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# Trophic status and metabolic rates of threatened shallow saline lakes in Central Spain: Providing diagnostic elements for improving management strategies

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A B S T R A C T

Shallow saline lakes in the La Mancha Húmeda Biosphere Reserve in Central Spain show diverse degrees of cultural and natural eutrophication, prompting urgent conservation measures. This study focuses on 17 representative lakes from the site to assess seasonal nutrient dynamics and their connection to plankton metabolism (photosynthesis and respiration) during two successive hydrological periods. Effect of environmental factors was evaluated on a combination of several response variables, demonstrating that source of the nutrient inputs (ranging from natural to anthropic) had the highest influence on the nutrients stoichiometry and metabolic rates. Regarding the source of eutrophication, the model demonstrated that effects of urban wastewaters exceed that of agricultural runoff, and moreover lead to more prolonged hydroperiods and contributes to desalination. Lakes affected by wastewater inputs or surrounded by volcanic lithology showed phosphorus enrichment in both water and surface sediments. Planktonic respiration rates in these cases closely correlated with photosynthesis, suggesting the utilization of algal-derived dissolved organic matter. Conversely, wastewater-free lakes, mainly fed by runoff, accumulated uncolored, likely recalcitrant dissolved organic carbon (DOC). These lakes exhibited a better-preserved condition, characterized by higher salinity, moderate metabolic rates, and lower production/respiration ratios compared to the previous state, implying a greater dependence on allochthonous organic matter. Enhancement of management strategies, which should consider salinity, volcanic lake vulnerability, and the multifaceted impacts of wastewater, will prove more effective in the conservation and restoration of these unique and fragile ecosystems.

## Introduction

The long-term sustainability of saline lakes is increasingly threatened by water extraction and climate change, as observed globally (Wurtsbaugh et al., 2020). This issue was previously highlighted by Williams (2002), who underscored the environmental threats to saline lakes worldwide, raising concerns that parallel those explored in this study—namely, changes in salinity and eutrophication as key drivers of ecological degradation. These prior studies emphasize the urgent need for targeted management and conservation efforts.

Shallow saline lakes in La Mancha Húmeda (Central Spain), a UNESCO Biosphere Reserve, are endorheic threatened systems, in which processes described previously converge (Camacho et al., 2017; Florín and Montes, 1999). Both cultural and natural eutrophication has led to an overall increase in nutrient availability in their basins, and most of them deserve urgent conservation and restoration actions. Lakes with high salinity levels, similar to those in La Mancha Húmeda, may serve as barriers against nutrient pollution due to specific interfaces, namely, the sediment-water interface and the freshwater-saltwater interface, yet still suffer from eutrophication when agricultural runoff intensifies N inputs (Valiente et al., 2022).

Shallow saline lakes from La Mancha Humeda are naturally temporary, which drives diverse process such as the patterns of nutrient transport in the catchment, the seasonal evaporative concentration of solutes and the productivity of the system (Camacho et al., 2017; Corrales-González et al., 2019; García-Ferrer et al., 2003). The hydroperiod of these lakes is the result of the transitional Mediterranean-continental climate condition of the area, which is characterized by warm and dry summers. Accordingly, seasonality plays an important role in the ecological functioning of these lakes compared to those from temperate

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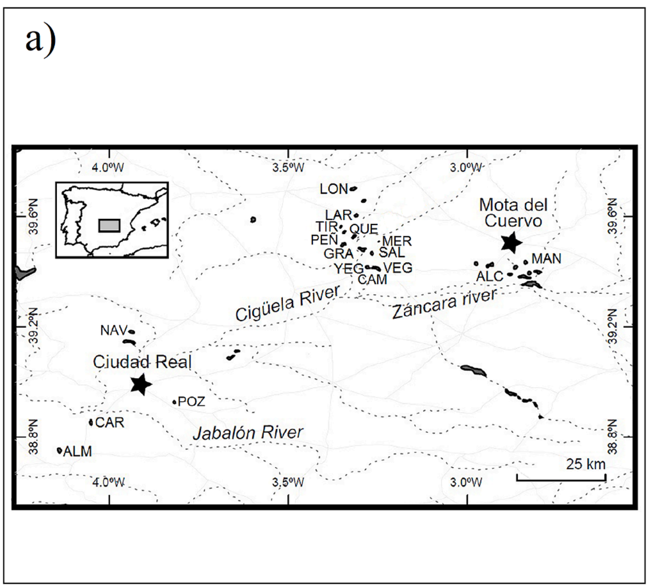
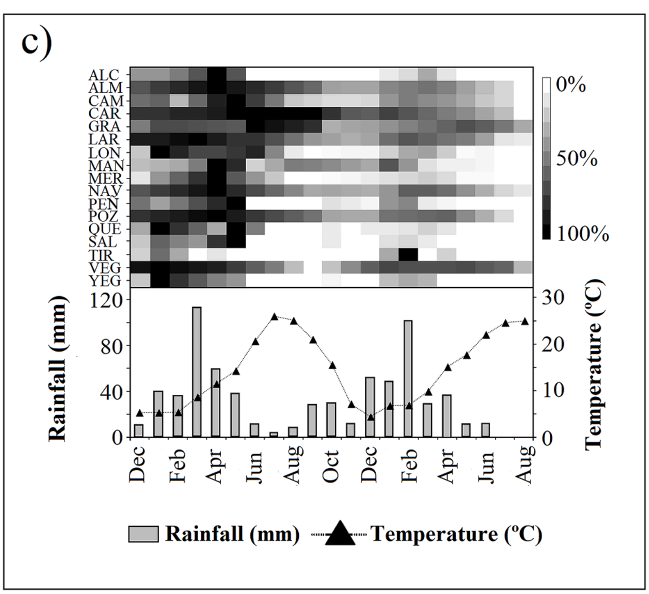
regions (Nõges et al., 2003). However, the occurrence of wastewater inputs in some of them has increased the hydroperiod while decreasing the salts content, as well as increasing the availability of nutrients compared to pristine conditions (Florín and Montes, 1999). Nevertheless, those lakes not affected by wastewaters may be impacted by the diffusive nutrient runoff originating from the catchments (Camacho et al., 2017), which are mainly dedicated to agricultural activities. Also, natural eutrophication resulting from the catchment lithology may play a role in some of these lakes. This is the case of the volcanic lakes from the location within the reserve known as Campo de Calatrava (Martín-Serrano et al., 2009), where the mechanisms allowing the phosphorus (P) immobilization in sediments are restrained compared to the non-volcanic lakes of the region (Cebriá and López-Ruiz, 1995; Corrales-González et al., 2019), thereby allowing a high availability of P in the water column.

