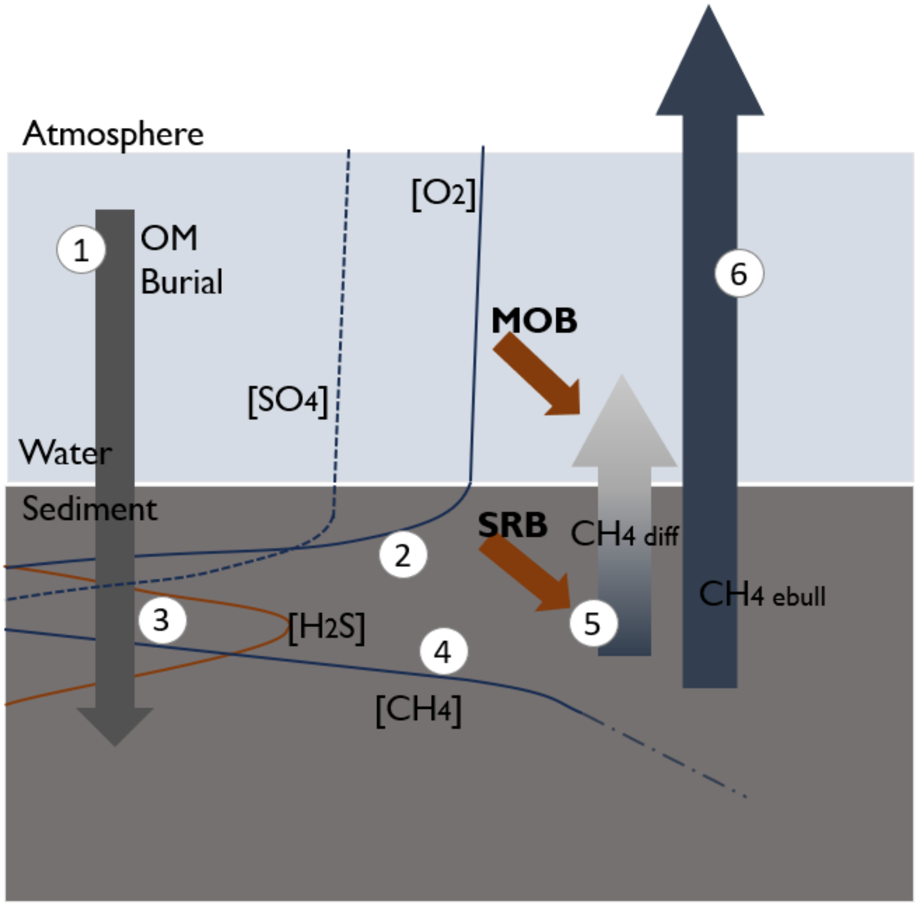


Figure 3-7 A conceptual mechanism for the CH_4 ebullition in saline aquatic ecosystems. 1. Organic matter (OM) produced in the lake/catchment is exported to the sediment and being oxidized. 2. Oxygen, oxidant with the highest energy yield, is used first, until it becomes depleted in the top layer of the sediment. 3. After oxygen (and other alternative electron acceptors) are consumed, SRB takes over the reminalization process, further oxidizing OM. 4. After SO_4 is depleted, methanogenesis becomes the ultimate step of OM oxidation, CH_4 concentration rises in the lower layers. 5. CH_4 produced in the methanogenesis layer diffuses into the upper layers and water column, where it is used as an organic substrate by the other respiratory processes (both oxic and anoxic), suppressing dissolved concentration and efflux to the amosphere. 6. Provided that CH_4 production rate is high enough, the CH_4 accumulates in the gas phase in lower layer constrained physically, and it is released as bubbles after passing a critical level and/or by a physical trigger (e.g. change in the atmospheric pressure, wind stress etc.)

Carbon dioxide

fCO_2 were all around negative in both sites and across salinities, indicating influx of CO_2 to the water column. Undersaturation of CO_2 in the water column means mesocosms were generally inclined to autotrophy, although varying degrees. As evidenced in the PCA analysis (Fig. 6) macrophyte dominated mid-salinity mesocosms had a tendency to have more negative fCO_2 while plankton dominated low and high salinity ends tend to be more heterotrophic, or less negative fCO_2. High water column levels of TP, chl-a and turbidity also aligned with the fCO_2.

Regression analyses were consistent with these general trends observed in PCA. Across salinity gradient in both sites fCO_2 was strongly associated with temperature, to a lesser degree with proxies of organic matter availability (particularly TP). In both sites, salinity was a minor negative effect; and Chl-a concentration had a slightly negative effect in overall dataset, and in cooler Ankara mesocosms. In addition, Mersin mesocosms had a negative site effect though which also had a positive interaction with temperature, as in the case of pCH_4, suggesting that fCO_2 in Mersin mesocosms will have a stronger response to the elevated temperature than in Ankara mesocosms likely due to the already warmer climate, potentially overruling the negative site effect at higher temperatures. In addition, the fact that respiration and methanogenesis are more temperature-dependent than photosynthesis (Allen et al, 2005, Yvon-Durocher et al, 2014; 2017), can explain this fixed site effect and its relationship to temperature.

Notably, macrophyte dominated mid-salinity mesocosms, specifically 8-23 ppt in Mersin and 6-40 ppt in Ankara, usually had lower fCO_2; while the plankton dominated, lower salinity mesocosms had less negative, and occasionally positive emissions (Fig.1B,D; Fig.3). This observation parallels the body of research that associates submerged macrophytes with the carbon sequestration in saline wetlands (Brown et al., 2016; Ward et al., 2021) and highlights the role of macrophytes for ecosystem resilience.

In the higher end of salinity gradient, cyanobacteria were the dominant primary producer (Pacheco et al., submitted), further contributing to negative fCO_2, and partially explaining the slight negative effect of salinity over fCO_2. This could also explain the negative association with Chl-a in Ankara and general dataset, while Mersin mesocosms' specific model did not show a negative association with Chl-a. In addition, temperature effect likely contributes to the interaction between salinity and Chl-a. Warmer Mersin site have presumably higher respiration rates and shorter succession periods, thus the balance between primary production and respiration produces more heterotrophic outcomes, and relatively less negative fCO_2.

Overall, our second hypothesis regarding the salinity stress causing more heterotrophic states in shallow lakes did not hold true. Because the ecosystem response to the salinization was a shift of primary producer community (to cyanobacteria) (Pacheco et al., 2025?) and the fCO_2 rates were explained by the interaction of temperature, plankton productivity, succession rates, and to a greater extent macrophyte presence; rather than a direct inhibitory effect of salinity due to biological stress.

Nitrous oxide

The remarkable discrepancy emerged between fN_2O and $totN_2O$ in both sites across whole salinity gradient. While fN_2O, derived from water concentrations, exhibited invariably low, close to baseline and often negative fluxes, suggesting undersaturation, $totN_2O$ was invariably positive and generally higher from previously reported values from saline lakes (Chapter 2, min max: 0-14, median: 0.5 mg N m^{-2} d^{-}). Therefore, the latter obtained from chamber measurements, likely includes a significant ebullitive component. Previous studies reported similar N_2O ebullition rates in freshwater environments (e.g., <10 µg N m^{-2} d^{-1}, Gao et al., 2013), and generally N_2O ebullition is considered a minor if not negligible pathway for N_2O emissions.

The fN_2O models produced rather inconclusive results, with limited explanatory power likely due to low variability around zero. In contrast, $totN_2O$ were significantly influenced by temperature, organic matter availability, particularly TN, and somewhat salinity. Although temperature showed a negative association across all three models, overall data showed that warmer siteMersin had a positive effect on $totN_2O$. This apparent contradiction can be attributed to the complex dynamic of microbial processes including the ones responsible for N_2O production (nitrification and denitrification) and consumption. Higher temperatures promote complete denitrification resulting in N2 with optimum temperature range being 15-35 while temperatures below 10 C usually promote incomplete denitrification. This could explain the temperature effect and the enhanced $totN_2O$ towards the end of sampling period (December) in Ankara site, where the temperature was well below this value (Fig 1C). Conversely in Mersin higher temperatures likely stimulated both processes, leading to increased N_2O production but also promoted N_2O consumption through complete denitrification. Yet Mersin mesocosms having higher $totN_2O$ suggests that N_2O production outweighed consumption under these conditions.

Similar to the observed pattern for $totCH_4$ (Fig 7.), the discrepancy between diffusive and total N_2O fluxes suggests a similar sediment and water column dynamic with its own specific conditions. N_2O production both through nitrification and denitrification primarily occurs within the suboxic top and the underlying anoxic sediment layers, respectively. The N_2O production zone was physically confined by the well mixed and oxygenated water column, which can facilitate N_2O accumulation, leading to supersaturation and subsequent ebullitive release, despite the high solubility of N_2O. However, in the transient zone with redox gradients where oxygen steeply declines, can create favorable suboxic conditions for nitrification, while denitrification requires anoxic conditions in the lower layer. The overall data and Ankara model shows TN, which includes NO_3 and organic nitrogen is the main positive driver of the N_2O emissions. This likely suggests that nitrification in the water sediment interface is a significant contributor to N_2O emissions. On the other hand, in Mersin site alone, TP, an indicator of organic substrate, and to a lesser extent

NO_3, was a positive impact, likely implying that denitrification, oxidation of organic matter with NO_3 in the anoxic layers of the sediment is a likely significant contributor to the totN_2O.

The effect of salinity over the totN_2O was not significant in the overall or Mersin site, but only appeared significant and as a positive effect in Ankara site. SO_4, a component of salinity, was associated with higher N_2O emissions in previous studies (Audet et al., 2020). Sulfide (H2S), which is produced by SO_4 reduction (e.g., by SRB) can inhibit the complete denitrification (from N_2O to N2) (Sørensen et al., 1980), and promote the sedimentary production of N_2O, likely explaining the positive association of salinity with totN_2O, and in overall high N_2O emissions across our eutrophic and high salinity mesocosms.

Conclusions and Limitations

Here we investigated the interactive effects of salinity, temperature and climate on the GHG dynamics of shallow saline lentic ecosystems. Although in our synchronized experiment across two mesocosm sites the main difference was temperature, the interaction between temperature and climate also produced different results and were differentiated. Our findings suggest that especially in the warmer regions ebullitive CH_4 emissions can still be a minor but non negligible pathway in the saline ecosystems. More remarkably, N_2O ebullition, which is often considered negligible, was revealed to be a minor but persistent contributor to N_2O emissions despite apparent undersaturation in water column, while its temperature dependence is more complex, and a result of the stochastic balance between N_2O production and consumption.

Yet, methodological restrictions necessitate cautious interpretation of our results. The gradual salinization process used relatively shortly before the experiment and samplings; this might mean that salt penetration to the sediment may not be fully representative of the conditions of natural saline ecosystems with stable salinity levels. However, our experimental design might be more of relevance to dynamic coastal brackish wetlands with considerable and frequent salinity fluctuations. Furthermore, in further tests carried out in the mesocosm (see Chapter 5, Discussion) flux chamber methods were shown to largely underestimate the ebullitive fluxes, because any steep rise of concentration in chamber due to an ebullition event was lost very rapidly, usually in a matter of hours, back to the water column through dissolution. This constraint limits the accurate quantification of ebullitive CH_4 (or N_2O for that matter) fluxes, and in turn applicability of our data to upscaling.