The different hydrological scenarios explained above are expected to produce different trophic statuses in waterbodies (They et al., 2017). P is usually the limiting nutrient, but nitrogen (N) may also limit algal growth (Camacho and de Wit 2003a, 2003b). High amounts of P in sediments may cause persistent eutrophication due to a chronic release (Søndergaard et al., 2003), which represents a problem which can remain for many years. This could be the case of the lakes in La Mancha Húmeda, in which sedimentary P is mainly occluded to calcareous and iron compounds, or immobilized in organic forms, but it can be released to the water column if the redox potential decreases because of organic matter (OM) degradation (Corrales-González et al., 2019). Also in these waterbodies, the salinity of the water might indirectly promote P desorption by facilitating oxygen depletion, leading to decreases in redox potential due to the reduced solubility of oxygen with increasing ionic strength (Corrales-González et al., 2019). On the other hand, water salinity is known to slow the rates of dissolved organic matter (DOM) breakdown (Minor et al., 2006; Seo et al., 2008), thereby influencing the release of carbon (C) and N. All the previously mentioned are internal lake processes that, jointly with the anthropogenic pressures, are




b)

| Lake | Code | Surface (ha) | Max depth (cm) | Wastewater |
|---|---|---|---|---|
| Alcahozo | ALC | 70.00 | 21 | No |
| Almodovar | ALM | 20.15 | 99 | No |
| Camino de Villafranca | CAM | 142.66 | 78 | Yes |
| Caracuel | CAR | 66.16 | 98 | No |
| Grande de Villafranca | GRA | 135.58 | 119 | No |
| Larga de Villacañas | LAR | 88.02 | 71 | Yes |
| Longar | LON | 93. 31 | 60 | Yes |
| Manjavacas | MAN | 230.4 | 48 | Yes |
| Mermejuela | MER | 9.57 | 68 | No |
| Nava Grande | NAV | 118.8 | 90 | No |
| Peñahueca | PEÑ | 113.87 | 19 | No |
| Pozuelo | POZ | 48.76 | 70 | Yes |
| Quero | QUE | 79.43 | 30 | No |
| Salicor | SAL | 58.15 | 20 | No |
| Tirez | TIR | 92.48 | 19 | No |
| Veguilla | VEG | 79.15 | 68 | Yes |
| Yeguas | YEG | 66.75 | 16 | Yes (in the past) |



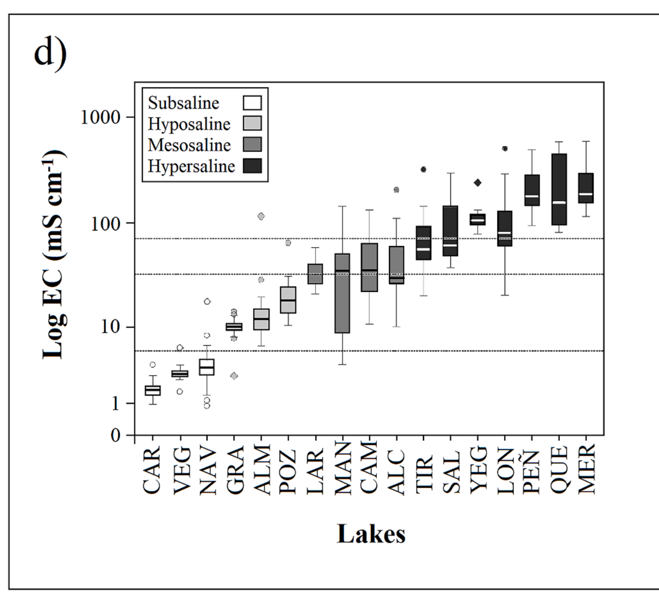




**Fig. 1.** Location and main limnological characteristics of the studied lakes: a) Situation map of lakes within La Mancha Húmeda Biosphere Reserve in Central Spain; b) Names, codes, bathymetric characteristics and impact by wastewaters; c) Annual variation of the hydroperiod of the lakes. Gray scale indicates the relative flooding level (%FL, with respect to maximum level) of lakes based on monthly observations (top chart), the white and black colors indicate 0 and 100 % of flooding, respectively. Monthly accumulated rainfall (bars) and average air temperature (black triangles) in the study area (lower chart); d) Water electrical conductivity (EC) of the lakes during the studied period. Based on these measurements, the salinity type (sensu Hammer, 1986) of each lake was defined.

expected to affect the nutrients stoichiometry. Unbalanced stoichiometries are in turn expected to impact on the metabolic function of the lakes as demonstrated by several experimental and observational studies (Elser et al., 2000; Peñuelas et al., 2011; Hilt et al., 2017; Vrede et al., 2009).

The study aims to assess the seasonal nutrient dynamics and the effects of natural and cultural eutrophication on the trophic status and metabolic processes of shallow saline lakes in the La Mancha Húmeda Biosphere Reserve. By evaluating the influence of different nutrient sources, such as wastewater and agricultural runoff, alongside environmental factors like salinity and seasonality, we seek to understand how these elements shape nutrient cycling, particularly phosphorus and nitrogen, and their impact on lake metabolism. An extensive survey was conducted to establish diagnostic parameters, using photosynthetic and oxygen consumption rates as indicators of ecosystem functioning, nutrient availability, and turnover. Ultimately, the study provides tools to improve management and conservation strategies for these vulnerable ecosystems, which are unique in Western Europe, focusing on addressing nutrient imbalances and enhancing restoration efforts.

## Methods

### *Study site*

Studied lakes are in the UNESCO La Mancha Húmeda Biosphere Reserve (Central Spain) (Fig. 1a). La Mancha Húmeda spans an area of over 400,000 hectares and stands as the largest wetland region within the Iberian Peninsula (Alonso, 1998). This site holds the status of a special bird protection area (SPAs) and is recognized as a wetland of international significance under the Ramsar Convention. It is situated in the upper basin of the Guadiana River, being characterized by a high density and diversity of lakes, a lithology dominated by marls and limestones, and a predominantly flat topography with minimal drainage.

### *Sampling and in situ physical-chemical determinations*

A total of 17 lakes were selected based on a gradient of water mineralization, including both lakes with and without wastewater inputs (Fig. 1). This selection was made to cover the range of conditions observed in the region. They are all shallow and range from subsaline to hypersaline. The lakes were sampled monthly over two hydrological cycles (Fig. 1). Precipitation and temperature data were obtained from the meteorological observatory in Herencia (JCCM, 2014).

The collection of physical-chemical data and sampling took place at the deepest points within the lakes. The depth of the water column was monitored using limnimeters. Subsequently, the relative flooding level of the lakes (%FL) was calculated by considering the recorded depths of the water column throughout the study period. Water's electrical conductivity (EC) was determined using a combination of a LF 91 conductivity meter and a KLE 1/T conductivity cell, both manufactured by WTW. Oxygen saturation and dissolved oxygen (DO) levels were measured using a WTW Multi 3410 instrument, paired with an FDO 924 IDS optical probe. A salinity correction was applied to the DO measurements. Classification of the lakes' saline type was based on conductivity measurements, following the methodology outlined by Hammer (1986). pH values of the water were measured using a portable pH meter from Hanna Instruments.

All containers utilized for sample collection were subjected to prior acid washing (using 10 % HCl) and subsequently rinsed multiple times with sample water before being filled. For the analysis of dissolved nutrient forms, water was immediately filtered in the field using Whatman GF/F glass filters and stored in 125 ml HDPE bottles. Unfiltered water samples were also gathered in identical bottles for analyzing the overall nutrient content. To determine the concentration of chlorophyll a (Chl-*a*), samples were passed through Whatman glass-fiber GF/F filters and then stored frozen until analysis. Monthly sampling of lake sediments was conducted between December 2013 and May 2014, involving the acquisition of 10 subsamples for each composite sample. These combined samples were homogenized in a 100 ml polyethylene container and filled without headspace to minimize potential sample alteration. All samples were preserved at −20 °C until they underwent analytical processing.

### *Nutrients analysis*

The nitrate ($NO_3$) concentration in the water was measured using the second derivative UV/Visible spectroscopy method (APHA 2005; Ferree and Shannon 2001) with a Beckman DU-7 UV–Visible spectrophotometer. This involved scanning water samples between 190 and 250 nm using a UV/Visible spectrophotometer. The second derivative of the absorption spectrum at 224 nm was then used to quantify nitrate concentrations. Method resulted advantageous because minimized interference from dissolved organic matter. The ammonium ($NH_4$) concentrations were determined using the modified Indophenol blue method (Verdouw et al., 1978). which forms a substituted indophenol complex avoiding the associated disadvantages of phenol use. This method can be applied effectively to seawater analysis. On the other hand, the total dissolved nitrogen (TDN) and total nitrogen in water (TNw) were measured using a Shimadzu TOC-V CSN analyzer, which includes a nitrogen determination module. This operated by oxidizing the nitrogenous compounds in the sample by high-temperature combustion and measure them by a chemiluminescence method. The proportion of dissolved organic nitrogen (DON) within the TDN was calculated by the difference between TDN and the sum of inorganic forms (namely nitrate and ammonia). The total nitrogen content in sediments (TNs) was quantified as nitrate after digesting the sediment samples using an alkaline persulfate oxidizer (NaOH 6 g $l^{-1}$ and $K_2S_2O_8$ 6 g $l^{-1}$ final concentration).

For the determination of soluble reactive phosphorus (SRP), a phosphomolybdic acid complex was formed by the reaction of phosphate ions with molybdate under acidic conditions. This complex was then reduced by ascorbic acid, resulting in the formation of a blue-colored compound. The intensity of the blue color, which correlates with the concentration of phosphorus in the sample, was measured spectrophotometrically (APHA, 2005).

Total phosphorus in water (TPw) and sediments (TPs) were determined in unfiltered water after conducting autoclave persulfate oxidation in an acidic environment (135 °C for 2 h) to hydrolyze any phosphorus-form into orthophosphate. The determination of released orthophosphate was carried out as described for SRP after neutralizing the sample's pH (APHA, 2005). The dissolved organic phosphorus in water (DOP) was estimated as the difference between TDP and SRP. Similarly, particulate phosphorus in water (PP) was calculated by subtracting TDP from TPw.

Total organic carbon (TOC) and dissolved organic carbon (DOC) concentrations in the water were measured using a Shimadzu TOC-V CSN Organic Carbon Analyzer. The measurement method is based on the total combustion of the sample, followed by the detection of the generated CO2 by Nondispersive infrared (NDIR) spectroscopy. To remove dissolved inorganic carbon from the samples, they were acidified and aerated beforehand. Total organic carbon (TOC) determination was carried out with the unfiltered samples, while dissolved organic carbon (DOC) was measured in samples previously filtered with Whatman GF/F filters.

### *Quantification of chlorophyll-a concentrations in water*

The concentration of Chl-*a* was used as a proxy for phytoplankton biomass. For this, the seston retained in Whatman GF/F filters was submerged in 90 % acetone overnight at −20 °C to extract photopigments, which were subsequently determined by HPLC according to

Picazo et al. (2013). The HPLC method reduced potential over-estimations by discriminating native Chl-*a* from its major degradation products, which may be abundant in shallow lakes because the strong interaction between the sediment and water column.

### Measure of gross photosynthesis and oxygen consumption rates in the plankton

To estimate the photosynthesis and aerobic respiration rates of plankton, the standardized oxygen-exchange method was employed (Camacho et al., 2012; 2016; Morant et al., 2020). The procedure began by collecting water from the water column at the sampling site, which was then distributed into eight 250 ml Winkler bottles.

The measurement of dissolved oxygen concentration at the beginning and end of the incubation allowed for the calculation of NPP and R rates. NPP was obtained from the transparent bottles, where net photosynthesis contributed to an increase in oxygen concentration, while R was calculated from the dark bottles, where the absence of light prevented photosynthesis and only oxygen consumption due to respiration occurred. To determine gross primary production (GPP), it was assumed that respiration rates in the illuminated bottles were equal to those measured in the dark bottles. Therefore, GPP was calculated by adding NPP and R. This assumption of equal respiration rates under light and dark conditions is common in such studies,

Finally, production/respiration (P/R) ratios were calculated as the quotient of GPP over R. A P/R ratio greater than 1 indicates an autotrophic metabolic balance, where production exceeds respiration, while a ratio less than 1 indicates a heterotrophic balance, where respiration exceeds production.

### Statistical analyses

A multivariate analysis of variance (MANOVA) with Tukeýs Honest Significant Difference for multiple comparisons was designed to evaluate the effect of the three studied factors (i.e., *Nutrient source, Salinity and Season*) on the measured variables. The effect size of the explored factors was assessed by observing partial eta-squared ($\eta^2$) provided by MANOVA analysis, which indicates the proportion of variance accounted for a given factor (Lakens, 2013).

A causal mediation analysis was performed to identify environmental variables (e.g., surface area, wastewater input, salinity, depth) that mediate the relationship between independent variables and outcomes such as pH, dissolved oxygen, and nutrient concentrations. The Baron and Kenny method (Baron and Kenny, 1986) was employed to test for mediating effects. The significance of mediation was determined using p-values $< 0.05$. All possible single-mediator models were explored, and results were ranked based on mediation intensity using the $R^2$ values, indicating the strength of the mediation effect.