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CRediT authorship contribution statement

GY: Conceptualization, investigation, data curation, formal analysis, original draft; PEA, CAA, LCL, MeltemK, MK: investigation; TAD, JA, NK: conceptualization, supervision; MB, EJ, KO: conceptualization, supervision, funding acquisition, project administration. The manuscript was reviewed/edited through the contributions of all authors. All authors have approved the final version of the manuscript.

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CHAPTER 4

IMPACT OF HEATWAVES ON GREENHOUSE GAS DYNAMICS IN SHALLOW SALINE LAKES: A SYNCHRONIZED MESOCOSM EXPERIMENT IN CONTRASTING CLIMATES

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ABSTRACT

Shallow lakes and ponds are significantly influenced by climate warming, salinization, and eutrophication, which in turn affect carbon cycling and greenhouse gas (GHG) dynamics. Climate change is not only increasing average temperatures but also intensifying and more frequently causing extreme weather events. These events can profoundly impact lake chemistry, ecosystem function, and

biogeochemical processes. To understand how GHG emissions from these ecosystems respond to such events under varying salinity conditions, we conducted a three-month factorial experiment. The experiment exposed two salinity levels (4 and 40 ppt) to a 15-day simulated heatwave (+6 °C compared to control), divided into pre-heatwave, heatwave, and recovery phases. Our experimental setup included 4 replicates of 2 treatments: salinity (2 levels) and heawave (HW and no heatwave) in 16 5000 L mesocosms in each site, which were filled with sediment, sand, and groundwater, inoculated with natural plankton communities, fish, and macrophytes from freshwater and brackish lakes. Salinity and heatwave conditions were controlled, where simulated heatwave was achieved via programmable electrical heaters. The experiment ran concurrently in Mersin and Ankara from August 29 to November 3, 2022. We measured diffusional and total fluxes of CH_4, CO_2 and N_2O, to see the extent of ebullition in saline systems in a weekly manner. Diffusional fluxes of CH_4 were minimal and close to baseline values and differed significantly across treatments (salinity and heatwave) and across sites, while low salinity mesocosms exhibited minor yet significantly higher ebullitive fluxes, reflecting the inhibitory role of salinity on CH_4 emissions in both climate zones. CO_2 fluxes were similar across the sites, but indicated slightly greater uptake in the less saline, macrophyte dominated mesocosms. The macrophyte dominated mesocosms notably responded less and recovered better to the heatwave, although differences across treatments were minor overall. N_2O fluxes were initially higher in the high salinity mesocosms at both sites, and were not effected by heatwave, however their significant changes in the duration of the experiment suggests the importance of seasonality and temperature patterns. Our findings indicate that a short term extreme heatwave event can induce minor but significant and interconnected alterations in the biogeochemical dynamics of shallow saline lentic environments.

INTRODUCTION

Shallow and small lakes, despite their relatively small global area, play a disproportionate role in biogeochemical cycles (Downing et al., 2006; Pi et al., 2022; Tranvik et al., 2009; Bastviken et al., 2011). However, their functioning is increasingly threatened by climate change and anthropogenic pressures (Wik et al., 2016; Jeppesen et al., 2015; Janssen 2021; Zhou et al., 2022).

Many lakes around the world have seen an increase in water temperature in recent decades (Woolway et al., 2022; Huang et al., 2024). A recent study indicated that lake heatwave (i.e. relatively short periods of extremely elevated water temperatures) can become warmer and longer, which can strengthen the connection between severe occurrences and climate change by the end of the twenty-first century (Woolway et al., 2021). Shallow lakes are likely more sensitive to increasing air temperatures due to higher atmosphere-water interactions compared to deep water bodies (Mooij et al., 2008; Zingel et al., 2018). Variations in temperature cause fluctuations in biotic and abiotic processes in the water column and the sediment, and when they exceed threshold conditions, they can cause adverse and potentially irreversible effects on the ecosystem functioning, individually or interactively with other environmental stressors. For instance, heatwaves in lakes are associated with harmful algal blooms (Duan et al., 2024; Huang et al., 2021); changes in thermal structure (Zhang et al., 2024), and nutrient cycling (Jeppesen et al., 2021) and GHG dynamics (Audet et al., 2017)

Shallow lakes, characterized by rapid water exchange, are particularly vulnerable to salinization. Precipitation and evaporation patterns, coupled with increased water abstraction, have driven water level fluctuations and heightened salinity levels in many water bodies, particularly in arid and semi-arid regions (Riveros-Iregui et al., 2017; Chen et al., 2019; Jeppesen et al., 2015). This heightened sensitivity can lead to pronounced physical, chemical, and biological alterations within these ecosystems (Jeppesen et al., 2023). Moreover, the combined effects of salinity and nutrient enrichment can exacerbate these impacts (Yang et al., 2013).

Fluctuations in hydrological regimes, including extreme precipitation events and altered runoff patterns and human activities (e.g., excessive water regulation and groundwater abstraction) can impact nutrient loadings of shallow lakes significantly and in relatively shorter time scales causing ecosystem level alterations. As a result of nutrient enrichment, the replacement of submerged plants by phytoplankton affects microbial diversity and abundance (Jeppesen et al., 2008), and hence carbon and nitrogen exchange mechanisms (DelSontro, 2018). Besides, climatic warming and its linked potential multiple stressors can lead to synergistic impacts on biogeochemical processes, further exacerbating these effects. Davidson et al., (2018) demonstrated that the combined impact of warming and nutrient enrichment on CH_4 ebullition in shallow lakes was substantially greater than the sum of their individual effects, leading to 6-to-17-fold increase in annual CH_4 emissions.

While the long-term implications of climate warming on carbon cycling and GHG dynamics are well-established (e.g., Yvon-Durocher et al., 2010; 2017), the impacts of short-term, extreme heat events, particularly in saline lakes, remain relatively unexplored. In order to investigate the effects of heatwaves on the GHG dynamics of the shallow saline lentic waters at different salinity regimes and climate zones, we conducted a synchronized mesocosm experiment in two sites, simulating a heatwave event. We hypothesized that intense short-term heating warming events can enhance respiratory processes and we predicted that heatwaves could elicit significant and potentially enduring shifts in carbon and nitrogen cycling, ultimately affecting GHG production, exchange, and ecosystem trophic status.

METHODOLOGY

Experimental design

Heatwave experiment was conducted at two coordinated mesocosm sites with identical setups in contrasting climates, one in Mersin (Mediterranean climate, 18.3°C, 600 mm precipitation) and the other in Ankara (semi-arid cold climate, 10°C, 600 mm precipitation), Türkiye, between 29 August and 20 November, 2022. At each site, we established 16 (32 total) 5000 L mesocosms, each containing 120 cm water and 30 cm of sediment and sand. These mesocosms were inoculated with natural plankton communities, fish, and macrophytes sourced from freshwater and brackish lakes prior to experiment.

To investigate how GHG emissions from saline shallow lake ecosystems respond to extreme heat events under varying salinity conditions, we conducted a three-month experiment with a factorial design with 4 replicates. We exposed two salinity levels (4 and 40 ppt) to a 15-day simulated heatwave (+6 °C compared to control), which was achieved by programmable electrical heaters. After the initial 3-week period (preHW), the heating period (HW) was started on 22 September, 2022, and followed by the recovery period (postHW). Target nutrient loading, 75 µg/l of total phosphorus (TP) and 1500 µg/l of total nitrogen (TN), were achieved by weekly additions of NO_3, NH_4 and PO_4. Details of the experiment, including the technical specifications of the mesocosm infrastructure and related samplings were described elsewhere (see "Experiment 2" section in Özkan et al., 2023).

Sampling and lab analyses

A similar approach described in the Chapter 3 was adopted for GHG and limnological samplings. For total GHG fluxes (totCH_4, totCO_2, and totN_2O) a floating chamber method and for diffusive fluxes (fCH_4, fCO_2, and fN_2O) a headspace method was adopted. Chamber sampling was done weekly and headspace sampling was done twice weekly. GC analyses for GHGs, flux estimations, collection of physical - temperature, pH, dissolved O2 (DO), Secchi transparency, TSS, conductivity - chemical, and biological – nutrients (TN, TP, NO_3, SRP), chl-a, alkalinity - variables were collected with the identical methods described in the Chapter 3.2

Statistical methods

Data was tested for normality and log-transformed when it fails normality with minimum offset addition. In order to test the significant differences between the means between phases and treatments, we performed mixed-effects ANOVA with heating phase and salinity as fixed effects and mesocosm site as random effect, followed by posthoc Tukey's HSD test. Furthermore, correlations between response and predictor variables were explored with Pearson's pairwise correlations.

RESULTS

The data was presented as the diffusive and total fluxes of CH_4, CO_2, and N_2O (diffusive: fCH_4, fCO_2, and fN_2O; total: $totCH_4$, $totCO_2$, and $totN_2O$, respectively), at two different sites, Ankara and Mersin, across varying salinities (4 and 40 ppt) and different phases of a heatwave (PreHW, HW, and PostHW) (Table 4-1.)

In low salinity Ankara mesocosms, fCH_4 were relatively stable across phases, with values ranging from 0.22 to 0.27 mg C m^{-2} d^{-1}, while $totCH_4$ showed a notable decline from 1.29 mg C m^{-2} d^{-1} PreHW to 0.57 mg C m^{-2} d^{-1} PostHW. Both fCH_4 and $totCH_4$ were significantly lower at the PostHW phase than the starting conditions. In high salinity mesocosms, fCH_4 were similar PreHW (0.13 mg C m^{-2} d^{-1}) to HW (0.16 mg C m^{-2} d^{-1}) and remained stable with no significant variation. The $totCH_4$ decreased significantly from 1.27 mg C m^{-2} d^{-1} PreHW to 0.48 mg C m^{-2} d^{-1} PostHW. At the warmer Mersin site, in 4 ppt, a significant reduction in fCH_4 flux was observed from PreHW (0.78 mg C m^{-2} d^{-1}) to PostHW (0.31 mg C m^{-2} d^{-1}). $TotCH_4$ also showed a marked decrease from 4.75 mg C m^{-2} d^{-1} PreHW to 2.29 mg C m^{-2} d^{-1} PostHW with no statistical significance. At 40 ppt salinity, fCH_4 fluxes reduced from 0.47 mg C m^{-2} d^{-1} PreHW to 0.21 mg C m^{-2} d^{-1} PostHW, whereas $totCH_4$ followed a similar trend, decreasing from 2.52 mg C m^{-2} d^{-1} PreHW to 1.25 mg C m^{-2} d^{-1} PostHW (Fig. 4.1)

At 4 ppt Ankara mesocosms, fCO_2 were consistently negative, indicating uptake, with values ranging from -25.8 to -31.0 mg C m^{-2} d^{-1} while at 40 ppt, fCO_2 showed a nonsignificant reduction in uptake from PreHW (-23.2 mg C m^{-2} d^{-1}) to HW (-21.3 mg C m^{-2} d^{-1}) and remained similar postHW. At warmer Mersin site (4 ppt) fCO_2 were also negative, with a slight reduction in uptake from PreHW (-28 mg C m^{-2} d^{-1}) to HW (-22.8 mg C m^{-2} d^{-1}) and remained stable PostHW.At 40 ppt, fCO_2 remained stable (Fig. 4.2).