The criteria for establishing the categories of these factors were as follow: A) Factor Nutrient source: Three different categories were established (i.e., catchment runoff, wastewater and volcanic substrate), which refer to the main sources of nutrients entering the lakes. Catchment runoff (*R*) indicates a major role of diffusive inputs of nutrients, which is mainly related to the surrounding land uses. On the other hand, lakes classified in the wastewater group (*Ww*) show furthermore point-source wastewater inflows from nearby towns. Finally, a lake was differentiated in the so-called volcanic category (*V*) because of the critical influence of this type of lithology, which provides large amounts of inorganic P (Cebriá and López-Ruiz, 1995; Corrales-González et al., 2019). Lake Almodovar is representative of the volcanic area of the "Campo de Calatrava", where other similar volcanic lakes occur. B) Factor Salinity: Four categories of water mineralization were established, namely, *subsaline, hyposaline, mesosaline* and *hypersaline*. Classification was carried out according to the ranges given by Hammer (1986), based on data of lake water conductivity (Fig. 1). C) Factor Season: Four groups were established for this factor: *Autumn*, when the lakes fill up; *Winter*, the period of maximum flooding; *Spring*, the most productive period associated with the onset of the drying process; *Summer*, the period when the lakes dry out, unless they remain artificially flooded by wastewater inputs.

The overall variability observed in the lakes was examined by principal component analysis (PCA) using descriptive variables of the trophic status (i.e., nutrients and Chl-*a*). A Spearman correlation analysis was performed to assess relationships between all the studied variables, and between the PCA-scores and metabolic rates. The data were log transformed, when required, to ensure a normal distribution for the statistical analyses. The raw (untransformed) data are reported in the figures and tables as average values. In all cases, the level of statistical significance was set to $p < 0.05$. All the statistical analyses were performed using the University of Valencia-licensed statistical package SPSS v. 22 (SPSS Inc., Chicago, IL, USA).

## Results

### Environmental conditions of the lakes

The water depth of lakes varied from centimeters to around 1 meter (Fig. 1b). The monthly cumulative rainfall and average air temperatures during sampling are shown in Fig. 1c. Monthly temperatures ranged from 5 °C to 25 °C. Rainfall peaked in autumn and early spring, decreasing with rising temperatures, causing a negative water balance explaining the seasonality of lakes. Some lakes remained flooded mostly due to wastewater inputs (Fig. 1c). Electrical conductivity (EC) ranged significantly, from 0.89 to 594 mS $cm^{-1}$ (Fig. 1d). Using Hammer's (1986) classification, lakes were grouped as subsaline, hyposaline, mesosaline, or hypersaline (Fig. 1d). EC increased across groups as hydroperiod advanced and depth decreased. Generally, water pH was slightly to moderately alkaline, averaging 8.62 ± 0.57 (Table S1 in supplementary material).

Lakes displayed oxygen saturation averaging 81.45 % to 120.91 % (Table S1). Lowest and highest levels occurred in hyposaline Almodovar and mesosaline Camino de Villafranca, respectively. Oxygen saturation peaked in winter (average: 122.25 ± 42.97 %) and dropped in summer-flooded lakes. Dissolved oxygen (DO) concentrations (range: 0.15–23.10 mg $l^{-1}$) exhibited hypoxia mainly in hypersaline lakes like Peñahueca, Mermejuela, and Longar (Table S1), with the highest concentrations in subsaline lakes during winter. Turbidity, caused by suspended particles or colloids, ranged from below 4 NTU in subsaline lakes to roughly tenfold higher in hypereutrophic Yeguas and volcanic Almodovar (Table S1).

### Nutrient enrichment and drivers of trophic status

Average P concentrations in water and sediment reflected significant trophic differences among lakes (Table S2 in supplementary material). Fig. 2 displays data grouped by MANOVA factors and corresponding post-hoc tests. The SRP generally increased with salinity, ranging from 0.26 to 24.67 μM in most lakes (10–20 % of total P). Notably, lakes Almodovar and Yeguas had high SRP accumulation, around 200 μM (Fig. 2a). The TPw concentrations in lake waters varied with SRP, and SRP:TPw ratios were exceptionally high (>0.5) in Almodovar, Yeguas, and Veguilla (Fig. 4a). The TPs widely varied, with lowest values in Alcahozo and highest in Yeguas and Veguilla (Table S2), both eutrophic with wastewater impacts. Almodovar's sediment accumulated P but less than other mentioned sites.

The *Nutrient source* factor was the primary explanation for variance in P fractions (Fig. 2a), with effect size measured by partial eta-squared ($\eta 2$) indicating explained variance proportion (Table S3 in supplementary material). The $\eta 2$ values were 0.45, 0.64, and 0.59 for SRP, TPw and TPs, respectively, accounting for 45 %, 64 %, and 59 % variance in these fractions. Post-hoc analysis for SRP and TPw showed significant subgroup differences ($p < 0.01$) (Fig. 2a). For TPs, lakes mainly fed by

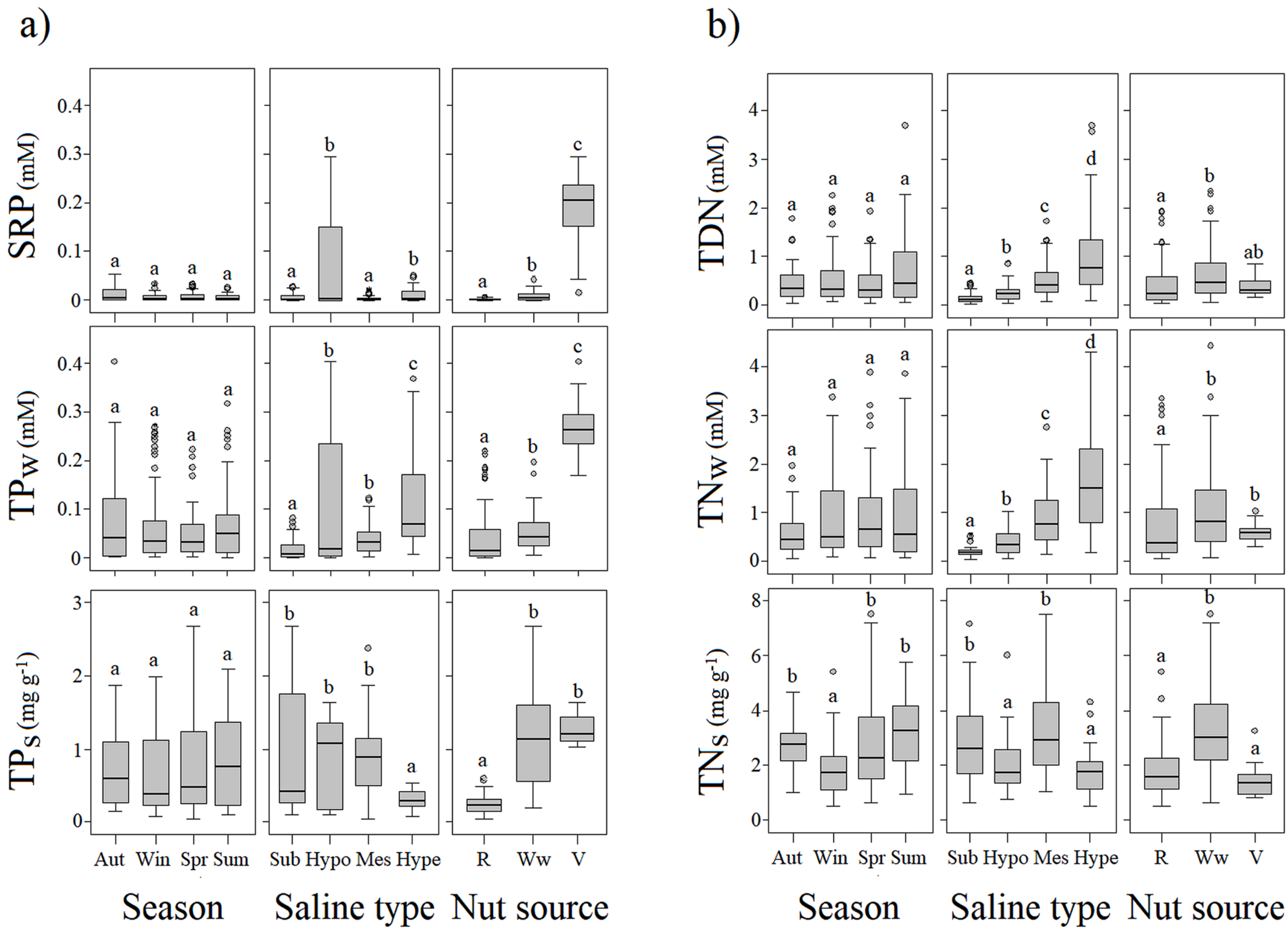



**Fig. 2.** Box plot charts showing the distribution of the concentration of phosphorus (a) and nitrogen (b) fractions in the studied lakes based on the factors explored in the MANOVA analysis. The fractions soluble reactive phosphorus (SRP), total phosphorus in water ($TP_w$), total phosphorus in the sediments ($TP_s$), total dissolved nitrogen (TDN), total nitrogen in water ($TN_w$), and total nitrogen in the sediments ($TN_s$). The subscripts 'W' and 'S' indicate water and sediment samples, respectively. The factors analyzed in the MANOVA are *Season* (Aut: autumn, Win: winter, Spr: spring, Sum: summer), *Saline type* (Sub. Subsaline, Hypo: hyposaline, Mes: mesosaline, Hype: hypersaline), and *Nutrient source* (R: run-off, Ww: wastewater, V: volcanic substrate). The box plot displays key statistics: The median is represented by a bold horizontal line. The interquartile range (25th-75th percentile) is shown as a box. The 10th-90th percentile range is depicted as whiskers. Outlier points are indicated by dots. Letters placed above the boxes represent the *post-hoc* groups determined by Tukey's HSD tests. The absence of a common letter denotes significant differences ($p < 0.05$) between subgroups.

catchment runoff (R subgroup) had significantly lower concentrations ($p < 0.01$), while volcanic Almodovar (V subgroup) and wastewater-impacted lakes (Ww subgroup) had no significant difference between them ($p > 0.05$) (Fig. 2a). The *Salinity* factor explained 55 % of TPw variance (η2 = 0.55) (Table S3). TPw was significantly lower ($p < 0.01$) in subsaline lakes. Hypersaline lakes had significantly lower average TPs (0.44 ± 0.54 mg $g^{-1}$) versus others, while subsaline lakes had higher TPs (0.96 ± 1.20 mg $g^{-1}$). No significant Season factor differences observed ($p > 0.05$).

The concentration of different nitrogen fractions in water and sediment were measured in the studied lakes (Table S2). Data grouped based on the MANOVA factors and the resulting post-hoc tests are shown in Fig. 2b. The total nitrogen in water (TNw) ranged from 0.05 mM to 13.79 mM, with higher values displayed by the *meso* and hypersaline lakes Manjavacas and Longar, respectively. Total dissolved nitrogen (TDN) represented around 50 % of total nitrogen in most of the lakes, and around half of this (48–66 %) was dissolved organic nitrogen (DON). In sediments, seasonal average concentrations of total nitrogen (TNs) ranged from 0.81 to 3.99 mg g-1, in lakes Tirez and Veguilla, respectively, and it was double in those lakes affected by wastewater inputs. The three factors of the MANOVA had a significant effect ($p < 0.05$) on the nitrogen concentrations both in water and sediments (Table S3). The *Salinity* factor explained most of the variance (η2 > 0.5) as shown in Table S3. In this case, both TDN and TNw increased significantly ($p < 0.01$) with salinity.

### *Organic carbon and nutrient stoichiometry as indicators of ecosystem functioning*

Total organic carbon (TOC) in lake waters, primarily dissolved (approximately 80 %), ranged from 2.00 ± 1.37 mM to 62.03 ± 65.77 mM in lakes Nava Grande and Mermejuela, respectively (Table S2). The *Salinity* factor accounted for most of the variance in both TOC (η2 = 0.63) and dissolved organic carbon (DOC) (η2 = 0.64) (Table S3). Post-hoc analysis revealed significant differences among all salinity subgroups ($p < 0.01$), with gradual TOC and DOC increase along salinity (Fig. 3). The *Nutrient source* factor significantly affected TOC and DOC, with higher concentrations in lakes with wastewater inputs ($p < 0.01$). Seasonally, TOC was slightly higher during summer (p-value = 0.04), aligned with increased temperatures and lake drying (Fig. 3).

Stoichiometric ratios of TOC, P, and N in water and sediments are shown by lakes and MANOVA groups in Fig. 4a and 4b, respectively. The TOC:TPw ratio varied from 12.50 to 3112.63, while the TNw:TPw ratio ranged from 0.83 to 213.03. These values exceeded Redfield ratios (106

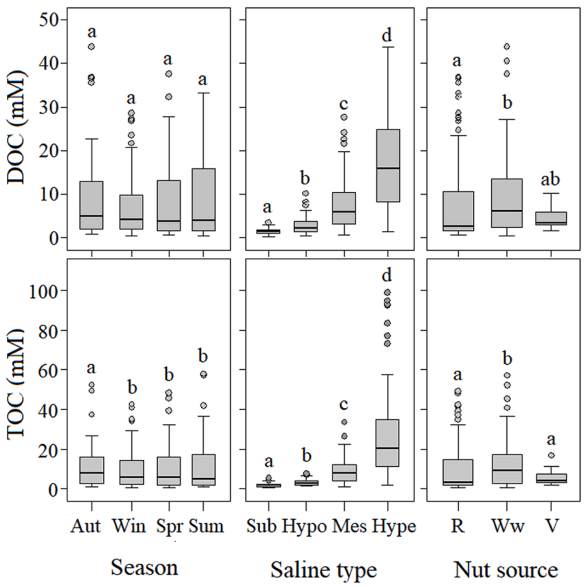



**Fig. 3.** Box plot charts showing the distribution of the concentration of dissolved organic carbon (DOC) and total organic carbon (TOC) based on the factors explored in the MANOVA analysis. The subscripts 'W' and 'S' indicate water and sediment samples, respectively. The factors analyzed in the MANOVA are *Season* (Aut: autumn, Win: winter, Spr: spring, Sum: summer), *Saline type* (Sub. Subsaline, Hypo: hyposaline, Mes: mesosaline, Hype: hypersaline), and *Nutrient source* (R: run-off, Ww: wastewater, V: volcanic substrate). The box plot displays key statistics: The median is represented by a bold horizontal line. The interquartile range (25th-75th percentile) is shown as a box. The 10th-90th percentile range is depicted as whiskers. Outlier points are indicated by dots. Letters placed above the boxes represent the post-hoc groups determined by Tukey's HSD tests. The absence of a common letter denotes significant differences ($p < 0.05$) between subgroups.