The greatest variability was observed in fN_2O while totN_2O did not show much variability across phases and only differed between sites. In low salinity Ankara mesocosms, fN_2O varied widely through phases, from a relatively high 14 µg N m^{-2} d^{-1} PreHW to a near-value during HW (-3 µg C m^{-2} d^{-1}) before stabilizing PostHW. At high salinity, fN_2O fluxes showed higher variability, with a large increase PreHW (328 µg N m^{-2} d^{-1}), a negative flux during HW (-9 µg N m^{-2} d^{-1}), and another spike PostHW (217 µg N m^{-2} d^{-1}). At 4 ppt Mersin mesocosms, fN_2O were consistently low, with slight fluctuations around zero, peaking at 8 µg N m^{-2} d^{-1} PreHW and dipping to -7 µg C m^{-2} d^{-1} during HW. On the other hand, at high salinity Mersin mesocosms fN_2O showed considerable variation, with a significant decrease during HW (-225 µg N m^{-2} d^{-1}) and a slight recovery PostHW (-161 µg N m^{-2} d^{-1}).

Table 4-1 Diffusive and total fluxes of greenhouse gas fluxes before (PreHW), during (HW), and after ther

		Diffusive			Total		
Site	Sal	PreHW	HW	PostHW	PreHW	HW	PostHW
		CH_4 mg C m-2 d-					
Ankara	4	0.27 ± 0.09	0.22 ± 0.06	0.26 ± 0.31	1.29 ± 0.5	0.97 ± 0.52	0.57 ± 0.34
Ankara	40	0.13 ± 0.06	0.16 ± 0.1	0.17 ± 0.21	1.27 ± 0.47	1.14 ± 0.88	0.48 ± 0.37
Mersin	4	0.78 ± 0.37	0.47 ± 0.22	0.31 ± 0.11	4.75 ± 3.79	4.64 ± 4.11	2.29 ± 3.12
Mersin	40	0.47 ± 0.09	0.38 ± 0.07	0.21 ± 0.03	2.52 ± 1.31	2.19 ± 0.4	1.25 ± 0.52
		CO_2 mg C m-2 d-					
Ankara	4	-29.6 ± 4.7	-25.8 ± 1.7	-31.0 ± 4.7			
Ankara	40	-23.2 ± 4.1	-21.3 ± 2.2	-23.8 ± 3.7			
Mersin	4	-28 ± 5.2	-22.8 ± 3.2	-24.8 ± 6.2			
Mersin	40	-22 ± 1.5	-20.7 ± 1.9	-21.8 ± 1.5			

		N_2O µg C m-2 d-					
Ankara	4	14 ± 20	-3 ± 7	1 ± 26	9 ± 1	10 ± 1	10 ± 1
Ankara	40	328 ± 328	-9 ± 170	217 ± 569	10 ± 2	10 ± 1	10 ± 2
Mersin	4	8 ± 13	-7 ± 10	3 ± 18	9 ± 1	8 ± 2	12 ± 5
Mersin	40	5 ± 263	-225 ± 93	-161 ± 108	9 ± 2	7 ± 0	10 ± 3

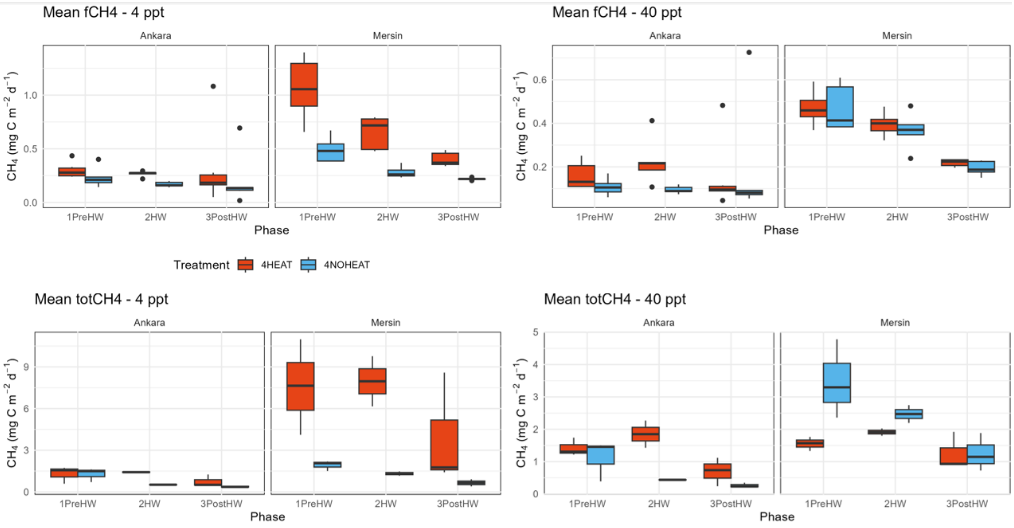


Figure 4-1 Mean diffusive (top row) and total (bottom row) CH_4 fluxes before, during, and after heatwave event. On the left: 4 ppt, right: 40 ppt.

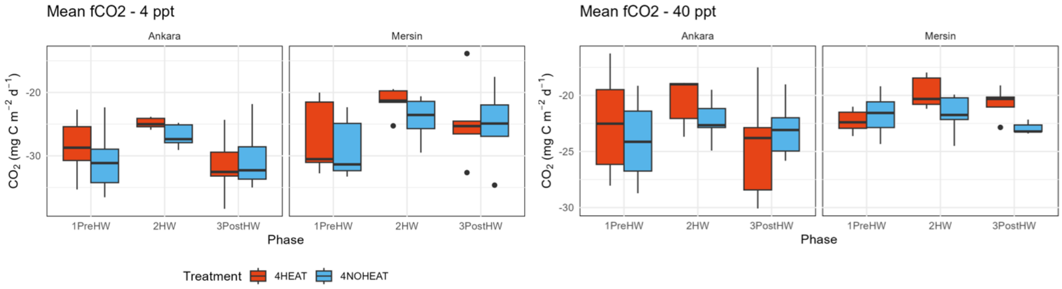


Figure 4-2 Mean diffusive and total CO_2 fluxes before, during, and after heatwave event. On the left: 4 ppt, right: 40 ppt.

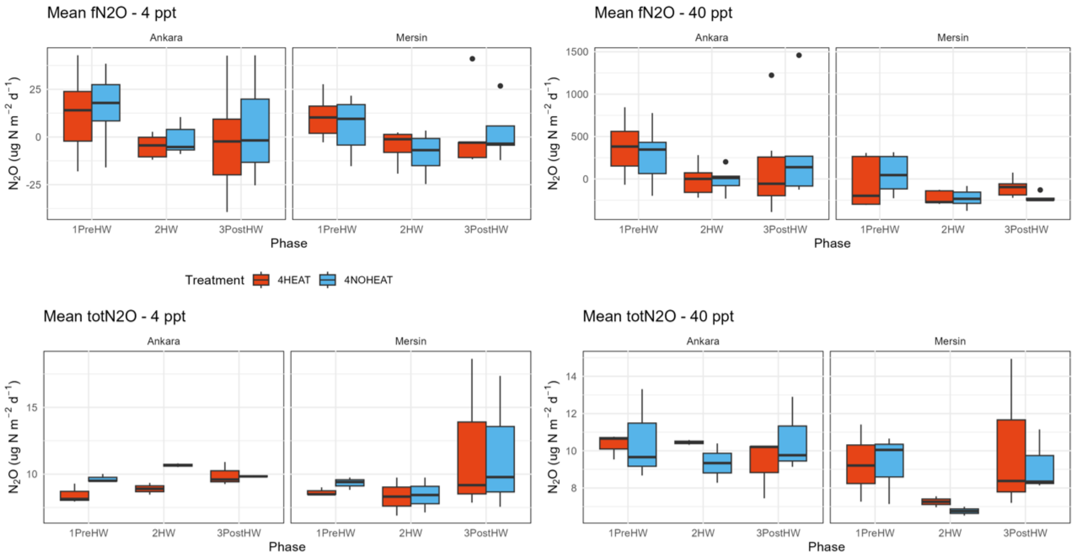


Figure 4-3 Mean diffusive (top row) and total (bottom row) N_2O fluxes before, during, and after heatwave event. On the left: 4 ppt, right: 40 ppt.

Physicochemical variables showed significant variation across salinities, heatwave phases, and between mesocosm site (Table 4.2). At both sites, higher salinity (40 ppt) generally lead to higher nutrient concentrations (SRP, TP, TN) and TSS, and lower water clarity. Mersin, compared to Ankara, exhibited higher chl-a, nutrient levels, and greater changes across the heatwave phases, especially in 40 ppt. During the heatwave (HW), nutrients such as SRP and TP increase significantly, particularly in Mersin, with further rises post-HW.

Table 4-2 Temperature (temp), Secchi depth (Secc), Chl-a, total suspended solids (TSS), ph, alkalinity (Alk), soluble reactive phosphorus (SRP), NO_3, total phosphorus (TP) and total nitrogen (TN) across mesocosm sites, salinity levels and heat treatments (Temp).

	Ankara											
	4 ppt						40 ppt					
Temp	NO	NO	NO	YES	YES	YES	NO	NO	NO	YES	YES	YES
Phase	1Pre HW	2 HW	3 Post HW	1Pre HW	2 HW	3Post HW	1Pre HW	2 HW	3Post HW	1Pre HW	2 HW	3Post HW
Secc	92	102	107	82	100	117	106	83	70	114	88	78
Chl-a	12	16	12	24	13	7	28	52	62	20	49	75
TSS	18	13	13	18	14	10	60	154	189	45	80	102
pH	9.89	10.15	10.18	9.6	9.87	10.12	9.2	9.7	9.7	9.03	9.4	9.24
Alk	5.43	6.43	5.23	4.55	5.5	5.46	4.08	5.14	4.78	3.34	3.74	3.73