and 16) (Redfield, 1958), except for polluted lakes Veguilla, Yeguas, and volcanic lake Almodovar. Almodovar and Yeguas had low ratios due to high TPw concentrations, while Veguilla's ratios resulted from low TNw and TOC. This contrasted with P-deficient lakes like Grande de Villafranca, Alcahozo, or Caracuel (Fig. 4a).

TOC:TPw and TNw:TPw ratios were significantly influenced by the *Nutrient source* and *Salinity* factors ($p < 0.01$) (Fig. 4b), particularly by the former, which explained around 50 % of the variance (Table S3). The interaction between these two factors was also significant ($p < 0.01$) (Table S3). However, no distinct pattern emerged for the TOC:TNw ratios (Fig. 4b), with no clear division between polluted and unpolluted lakes. Nevertheless, the factor *Salinity* significantly explained 21 % of the variance ($p < 0.01$) for the TOC:TNw molar ratio (Table S3), and the interaction between this and the *Season* factor accounted for nearly 10 % of the variance (p-value = 0.01). In this context, the lowest TOC:TNw ratios were observed in summer for subsaline lakes, while the highest occurred in autumn during the flooding period in the hypersaline lakes (Fig. 4b).

The TNs:TPs molar ratios in sediments revealed a relative phosphorus enrichment compared to the water column (Fig. 4). Similar to the water column, significant differences were evident between groups based on both *Nutrient source* and *Salinity* factors ($p < 0.01$) (Fig. 4b), yet only the *Nutrient source* factor explained a significant portion of the variance ($\eta2 = 0.53$). In this context, sediment phosphorus enrichment was more pronounced (i.e., TNs:TPs molar ratio <16) in polluted lakes, particularly in the volcanic lake Almodovar (Fig. 4a). In contrast, lakes primarily fed by nutrient runoff (R subgroup) displayed average TNs:TPs molar ratios around 20.

*Phytoplankton biomass and metabolic rates in relation to trophic conditions*

Chl-a concentrations in the water column exhibited a notable variation across the lakes (Fig. 5a), with average values spanning from oligo-mesotrophic ($2.45 \pm 2.76$ µg $l^{-1}$) to hypertrophic ($185.14 \pm 201.15$ µg $l^{-1}$) conditions. High concentrations were evident in lakes still impacted by wastewater inputs, such as Larga de Villacañas or Longar, as well as in those where previous inputs account for the existing internal load (e.g., Lake Yeguas). The *Nutrient source* predominantly accounted for the variance in Chl-a concentrations ($\eta2 = 0.21$; $p < 0.01$), while the *Salinity* factor explained a minor portion (around 10 %) of the variance (Table S3). Chl-a concentrations were lower in sub- and hyposaline lakes compared to meso- and hypersaline lakes (Fig. 6a). On the other hand, no significant seasonal differences were observed ($p > 0.05$) (Fig. 6a).

The GPP of plankton varied according to the trophic status of the lakes. Lake Longar exhibited extremely high GPP values (>300 µmoles $O2\ l^{-1}\ h^{-1}$), whereas lower values were observed in Lake Nava Grande (Fig. 5b). Similarly, the highest average oxygen consumption rates (R) were recorded in Lake Longar, while oligotrophic and mesotrophic lakes such as Alcahozo, Grande de Villafranca, and Quero showed the lowest rates (Fig. 5b). All three MANOVA factors significantly affected GPP rates ($p < 0.01$) (Fig. 6b), with the *Nutrient source* ($\eta2 = 0.27$) and *Salinity* ($\eta2 = 0.19$) factors explaining most of the variance (Table S3). The pattern was similar for oxygen consumption rates (Fig. 6b), with slightly lower η2 values. Notably, lakes influenced by wastewaters and hypersaline lakes displayed significantly higher rates ($p < 0.01$) of both GPP and R (Fig. 6b).

The Production/Respiration ratio (P/R) roughly increased with trophic status and consistently exceeded 1 (Fig. 5d). Higher ratios were observed in eutrophic lakes such as Almodovar and Veguilla, while lower ratios were seen in oligotrophic lakes Tirez and Alcahozo. The increase of the metabolic rates with salinity was more pronounced for respiration, leading to decreased P/R ratios (Fig. 6b). GPP and R rates were significantly higher in summer ($p < 0.01$), exhibiting similar patterns over the study period and resulting in relatively stable P/R ratios throughout the hydroperiod (Fig. 6b).

*Multivariate analysis: linking trophic status to ecosystem processes*

The sorting of samples resulting from the principal component analysis (PCA) is illustrated in Fig. 7. The first (PC1) and second (PC2) components accounted for 34 % and 29 % of the total variance, respectively. PC1 exhibited substantial positive loadings for all P stocks and Chl-a concentrations, thereby organizing samples based on their trophic status. Samples most impacted by point-source pollution were positioned on the positive side of this axis, while those related to runoff were on the negative side. Lake Almodovar samples, despite lacking wastewater inputs, were on the positive side due to substantial P dissolution in the water column. Conversely, PC2 had the highest positive loadings for TOC and TNw. Samples associated to longer water residence times and evaporative concentration processes were situated on the positive side of this axis (Fig. 7). TNs played a smaller role in lakes clustering as indicated by lower loadings. PCA scores of samples for both components increased with salinity in both wastewater and runoff subgroups (Fig. 7). However, the volcanic Lake Almodovar displayed the highest average scores for the first component and the lowest for the second, deviating from the general pattern. The Spearman correlations between the variables studied, along with their statistical significance, are shown in Table 1. In general, both water nutrient concentrations and EC exhibited negative correlations with water column depth, indicating evapo-concentration of solutes. P levels in water demonstrated significant positive correlation with sediment P content. However, no N fractions in water displayed statistically significant correlation with sediment N. The Chl-a concentration displayed positive correlations with water nutrient concentrations and $TP_s$.

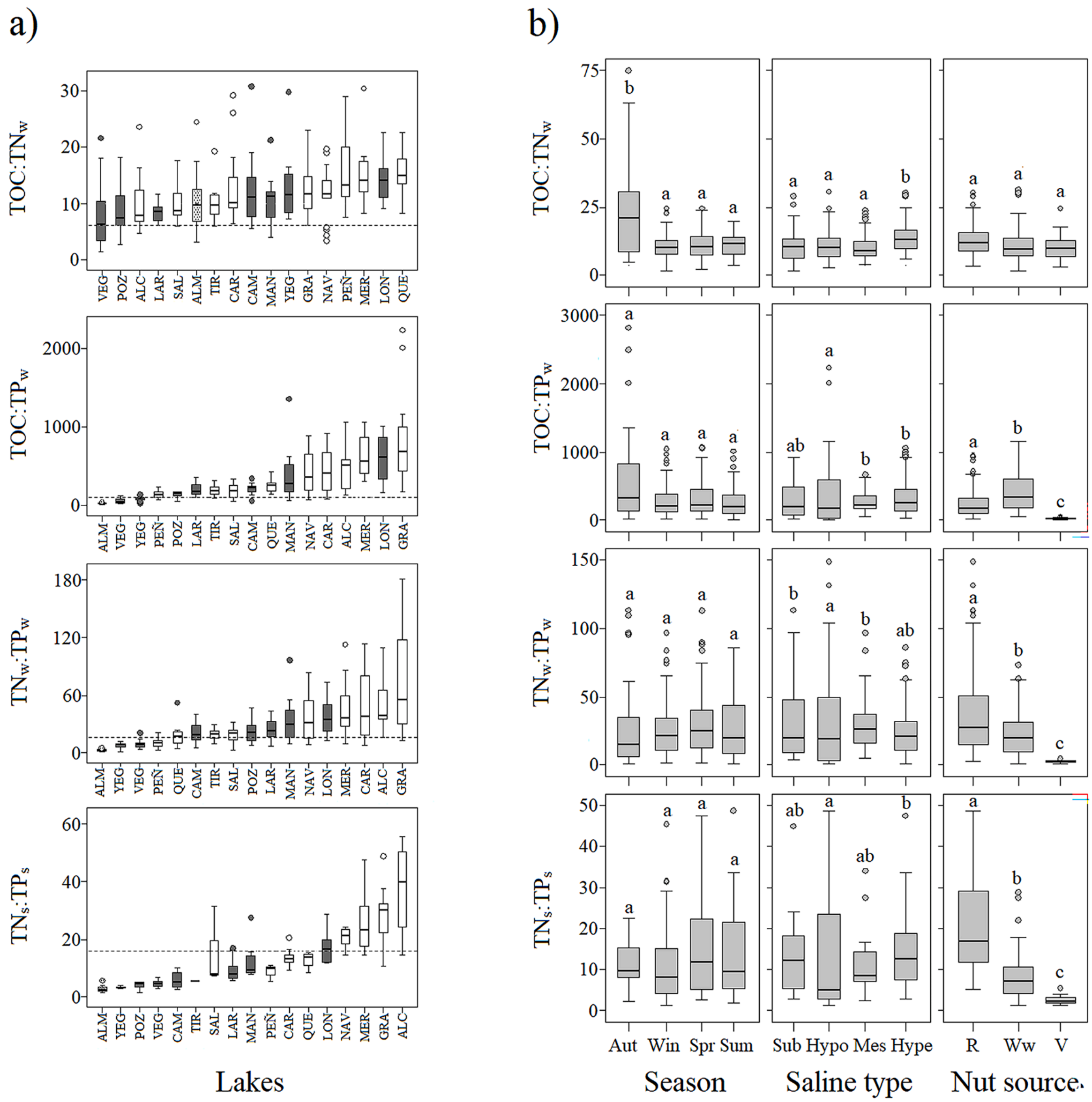



**Fig. 4.** Box plot charts showing the distribution of the molar relationships of nutrients in the water ($TOC:TN_w$, $TOC:TP_w$ and $TN_w:TP_w$) and sediments ($TN_s:TP_s$) of the studied lakes. a) Distribution of stoichiometric ratios for each individual lake. Dark grey and white boxes represent lakes with and without wastewaters inputs, respectively. b) Distribution of stoichiometric ratios based on the factors explored in the MANOVA analysis. The subscripts 'W' and 'S' indicate water and sediment samples, respectively. The factors analyzed in the MANOVA are Season (Aut: autumn, Win: winter, Spr: spring, Sum: summer), Saline type (Sub. Subsaline, Hypo: hyposaline, Mes: mesosaline, Hype: hypersaline), and Nutrient source (R: run-off, Ww: wastewater, V: volcanic substrate). The box plot displays key statistics: The median is represented by a bold horizontal line. The interquartile range (25th-75th percentile) is shown as a box. The 10th-90th percentile range is depicted as whiskers. Outlier points are indicated by dots. Letters placed above the boxes represent the post-hoc groups determined by Tukey's HSD tests. The absence of a common letter denotes significant differences ($p < 0.05$) between subgroups.

Correlations between GPP and R were examined to determine whether carbon supporting plankton's secondary production primarily originates from planktonic photosynthetic rates (stronger correlations) or external sources (weaker correlations). The complete dataset revealed a robust correlation ($r = 0.84$; p-value $< 0.001$) between both rates. Correlations, sorted by *Season* factor, remained significant, although lower during winter ($r = 0.70$; p-value $< 0.001$) and higher in summer ($r = 0.91$; p-value $< 0.001$). Across saline types, correlations ranged from lowest in mesosaline ($r = 0.79$; p-value $< 0.001$) to highest in hypersaline ($r = 0.95$; p-value $< 0.001$) subgroups. Sorting data by *Nutrient source* factor indicated significant correlations (p-values $< 0.001$) for both wastewater (Wv) and runoff (R) subgroups ($r > 0.80$), while Lake Almodovar, the sole volcanic lake, showed a lower but still significant correlation ($r = 0.71$; p-value $= 0.047$).

The correlation between the PCA-scores of the samples (cause variables) and the metabolic rates (effect variables) was also examined. The scores of the first component of the PCA, representing the lakes' trophic status, showed a positive correlation with GPP ($r = 0.68$; $p < 0.001$) and, to a lesser extent, with R ($r = 0.46$; $p < 0.001$). However, no statistically significant correlation was observed between these metabolic rates and the scores of the second component of the PCA, which corresponds to longer water residence times and increased evapo-concentration processes.