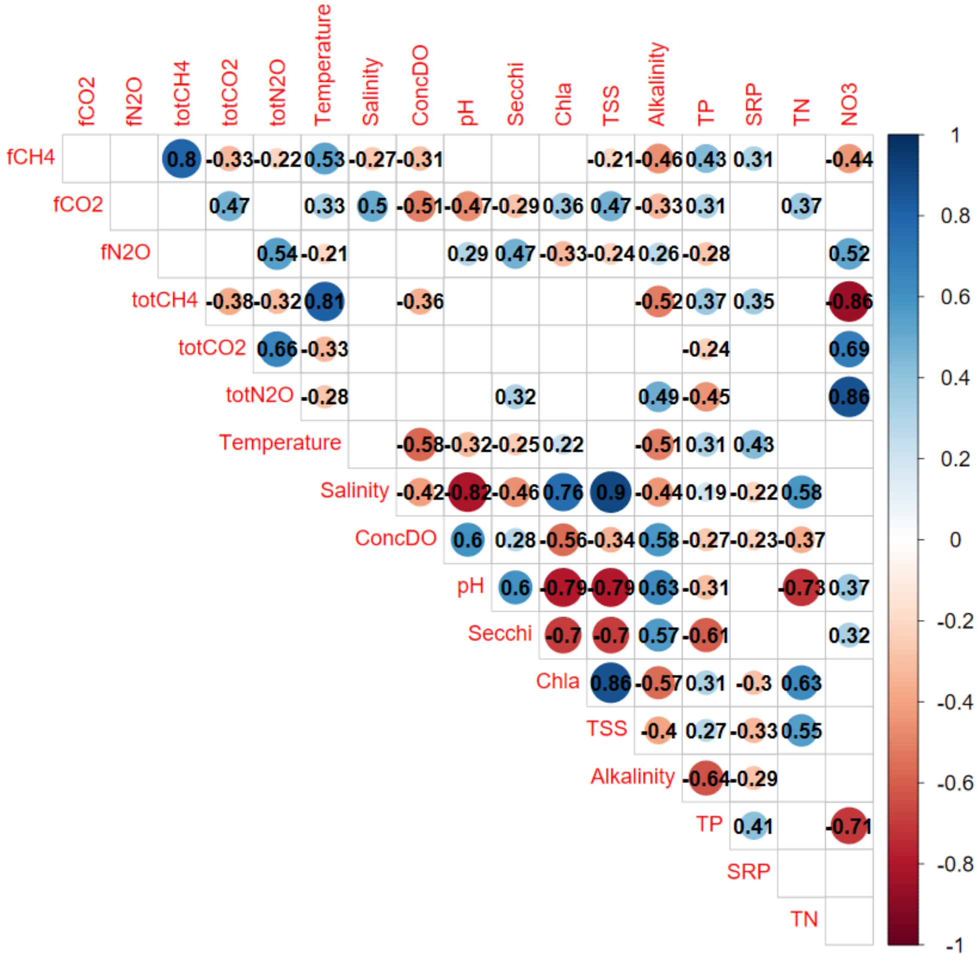
SRP	15.9	12.5	10.8	18.4	20.9	21.1	23.8	17.4	15.4	21.9	18.1	16.5
NO_3	670	347	210	534	204	72	439	138	454	595	168	384
TP	32	42	43	46	44	54	52	64	75	35	57	66
TN	990	737	1098	954	716	929	1340	1309	1835	1305	1233	1670

	Mersin											
	4 ppt						40 ppt					
Temp	NO	NO	NO	YES	YES	YES	NO	NO	NO	YES	YES	YES
Phase	1Pre HW	2 HW	3 Post HW	1Pre HW	2 HW	3Post HW	1Pre HW	2 HW	3Post HW	1Pre HW	2 HW	3Post HW
Secc	75	78	106	85	82	111	68	40	23	65	44	25
Chla	41	12	5	29	15	7	70	128	100	112	141	125
TSS	19	10	7	17	11	9	72	194	303	71	138	284
pH	10.1	10.36	10.3	10.03	10.03	9.96	9	8.74	9	8.85	8.43	8.71
Alk	2.88	3.1	3.47	2.93	2.75	3.21	1.49	1.44	2.45	1.38	0.94	1.69
SRP	25	59.1	141	31.9	66.9	120.6	20.2	20.1	16	17.4	28.5	32.2
NO_3	NA	94	22	NA	50	30	NA	12	29	NA	17	18
TP	121	162	304	128	221	387	129	283	359	123	207	281
TN	NA	890	725	NA	941	846	NA	2098	386	NA	2293	1125

Pairwise correlations displayed considerable variability. Both fCH_4 and $totCH_4$ were significantly correlated with temperature and TP, which is a proxy for organic matter. The temperature association was considerably higher for $totCH_4$. Conversely, fCH_4 significant negative associations were salinity, DO, TSS, alkalinity, and NO_3 with the latter was more significant and negative for NO_3.

fCO_2 were positively associated with temperature, salinity, Chl-a, TSS, TP and TN. On the other hand, it was negatively related with DO, pH, Secchi tranparency, and alkalinity.

fN_2O was negatively related with temperature, Chl-a, TSS, and TP, while it showed significant positive correlations with pH, Secchi transperency, alkalinity and NO_3.



	fCO2	fN2O	totCH4	totCO2	totN2O	Temperature	Salinity	ConcDO	pH	Secchi	Chla	TSS	Alkalinity	TP	SRP	TN	NO3
fCH4			0.8	-0.33	-0.22	0.53	-0.27	-0.31				-0.21	-0.46	0.43	0.31		-0.44
fCO2				0.47		0.33	0.5	-0.51	-0.47	-0.29	0.36	0.47	-0.33	0.31		0.37	
fN2O					0.54	-0.21			0.29	0.47	-0.33	-0.24	0.26	-0.28			0.52
totCH4				-0.38	-0.32	0.81		-0.36					-0.52	0.37	0.35		-0.86
totCO2					0.66	-0.33								-0.24			0.69
totN2O						-0.28				0.32			0.49	-0.45			0.86
Temperature								-0.58	-0.32	-0.25	0.22		-0.51	0.31	0.43		
Salinity								-0.42	-0.82	-0.46	0.76	0.9	-0.44	0.19	-0.22	0.58	
ConcDO									0.6	0.28	-0.56	-0.34	0.58	-0.27	-0.23	-0.37	
pH										0.6	-0.79	-0.79	0.63	-0.31		-0.73	0.37
Secchi											-0.7	-0.7	0.57	-0.61			0.32
Chla												0.86	-0.57	0.31	-0.3	0.63	
TSS													-0.4	0.27	-0.33	0.55	
Alkalinity														-0.64	-0.29		
TP															0.41		-0.71
SRP																	
TN																	

Figure 4-4 Pearson’s correlations between diffusive (fCH_4, fCO_2, and fN_2O) and total ($totCH_4$, $totCO_2$, and $totN_2O$) GHG emissions and limnological variables. temperature (°C), salinity (ppt), ConcDO: dissolved oxygen (mg/L), Secchi (cm), TSS: total suspended solids (mg/L), TP: total phosphorus, SRP: soluble reactive phosphorus, TN: total nitrogen, and NO_3. Circle size indicates significance level, with larger circles representing lower *p*-values (more significant correlations). Correlations with $p > 0.1$ are not shown on the table.

DISCUSSION

As detailed in Chapter 3, methodological limitations associated with chamber-based measurements led to unreliable $totCO_2$ flux estimates. Consequently, only diffusive

CO_2 fluxes (fCO_2) were considered for further analysis. Overall, the data reveals limited variability in GHG fluxes (CH_4, CO_2, N_2O) across sites, salinities, and heatwave phases. CH_4 and N_2O fluxes demonstrate considerable fluctuations, particularly in Mersin site, which has higher average temperatures. fCO_2 consistently indicate carbon uptake, with minimal impact from the heatwave. The changes in CH_4 and N_2O fluxes suggest a complex response to environmental conditions, potentially driven by site-specific factors and salinity levels.

fCH_4 were elevated in low-salinity mesocosms and at the warmer Mersin site, consistent with previous studies highlighting the stimulatory effect of temperature (Aben et al., 2017) and inhibitory role of salinity (Bartlett et al., 1985) on CH_4 production. In both sites fCH_4 and $totCH_4$ declined towards the end of experiment, likely reflecting the effect of temperature, and possibly the seasonal succession in the microbial community. Despite the pronounced temperature related fCH_4 differences between sites, the heatwave event did not significantly influence fCH_4 fluxes within site, while it created a significant effect on $totCH_4$, only in Ankara mesocosms. This could be attributed to several reasons.

The simulated heatwave, occurring at the end of summer (Özkan et al., 2023), induced only a gradual temperature increase, potentially limiting its impact on microbial communities and ecosystem processes. Consequently, the heatwave’s influence on CH_4 dynamics was minimal. In the case of Ankara, the heatwave may have counteracted the natural temperature decline, leading to a more pronounced emission response. Several factors may have contributed to the muted response of CH_4 emissions to the heatwave. Increased temperature can stimulate both CH_4 production and oxidation pathways, potentially offsetting the overall effect. Additionally, the presence of macrophytes, more abundant in low-salinity mesocosms, can enhance CH_4 oxidation, further complicating the relationship between temperature and CH_4 emissions. The observed heterogeneity in CH_4 emissions among replicates, particularly evident in the 4 ppt heated tanks where a consistently high emission mesocosm drive the average flux, was due to the influence of unaccounted factors or experimental variability.

Finally, the strong negative correlation between NO_3 concentrations and CH_4 emissions suggests potential competition between methanogens and denitrifying bacteria. However, the exact mechanisms underlying this relationship, including the potential role of coupled methanotroph-denitrifier processes, require further investigation.

In the case of CO_2 emissions, mesocosms showed a surprisingly minor response to the heatwave, with impact on high salinity mesocosms were slightly more prominent, this pattern was likely influenced by the reduced macrophyte dominance in these systems, which may have contributed to lower ecosystem stability. The muted response to the heatwave may be related to the relatively short duration of the heating event, as it is discussed in the Chapter 5. Significant positive associations with salinity, TSS and Chl-a were also relevant with the macrophyte dominance, as high salinity mesocosms lack the macrophytes.

Higher variability of fN_2O in higher salinity in both sites, and relative stability in the low salinity, plant dominated tanks suggest a stabilizing effect of macrophytes also on the N_2O emissions. The strong association between NO_3 and negative association with temperature suggests N_2O emissions were the result of the dynamic balance between production and consumption of N_2O, as detailed in the Chapter 3.

CONCLUSION

The simulated heatwave event had a limited impact on overall GHG emissions, particularly for CH_4. While temperature is a primary driver of microbial processes influencing GHG production, the relatively short duration of the simulated heatwave in this study may not have been sufficient to induce pronounced changes in ecosystem metabolism. However, the observed decrease of N_2O fluxes in the warmer Mersin site highlights the potential for more significant impacts under prolonged or more intense heatwave conditions. The complex interplay between temperature, salinity, and other environmental factors govern GHG emissions from saline lakes.

Future research focusing on the long-term consequences of heatwaves and their interaction with other stressors is necessary to gain a better understanding of the fragility of these ecosystems to climate change.

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DISCUSSION AND CONCLUSIONS

This doctoral research aims to investigate the complex interactions between climate change, land use pressures (primarily agriculture) in driving GHG dynamics within saline lake ecosystems and other lentic environments experiencing salinization. A multifaceted approach, encompassing historical data, literature reviews, remote sensing, field surveys, and controlled experiments, is employed to comprehensively address this complex topic. From an ecosystem ecology perspective, our study examines the ecosystem-level impacts of climate change and increasing agricultural pressures. These factors interact to influence biogeochemical processes, altering carbon and nitrogen cycles within lake ecosystems and as an extension of these. Major consequences include salinization, intensified eutrophication as a result of agricultural intensification, lake shrinkage, and subsequent biogeochemical and ecological alterations.

The main study region is the predominantly shallow saline lakes that are situated in west central Türkiye (the Burdur and Konya Closed Basins), and the southern coast of Türkiye. This region is representative of the Mediterranean region, a highly vulnerable area to climate change (Giorgi et al. 2006; IPCC, 2013). Rising temperatures, reduced precipitation, and more frequent droughts are expected to intensify in this already arid region and the intensity and frequency of extreme weather events are also expected to rise (IPCC, 2013; Wang et al., 2023) while agricultural water use further exacerbates water scarcity. Agricultural intensification is driven by higher need for food production but also global market demands, as evident from the rising share of so-called money crops (e.g., corn and sugar beet) in agricultural production. The Konya Basin, a prime example, is experiencing lake dry outs due to these combined pressures (Chapter 1). This trend is indicative of a future marked by water scarcity in the Mediterranean and semiarid climates. Similar challenges are evident in other semiarid regions, such as California, where groundwater levels are declining, and lakes are under stress (California's

Groundwater Live: Groundwater Levels, 2021). These changes have already had severe consequences, including habitat degradation, ecosystem health decline, and a reduction in ecosystem services, and our research suggests that this trend will intensify, leading to even more extreme changes. Thus, this thesis aimed to provide a broader understanding of GHG dynamics in such environments under environmental change. By investigating the interactions between climate change, land use pressures, and GHG emissions, we aimed to inform policies to mitigate the negative impacts on saline lake ecosystems and promote their resilience.

Our research examined GHG dynamics in a diverse array of saline ecosystems, including coastal shallow lakes, deep tectonic lakes, hypersaline salt pans, and endorheic brackish lakes, spanning various regions, origins, salinities, trophic states, hydrology and morphologies. We focused on understanding how changes in these ecosystems affect GHG emissions. Since GHG dynamics are closely intertwined with carbon and nitrogen cycles, lake metabolism, nutrient dynamics, biogeochemistry, and hydrological regimes, we incorporated these factors into our investigation. Following a descriptive analysis of GHG emissions of natural lakes (Chapter 2), we conducted mesocosm experiments, which can be considered as simplified simulations of natural lakes to gain a more mechanistic understanding of GHG dynamics (Chapter 3 and 4). These experiments, including a salinity gradient experiment, a heatwave experiment, and additional short-term tests, allowed us to isolate factors like salinity, climate, and temperature effects and provided a process-oriented understanding of GHG dynamics in saline aquatic environments. They also enabled us to investigate and differentiate the effects of various emission pathways, such as ebullition, which requires continuous sampling and may not have been feasible in snapshot studies.

Our study, through the investigation of land use changes, climate record trends, field GHG measurements, and long-term mesocosm experiments (including salinization and heatwave experiments), identified five distinct ways in which environmental changes can influence GHG dynamics within aquatic ecosystems. These factors are interconnected and can interact in complex ways, to unexpected ends:

1. Temperature/temperature rise: Temperature plays arguably the most crucial role in GHG dynamics, directly influencing microbial processes and chemical reactions that govern GHG production and emission.
2. Eutrophication and nutrient enrichment: Excessive nutrient inputs through agricultural runoff can stimulate primary production and organic matter accumulation, providing fuel for respiratory processes, leading to changes in microbial communities and biogeochemical processes that affect GHG emissions.
3. Salinity/salinization: Increased salinity can alter microbial communities, affect enzyme activities, and modify aquatic chemistry, impacting GHG dynamics.
4. Community/ecosystem alterations: Shifts in aquatic communities, driven by factors like temperature, eutrophication, and salinization, can have cascading effects on biogeochemical processes and GHG emissions.
5. Lake area losses: Reductions in lake area decrease water depth, increases internal nutrient concentrations, and lead to habitat fractionation, influencing microbial communities and GHG dynamics.

In this final discussion section, we examine each factor individually and their interactions to understand how environmental changes drive GHG dynamics and draw conclusions This synthesis will provide valuable insights for researchers and policymakers.

Temperature/Temperature Rise

Temperature is a primary driver of respiratory processes within aquatic ecosystems. By increasing metabolic rates of bacteria and plankton, it stimulates respiration, including oxygen respiration (leading to CO_2 production) (Allen et al., 2005) and anaerobic respiratory processes like methanogenesis (producing CH_4) (Aben et al., 2017) and denitrification/nitrification (Bloemerts and Vries, 2009). Consequently, a rise in temperature generally results in increased GHG fluxes when considered in isolation. This aligns with existing research (Aben et al., 2017; DelSontro et al., 2016; Yvon-Durocher et al., 2010) indicating that temperature dependency alone can lead to higher CH_4 emissions.

Our mesocosm experiments revealed that temperature was a primary driver of CO_2 emissions, diffusional and ebullitive CH_4 fluxes across various timescales, while N_2O fluxes exhibited a more complex response. CO_2 and CH_4 fluxes, particularly ebullitive CH_4, were strongly positively correlated with temperature (Chapter 3). General decline of CH_4 fluxes towards winter (Chapter 3, 4) corroborated with this observation. In the warmer Mersin site (8-10°C higher than Ankara), average total CO_2 and CH_4 fluxes were higher than in Ankara. Additionally, CO_2 and CH_4 emissions in Mersin were more sensitive to temperature changes, suggesting that a given temperature increase would result in a larger GHG response in warmer regions. Even more so, ebullitive CH_4 emissions were more responsive to temperature changes than diffusive CH_4, aligning with the previous research (e.g., DelSontro et al. 2016; Qi et al., 2024). This suggests that warmer climates may experience more significant CH_4 emissions in response to climate change. In Ankara, ebullition was less prominent, with diffusive fluxes accounting for approximately 50% of total CH_4 emissions. Conversely, in Mersin, ebullitive fluxes were much higher (83% of total on average) and more variable (2 to 100 times higher than diffusive flux) across salinities, emphasizing the importance of temperature. Our hypothesis in Chapter 4 suggested that short-term temperature spikes, like heatwaves, could trigger system alterations due to metabolic responses. While not observed in our experimental lakes, repeated tests with similar setups indicated that such effects might be relevant over longer periods e.g., over 30 days, (see 5.2.1 below).

In contrast to CO_2 and CH_4, N_2O emissions exhibited a more complex response to temperature, a previously reported phenomenon (Dijkstra et al., 2012). In the same site, N_2O fluxes were negatively associated with temperature, with colder temperatures generally leading to higher N_2O emissions. N_2O emissions in the season end will likely increase only as a response to temperature, as regression analysis (Chapter 3, Table 4), PCA results (Chapter 3: Fig 3-6), and Pearson pairwise correlation (Chapter 3: Fig 3-5; Chapter 4: Fig 4-7) also reveal the negative associations. This can be attributed to the multi-step nature of denitrification, the primary pathway for N_2O production. While complete denitrification results in N2 production, incomplete denitrification leads to N_2O release. This explains why declining temperatures at the end of the season promote N_2O formation, as the optimum temperature conditions for complete denitrification resulting in N_2 formation is 15-35°C and at temperatures below 10°C the complete denitrification final step that converts N_2O to N2 is significantly inhibited (Liao et al., 2018). Regression analysis, PCA results, and pairwise correlations consistently revealed this negative association between N_2O emissions and temperature. However, our analysis also indicated a positive effect of the warmer Mersin site on N_2O emissions, seemingly contradicting other findings. This inconsistency can be explained by the fact that N_2O is an intermediate product, and its net emission is determined by a stochastic balance between its production and consumption through microbial activities. In warmer conditions, N_2O production increases, and while consumption may also rise, the overall balance determines net N_2O emissions (Chapter 4).

In addition to its direct effects on GHG emissions, temperature can indirectly influence aquatic ecosystems through its impact on species distribution, food web interactions, and biogeochemical processes. Rising temperatures can push species beyond their thermal tolerance limits, leading to local extinctions and shifts in species distribution. This is particularly concerning in low latitude lakes, where extreme temperature increases can occur more rapidly due to lower natural variability in temperature and exceeding conditions will be more readily attained (Huang et al., 2024). These changes can disrupt food webs and trophic interactions, leading to ecosystem shifts that may influence biogeochemical processes. Furthermore, higher temperatures can intensify thermal stratification, limiting oxygen supply in deeper waters and favoring CH_4 production (Davidson et al., 2024). Such conditions are expected to reach to a no analogue conditions (Huang et al., 2024) contribute to harmful algal blooms and fish kills, further altering the ecosystem structure. In summary, a rise in temperature can directly stimulate GHG emissions and indirectly influence other ecosystem processes, ultimately impacting the overall health and function of aquatic ecosystems.

Salinity/Salinization

Salinity exerted a primary control over all GHG emissions through various pathways. The strong effect of salinity over CH_4 emissions was apparent in our snapshot study (Chapter 2) and is in line with the previous research. Studies dating back to the 1970s (Barnes & Goldberg, 1976; Bartlett et al., 1987) have demonstrated that salinity suppresses CH_4 emissions through mechanisms involving sulfate competition and SRB activity. In presence of SO_4, SRB effectively outcompete methanogens for organic substrates, as they produce more energy from the same amount of organic substrate, following the thermodynamic ladder of geomicrobiology (Bethke et al., 2011). This competition, rather than direct CH_4 oxidation, primarily suppresses CH_4 production as it was also suggested by Barnes and Goldberg (1976). Later studies focusing on the sedimentary interaction between SRB and CH_4 formation (Kuivila et al., 1989) demonstrated that CH_4 production commences at a certain depth following the depletion of SO_4 in the interstitial water. However, above this depth, CH_4 production is inhibited and exhibits high sensitivity to SO_4 concentrations at different levels. Previous research has shown that (e.g., see Poffenbarger et al., 2011) even relatively low salinity levels can significantly inhibit diffusive CH_4 emissions, while under this threshold CH_4 emissions are remarkably higher and showed a significant variability, as also was the case in our snapshot study (Chapter 2). On the other hand, in the mesocosm salinity gradient experiment (Chapter 3) the high salinity levels in mesocosms already exceeded this inhibitory threshold, which may explain why salinity did not appear to be a significant factor in regression models, except in one (Ankara specific model).

Perhaps the most remarkable finding of the study is the co-occurrence of near-zero, even occasionally slightly negative diffusional CH_4 fluxes with the minor yet consistent ebullition (Chapter 3). This suggests that while competition by the SRB is the primary control for overall CH_4 production, methanotrophic activity, stimulated plausibly by the SO_4 availability, is also significant as this contrasting observation necessitates the removal of dissolved CH_4 in the water through oxidative processes. Dissolved CH_4 in the water is oxidized in the redox transient zone (Bastviken et al., 2002) while moving upwards from the sediment, leading to near-zero diffusional fluxes. Involved CH_4 oxidation pathways likely comprise aerobic oxidation of methane and the coupled processes between SRB and methanotrophs (S-AOM) (Lambrecht et al., 2020).

Salinity also significantly influenced CO_2 and N_2O emissions (Chapter 2 and 3). The negative effect on CO_2 may be attributed to salinity-induced biological stress, reducing microbial activity (Ollivier et al., 2019). In addition to negative effect in regression analyses in Chapter 2 in natural lakes, in Chapter 3, mesocosms with high salinity (over 23 ppt) showed more negative diffusional N_2O fluxes in natural lakes, with the effect being more consistent in Mersin mesocosms. In line with the negative association between salinity and N_2O fluxes in Chapter 2, this could be attributed to the direct salinity inhibition over nitrification pathways; specifically, the conversion of NO_2^- to NO_3^- is more strongly inhibited than the conversion of NH_4^+ to NO_2^-, leading to an accumulation of NO_2^- in saline soils, which can enhance N_2O, Salinity affects the activity of nitrifying bacteria. Also, salinity suppress the overall microbial activity involved in nitrification and denitrification, thereby reducing N_2O emissions (Fagodiya et al., 2022; Li et al., 2020).

Given these observations presented, salinization will likely decrease GHG emissions, particularly CH_4 emissions from the lake ecosystems, significantly mitigating the GWP of the emissions from the lake ecosystems. However, this effect can be complicated by other factors, such as eutrophication and temperature. Increased nutrient and organic matter loading, and eutrophication will likely increase the N_2O and CO_2 emissions, potentially counteracting the positive effects of salinization on GHG reduction. Furthermore, recent studies suggest that the interaction between salinization and temperature can influence methanogen activity and CH_4 emissions. In unrestored saline ponds salinization can strengthen the temperature dependence of the methanogens, through stimulation of alternative methanogenic pathway, thereby counteracting the decline in CH_4 emissions with salinization (Chamberlain et al., 2020).

Beyond its direct effects on GHG emissions, salinity can have broader implications for aquatic ecosystems (Jeppesen et al., 2023). Salinization stress can inhibit primary production, alter the balance between respiration and production, shifting the ecosystem towards a more heterotrophic state. Another major impact of salinization is species richness reduction and food web alterations (Jeppesen et al., 2023; Vidal et al.,2021). While this have many grave, long-term implications on the functioning of ecosystems, one immediate risk is the decline or extinction of macrofauna and submerged vegetation. This can severely impact ecosystem services, as macrophytes play crucial roles in habitat provision, water quality improvement, and nutrient cycling.

Nutrient enrichment/Eutrophication

Elevated nutrient concentrations and eutrophication can severely impact lake ecosystems. Nutrient enrichment leads to organic matter (OM) production, which serves as the substrate of all respiratory processes, including O_2 respiration, SO_4 reduction, nitrification and denitrification, and methanogenesis.

The difference between coastal and inland lakes can largely be attributed to their different nutrient levels (Chapter 2; Fig. 5-1). Coastal lakes with presumably shorter residence times generally have lower nutrient and DOC concentrations compared to inland saline lakes, which have higher residence time and an inclination to accumulate nutrient and organic matter along with dissolved minerals. (Fig 5-1). Field surveys and mesocosm experiments revealed that nutrient and OM concentration were the main drivers of CH_4, N_2O and CO_2. In natural lakes, DOC was the main driver of CH_4. In mesocosms, while we lack the direct DOC measurements, TP, also a proxy of OM abundance, was strongly associated with CO_2 and ebullitive CH_4 fluxes, corroborating with the previous research associating the high OM content/eutrophic conditions with elevated CH_4 emissions (Beaulieu et al., 2019). Regression analysis showed a strong association of CO_2 also with TP, in mesocosms.

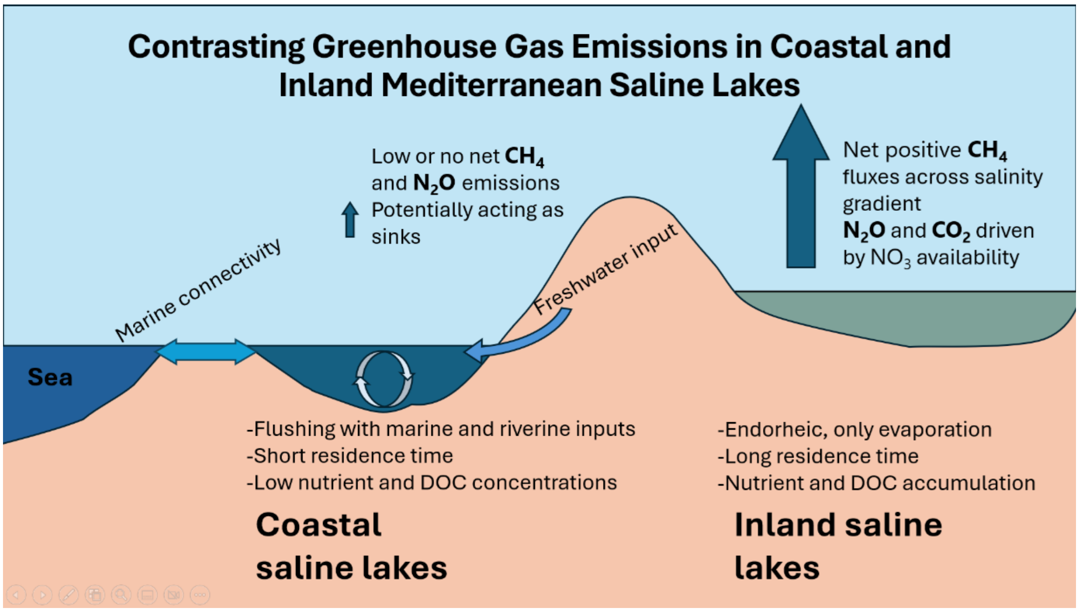

Figure 5-1 Graphical representation of the causes of the contrast between coastal and inland saline lakes.

However, we observed somewhat contrasting results between natural lakes and mesocosms regarding the drivers of CO_2 and N_2O emissions. While NO_3 concentration was the main driver of CO_2 and N_2O emissions in natural lakes, TP and TN were more important in the mesocosm studies. In addition, CO_2 fluxes were consistently negative in mesocosms but more variable and generally positive in the natural lakes.

This discrepancy between mesocosms and natural lakes can be attributed to the presence of allochthonous OM in natural lakes, which is terrestrially generated and transported from the catchment via runoff. Mesocosms, however, primarily contain autochthonous OM, which was produced exclusively in the water column. Thus, in mesocosms, OM is likely a limiting factor, restricting CO_2 emissions. In contrast, natural lakes receive significant amounts of allochthonous OM from the catchment, leading to higher DOC concentrations. A comparison of TP concentrations between inland lakes and mesocosms in Chapters 2 and 3 confirms that our mesocosms had lower TP levels than the natural lakes. This disparity in OM availability likely explains the observed differences in CO_2 emissions between the two environments. Furthermore, the absence of allochthonous organic matter in the mesocosms likely created a substrate limitation also for all N_2O, which could explain why TN, rather than NO_3, was a significant predictor of N_2O emissions in mesocosms. In natural lakes with higher organic matter availability, NO_3 might be the limiting factor. However, in mesocosms, organic nitrogen and organic matter in general were more likely to be limiting, leading to the observed patterns in Chapter 3.

The interaction between DOC and salinity can also influence GHG emissions. CH_4 flux was strongly associated with the DOC to salinity ratio Chapter 2, corroborating a recent study (Soued et al., 2024). High substrate availability can modulate the negative effect of salinity on CH_4 emissions by weakening the substrate competition, allowing methanogenesis and SRB to co-occur.

In addition to its direct effects, nutrient availability can interact with temperature to drive GHG emissions synergistically. A well-known example is the coupling between temperature rise and eutrophication. Davidson et al. (2018) demonstrated that nutrient enrichment combined with temperature treatment increased CH_4 ebullition by up to 17-fold in mesocosms. CH_4 emissions in natural lakes will continue to rise until the end of the century with the synergistic effects of increased average temperature and eutrophication (Beaulieu et al., 2019; DelSontro et al., 2016).

Beyond their direct effects on GHGs, nutrient enrichment and warming can also alter ecosystem structure and function, leading to increase in algal biovolume and diversity loss, phytoplankton community alterations, and taxonomic and functional reorganization of phytoplankton communities in lakes (Dory et al., 2023), influencing biogeochemical cycles and GHG dynamics.

Ecosystem alterations/community shifts/Macrophytes.

Ecosystem and community alterations, including species extinctions, biodiversity losses, changes in food web structure caused by these multiple stressors can significantly impact the functioning and biogeochemistry of lakes, potentially shaping their GHG dynamics. Findings from our field surveys and experiments highlight the crucial role of macrophytes in regulating GHG emissions. These findings also concur with the previous research that reveals the importance of submerged macrophytes on carbon burial and GHG mitigation (Brown et al., 2016; Fourqurean et al., 2012). Macrophytes are responsible for substantial uptake of CO_2 and consequential burial to the lake sediments in saline wetlands (Brown et al., 2016). They also oxygenate sediments (Desmet et al., 2011; Woodward and Hofstra, 2024), and they provide surface for methanotrophic bacteria (Heilman and Carlton, 2001), suppressing CH_4 production, promoting CH_4 oxidation and actively drawing CO_2 from the atmosphere. Our mesocosm experiments demonstrated that macrophyte-dominated ecosystems exhibited higher rates of CO_2 uptake in the water column, aligning with recent studies emphasizing the importance of macrophytes in carbon sequestration. While we didn't observe a direct correlation between macrophytes and CO_2 emissions in our natural lake regression models, the negative correlation between CO_2 fluxes and plant volume index (PVI) in coastal lakes suggests a similar relationship.

Macrophytes also contribute to ecosystem resilience by competing with phytoplankton for nutrients and mitigating eutrophication. The theory of alternative stable states in shallow lake ecosystems posits that macrophytes can help maintain clear water conditions in lakes, even under conditions of nutrient enrichment (Scheffer et al., 1993). However, more recent studies suggest that long-term exposure to high nutrient loading, the alternative states tend to converge, finally reflecting the nutrient conditions (Davidson et al., 2023) of lakes, which can in the long run damage macrophyte communities, leading to a loss of their GHG mitigation benefits. In addition to eutrophication, salinization can further exacerbate the negative impacts on macrophytes, as many species have limited salinity tolerance. The decline of macrophytes due to salinization in turn can intensify eutrophication, stimulate GHG emissions, and negatively affect other aquatic organisms like fish and zooplankton, ultimately impacting carbon and nitrogen cycles.

Lake area loss/Desiccation.

Overutilization of water resources for irrigation, combined with climate warming, is expected to increase the frequency and severity of temporary lake dry outs, amplify the water level fluctuations or complete desiccation of lakes. Seasonal desiccation affects 18 % (~800000 km^2) of the global surface area of inland waters, exposing littoral sediments to the atmosphere, and this rate is expected to rise (Pekel et al., 2016). These changes will cause several outcomes in terms of biogeochemical processes and GHG dynamics of lakes (Beaulieu et al., 2018; Cobo et al., 2024; Pouladi et al., 2022). The first and immediate effect is the exposure of previously submerged sediment to the atmosphere, which causes the rapid oxidation of OM in the sediment (Catalan et al., 2014; Marcé et al., 2019; Obrador et al., 2018). Although it is often excluded from GHG estimates from lakes, this rapid oxidation can account for 6 % of CO_2 emissions from lakes (Keller et al., 2020).

Lake desiccation has also significant indirect impacts on the biota and biogeochemical processes of aquatic ecosystems. It alters microbial communities, carbon exchange, and nutrient dynamics. Microbial communities in littoral zones, which are critical for processing organic carbon, may experience shifts in composition due to varying water levels. The drying process can alter sediment chemistry, impacting the availability of nutrients in the water column. This change can lead to decreased phosphate adsorption capacity in sediment. Prolonged desiccation can reduce taxonomic richness in macrophytes and benthic invertebrates, potentially disrupting food webs and ecosystem functions, including nutrient cycling and habitat provision for other species (de Vicente, 2021), further diminishing the potential mitigation role of macrophytes. The long-term effects of lake desiccation encompass a cascade of ecological and biogeochemical responses that can fundamentally alter the structure and function of aquatic ecosystems.

Understanding these impacts is crucial for effective freshwater resource management in the context of climate change and increasing anthropogenic pressures.

Caveats and Limitations

There are two main caveats of the study is further discussed below, they add additional dimensions by highlighting the shortcomings and alternative insights to the study. First one is the contrasting findings about the effect of heating events. This finding is contrasting to the findings in Chapter 4, where short term heating did not elicit a significant GHG response. In this experiment we did see a shift in trophic structure of the mesocosm. But this study was conducted in only one site and also the duration and samplings are limited. Thus it can only give an idea about the response of the lakes to abrupt heating events.

The temperature effect on the trophic state of lakes

The temperature is arguably (Davidson et al., 2015) the most important factor at play in production and transfer of GHGs in aquatic ecosystems (Yvon-Durocher et al., 2010). Additionally, in previous experimental studies (Audet et al., 2017) heatwaves were demonstrated to have a significant effect on GHG dynamics. However in this study (Chapter 4), heatwave effects were mostly insignificant or minor. To understand the dynamics at play, we performed additional tests and measurements the following year in September-October, 2023, in Mersin mesososms.

Experimental design was identical to the one described in the Chapter 4 (two levels of salinity: 4 vs 40 ppt; two temperature levels: heated vs ambient; contant nutrient loading through weekly additions, same season), except the heating was 4.5 C instead of 6 C of the previous experiment. In the experimental period, 4 ppt mesocosms were completely covered with macrophytes (PVI: 100 %, *S. Pectinata*) while in 40 ppt mesocosms there were no macrophyte growth, as was in the case of heatwave experiment in Chapter 4. 1 month after heating started we started sampling the mesocosms with a real time photoacoustic GHG monitor (LumaSense, 1410i), fitted to a floating chamber. The samplings were carried out every afternoon (same hour with the previous year's GHG sampling) for one week, where fluxes were measured for 10-15 minutes in every tank to determine gas exchange rates.

Our heat treatment test revealed a significant rise in CO_2 emissions in 40 ppt mesocosms. Heated tanks exhibited an average CO_2 flux rate of 1 ppm min^{-1}, while unheated mesocosms showed a negative flux of 2.5 ppm min^{-1} while CH_4 and N_2O fluxes remained similar. However, in mesocosms with high macrophyte presence and low salinity, heating had no significant effect on CO_2, CH_4, or N_2O fluxes (Fig. 5.2.)

The shift from CO_2 sinks to net sources in heated mesocosms was accompanied by changes in pH, alkalinity, and dissolved oxygen levels, further corroborating the CO_2 emission pattern. Additionally, chlorophyll-a concentration remained unaffected by heating, suggesting that primary production did not change significantly while respiration rates increased, leading to a heterotrophic ecosystem. These findings align with previous research indicating that plankton-dominated ecosystems are more susceptible to heat alterations, resulting in elevated respiratory rates, shorter succession periods, and heterotrophic metabolism, which can contribute to CO_2 emissions.

In contrast to a previous experiment, this study employed a longer heatwave duration (30 days) with a less pronounced temperature increase. Despite the milder temperature difference, the extended heatwave period elicited a more pronounced ecosystem response, emphasizing the importance of both temperature and duration in driving ecological changes. This also highlights the crucial role of macrophytes in enhancing ecosystem resilience.

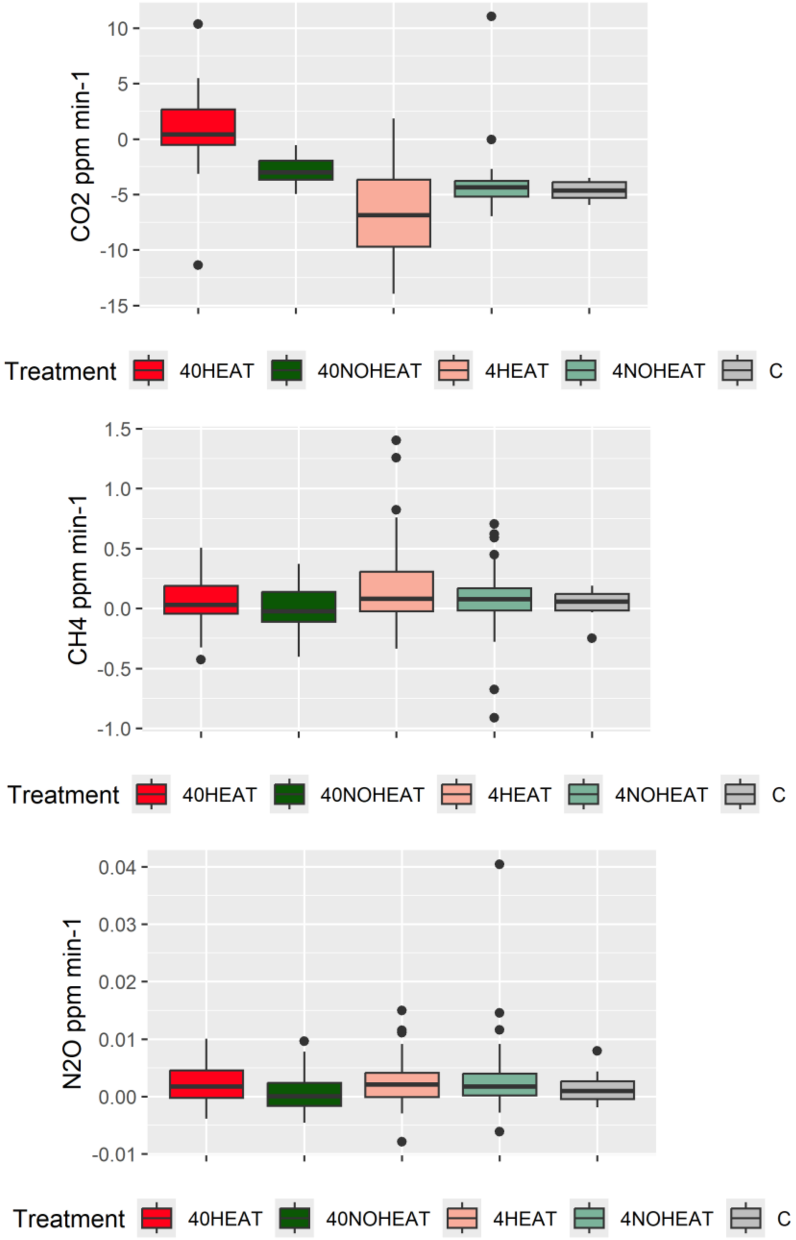

Figure 5-2 The gas emission rates obtained from high frequency chamber measurements.

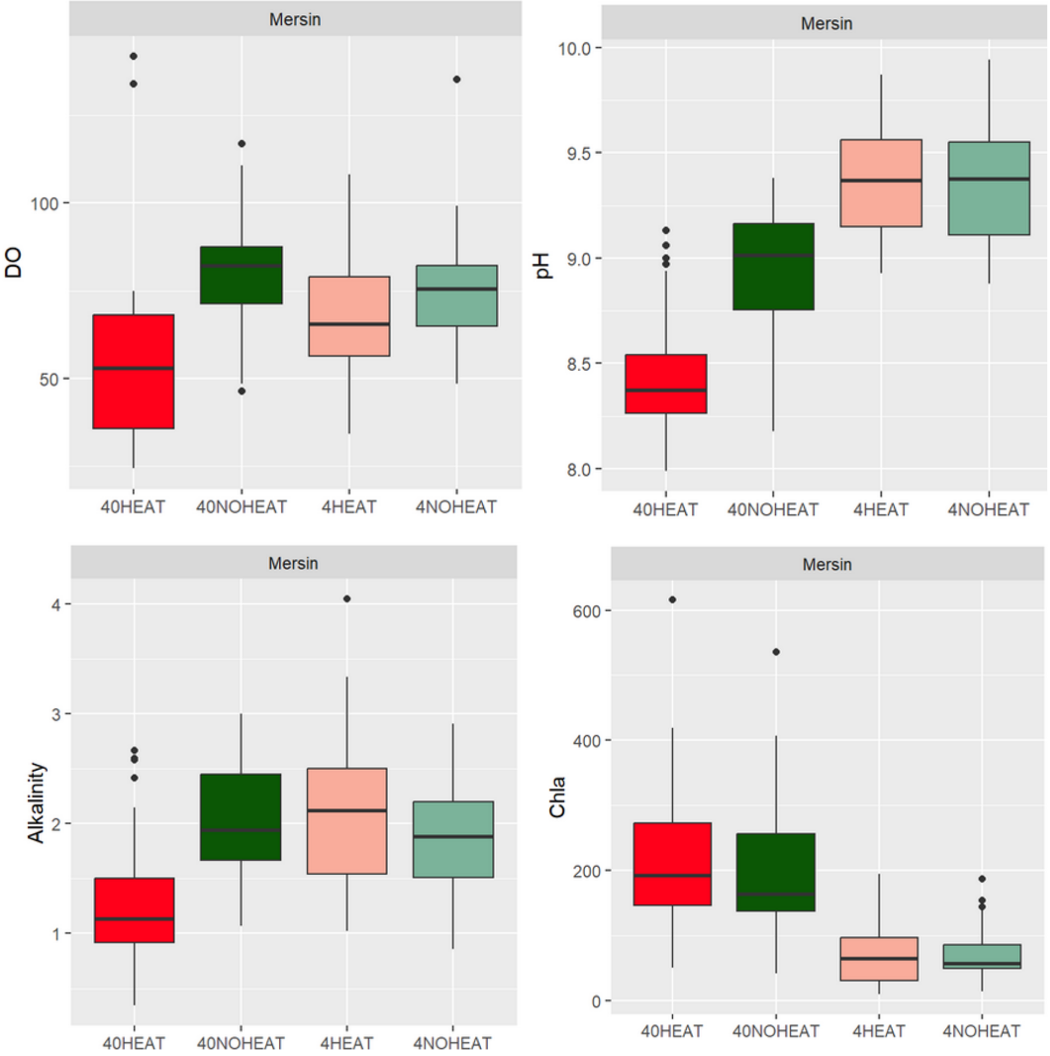

Figure 5-3 Relevant limnological parameters before and during the gas sampling.

Limitations of flux chambers

Flux chamber methods are advantageous in measuring diffusive fluxes, as they allow direct measurement of flux, compared to the methods deriving flux rates from dissolved gas concentrations (e.g., headspace), in which estimations of gas transfer rates can be challenging and variable depending on the chosen gas transfer model (Dugan et al., 2016). However, chambers are also prone to several limitations. Firstly, although they measure the flux from the water surface directly without a need for estimations, they can interfere with the wind stress, which is a major factor in diffusion of gases. Moreover, they perform best in short-term measurements but usually not appropriate in longer durations, and cause uncertainties. This uncertainties may stem from (i) back dissolution of the gases, (ii) microbiological uptake and release (e.g., for CO_2), (iii) biofouling of the gas and or other microbial activity within the chamber interfering with the results, and (iv) enclosure reaching to saturation with gas, (v) large animal interference (e.g., insects trapping in).

Gas back-dissolution following the events of ebullition can be potentially significant and in our samplings it likely played a significant role as well. In order estimate the rate of the gas loss back to water column, we conducted a standard gas spike experiment in October, 2023. For this we placed a floating chamber on three mesocosms (40 ppt, 4 ppt and freshwater) and connected the chambers to the LumaSense 1410i Gas Monitor. While taking continuous measurements we spiked the chambers with standard CH_4 to a final concentration of 600 and 120 ppm, three replicates for each (n=30). Results revealed that CH_4 loss in chambers was remarkably high, and rate of loss is dependent on the partial pressure of the gas. The loss rate were 2 to 3 ppm min^{-1} at 600 ppm initial, and 0.7 ppm min^{-1} at the 120 ppm (Fig. 5.4). This suggests that even a typically large ebullition event (e.g., 100-1000 ppm) captured by the chambers will dissipate in a matter of hours, if not minutes. Thus this additional test suggests due to this methodological incompatibility, we have potentially underestimated the ebullitive fluxes in the previous experiments, as six day long sampling periods are too long to capture ebullition events, except the ones that incidentally happened a short time ago before the sampling of the chamber. Thus our data is potentially an underestimation of total fluxes, and should not be fit for any upscaling study. Nevertheless, although ebullitions are episodic events, in a time period as long as a week, even the underestimated values should give an intercomparable estimate of the average ebullitive fluxes between the mesocosms of controlled and similar conditions.

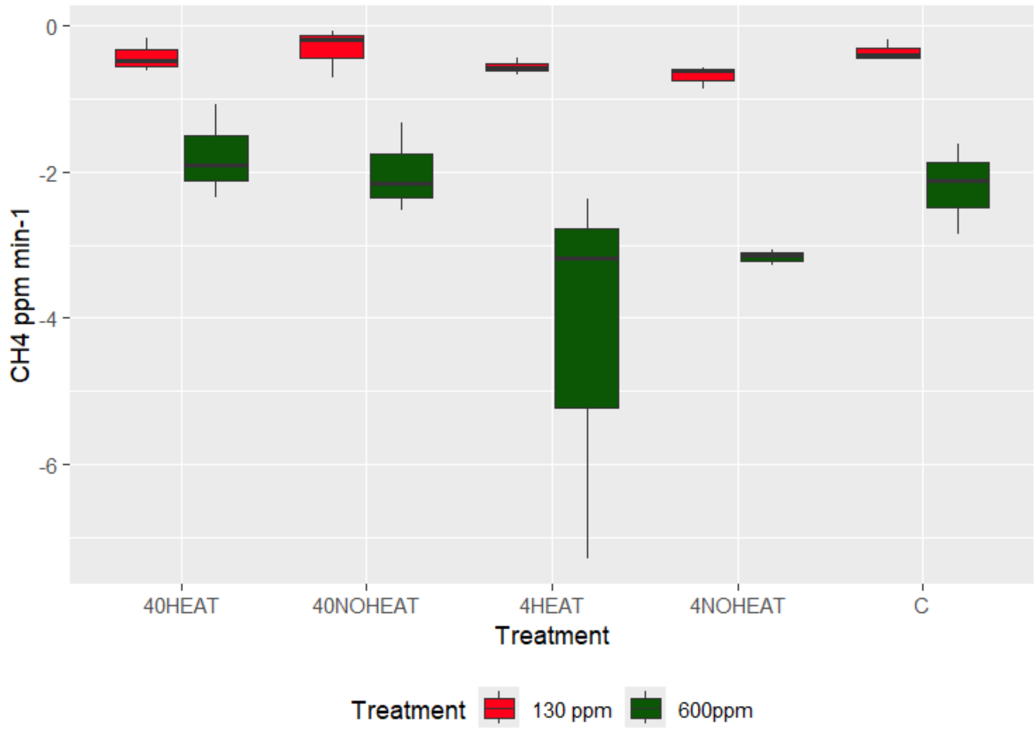

Figure 5-4 Loss rates of CH_4 in the chamber spike tests.

The other problem that may have interfered with our findings is the saturation issue. Gases with high solubility, such as N_2O, have lower partial pressures at equilibrium with the atmosphere, which means under a certain level, i.e., the partial pressure reaches the equilibrium in the chamber with concentration stabilized in the chamber, not allowing further buildup of gas, leading to an underestimation of emissions. This might have been a potential interference in three studies (Chapter 2, 3, 4) pN_2O had a mean maximum c. 0.8 ppm at various time scales (40 minutes to 6 days). This value indicates %100-160 saturation in the relevant temperature scales (20-35 C), and may cause an underestimation of flux. Fig. 5-5 shows a day long observation with real time gas monitor, where N_2O flux into the chamber coming to a halt around a similar value, potentially suggesting saturation interference.

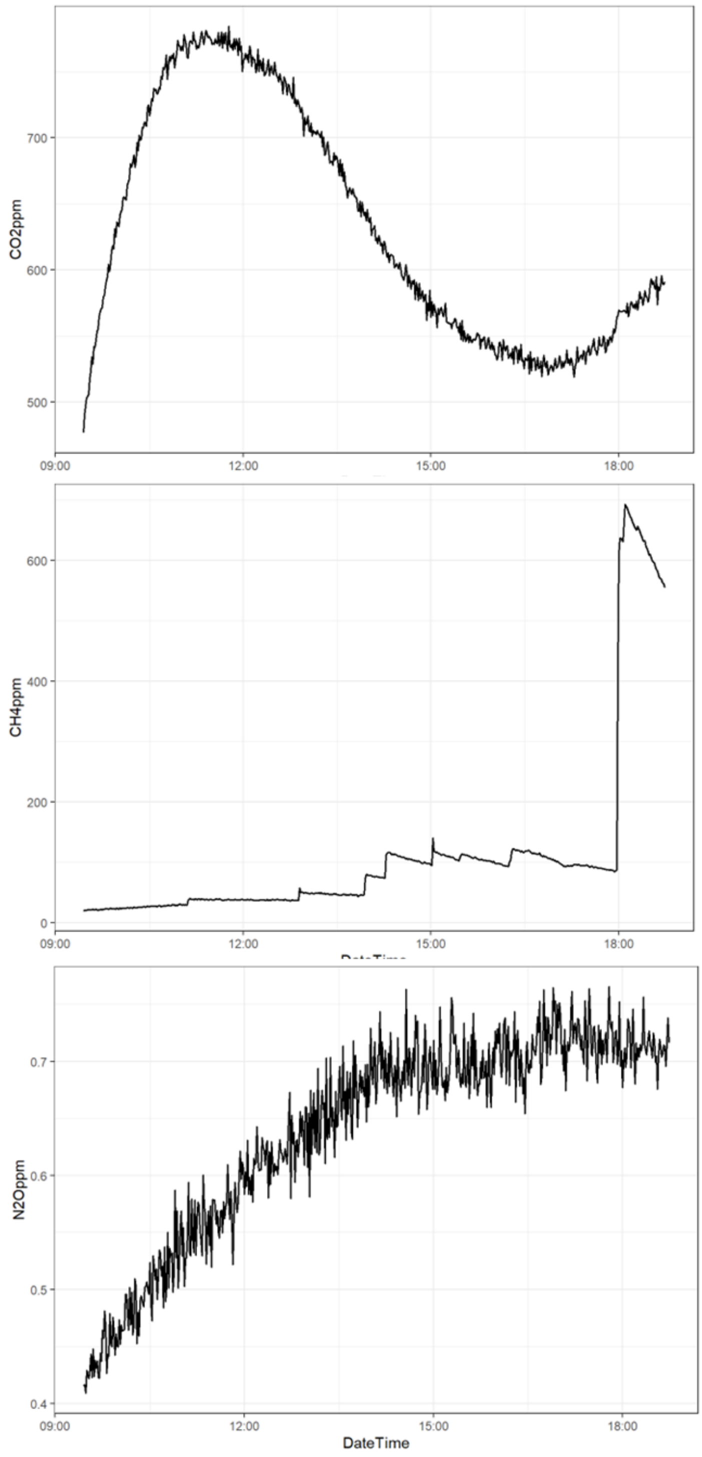

Figure 5-5 Daily patterns of chamber concentrations of CO_2, CH_4 and N_2O monitored by LumaSense GHG monitor. Note that CO_2 follows diurnal cycle, CH_4

increases through sporadic ebullition events, followed by stable decline, and N_2O becomes stabilized after a threshold.

Conclusions

Climate change and land use pressures are driving changes in GHG emissions from saline lakes. These changes are influenced by factors such as temperature, salinity, nutrient availability, and community composition. Temperature is a primary driver of GHG emissions, influencing respiratory processes and microbial activity. Higher temperatures can increase the frequency and intensity of ebullition, specifically in the warmer regions. Salinity exerts a significant influence on GHG emissions, primarily by suppressing CH_4 production and reducing diffusive and ebullitive emissions, and future salinization will likely reduce CH_4 emissions from the lakes, weakening the positive feedback loop of temperature rise and CH_4 emissions. Experimental studies have shown that CH_4 ebullition can be a minor yet non-negligible emission pathway in saline lakes, even when diffusive fluxes are near zero. Furthermore, CH_4 ebullition was likely underestimated in this study because (i) our floating chamber method is prone to largely underestimate ebullition because of the back dissolution of gases, and more importantly (ii) organic matter, the fuel of methanogenesis and other GHG production pathways, is limited to autochthnous organic matter in mesocosms, thus very limited compared to the natural lakes. These two factors together likely lead to underestimating the actual GHG emissions from the lakes, i.e., in natural lakes, the ebullitive fluxes may be much higher than observed in the mesocosms, further emphasizing the importance of ebullition in saline lakes. On top of that, rise in organic matter availability stimulate CH_4 even in hypersaline conditions, and potentially N_2O emissions. Lake level fluctuations, including temporary and permanent dry outs, also potentially lead to the release of stored carbon. Finally, macrophytes play a crucial role in regulating GHG emissions by sequestering carbon and providing habitat for methanotrophic bacteria. The combined effects of salinization, eutrophication, and lake desiccation can severely impact macrophytes, leading to their decline and loss. This can deteriorate ecosystem resilience and stimulate GHG emissions.

Future research

Addressing the underestimation of ebullitive fluxes due to gas back-dissolution is crucial for future research. Employing bubble traps and optimizing measurement frequency can improve data accuracy. Furthermore, the integration of sensor-based, real-time monitoring systems offers a promising approach to capture the dynamic nature of ebullition events and carbon cycling processes. While technological challenges remain, their implementation in controlled experimental settings is feasible. This advanced methodology will provide more precise estimates of ebullitive fluxes and enable a better understanding of diurnal carbon dynamics in aquatic ecosystems.

Building upon the findings of this study, future research may explore several research topics which are distinct but not necessarily mutually exclusive. Firstly, as a very important mediator of GHG cycles, impact of macrophytes can be a plausible research focus, including interaction of macrophytes with carbon cycles, nutrient uptake, oxygenation and GHG response to different macrophyte assemblages. Secondly, interactions between macrophytes, sediment and other biotic factors (e.g., macrofauna, zooplankton) can provide new insights into the effects of bioturbation on GHG dynamics. Lastly, the microbial response to expected or simulated environmental alterations in terms of traits, gene expressions might be of relevance.

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