A causal mediation analysis was conducted to identify environmental factors that serve as mediators between the independent variables, which main results are shown in Table S4. In the mediation analysis, the strongest mediations, with $R^2$ values above 0.9, involve nitrogen and carbon processes. For instance, the relationship between

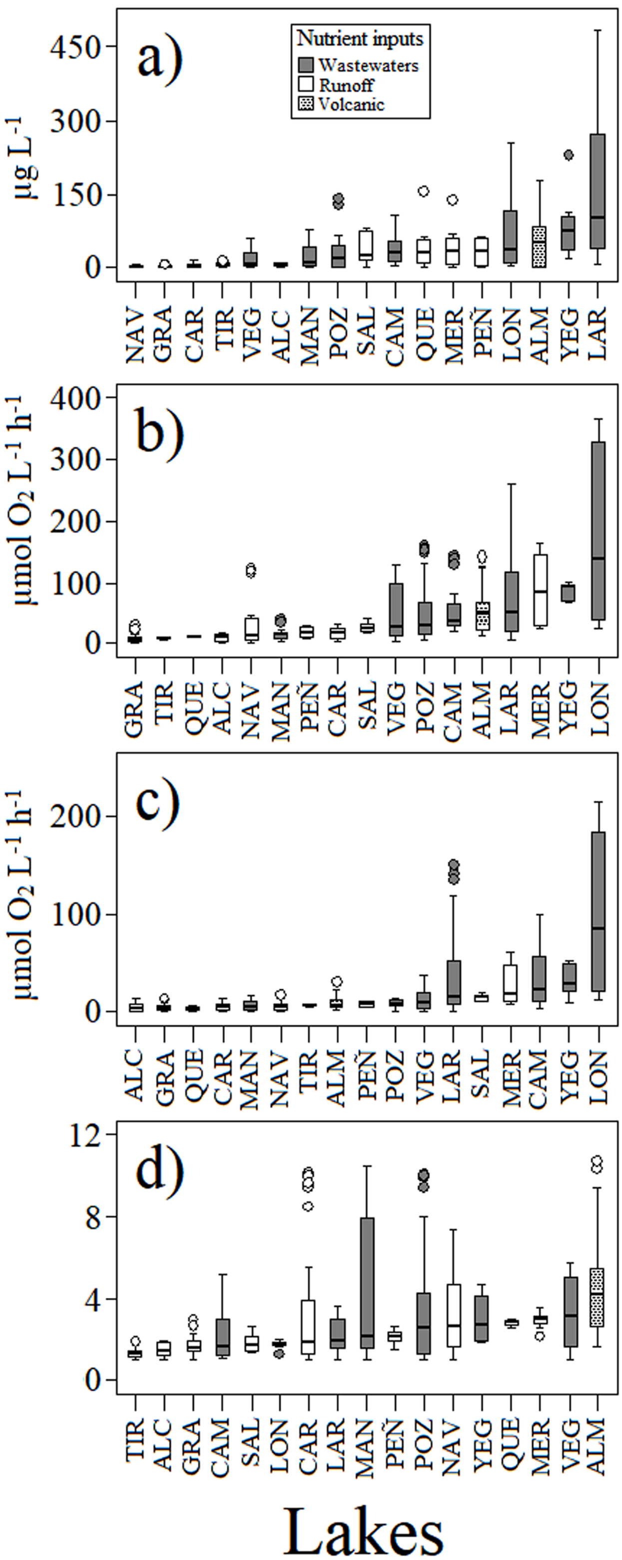



**Fig. 5.** Planktonic algal biomass and metabolic rates in the lakes: a) Chlorophyll a concentration (Chl-a), b) gross photosynthetic production (GPP), c) respiration rates (R), and d) production/respiration ratio (P/R). Dark grey and white boxes represent lakes with and without wastewaters inputs, respectively. The box plot displays key statistics: The median is represented by a bold horizontal line. The interquartile range (25th-75th percentile) is shown as a box. The 10th-90th percentile range is depicted as whiskers. Outlier points are indicated by dots.

Max depth and DOC (mM) mediated by TDNw (mM) ($R^2$ = 0.959, p-value = 0.179) underscores the depth's influence on dissolved organic carbon via nitrogen processes. Phosphorus variables, such as TPw (µM) and SRPw (µM), were also involved in mediations, particularly with pH, although only SRPw showed statistical significance (p-value = 0.046, $R^2$ = 0.267).

The concentration of Chl-a showed weaker mediations, particularly related to phosphorus variables like TPw and SRPw, suggesting a role in productivity but with less robust effects. Lastly, the lake's surface area influenced the amount of phosphorus in sediments, which in turn affected nitrogen accumulation in the sediments (p-value = 0.044, $R^2$ = 0.613), emphasizing the interconnectedness of nutrient cycling and physical lake characteristics.

Additionally, TPs mediated the effect of lake depth on pH (p-value = 0.043, $R^2$ = 0.358), demonstrating sedimentary phosphorus' role in regulating water chemistry. TPw also served as a mediator between lake depth and pH (though not statistically significant, $p$ = 0.051, $R^2$ = 0.292).

## Discussion

### *Environmental pressures and global challenges*

The Biosphere Reserve of 'La Mancha Húmeda' exhibits a high abundance and diversity of shallow lakes, which contrast in water salinity, management methods, and trophic status. The UNESCO Man and Biosphere Program aims to reconcile nature conservation and human development, a goal that is not free from potential conflicts. The functioning of the studied lakes is influenced by a range of distinct environmental factors, encompassing anthropic pressures, the biogeochemical characteristics of catchments, and seasonal variations. These factors are interconnected, exerting mutual influence upon each other. Wastewater discharges have induced modifications in the water dynamics of some of the studied lakes, leading to changes in their natural hydroperiod. This transformation has changed the condition from temporary to semi-permanent waterbodies. The distinct seasonality observed in these Mediterranean shallow lakes sets them apart from cold-temperate lakes in central Europe (Nõges et al., 2003), underlining the need to preserve these unique ecological environments. Urban wastewaters, regardless of their treatment status, directly contribute to desalination processes, as evidenced in this study.

Wurtsbaugh et al. (2020) highlights how these pressures are leading to the decline of saline lakes worldwide, which could result in severe biodiversity losses and ecosystem degradation, as also evidenced in the present study. In particular, the effect of cultural eutrophication related with agricultural expansion and drought had been observed in shallow lakes from Canada's Boreal Plains, being some of them also saline (Bayley et al., 2013). Nevertheless, findings of the present study indicates that the impact of extensive agriculture in La Mancha Húmeda could be quantitatively less significant when compared to the pollution associated to the pouring of wastewaters.

A study conducted in North Kazakhstan (Central Asia) shows that shallow saline lakes with endorheic conditions experience chemical dynamics similar to those observed in La Mancha Húmeda (Boros et al., 2017). The study demonstrates how increasing salinity caused shifts in dominant ions and mineral precipitation, such as gypsum and halite, which contributed to altering the lakes' trophic state and pushed them toward hypertrophic conditions. A previous study conducted in these same lakes from La Mancha Humeda already desmostrated how changes in water chemistry not only can alter their physical properties but also has an impact in their ecological balance by promoting nutrients release from sediments (Corrales-González et al., 2019). Not only the sediment-water interface is a critical factor, but also the freshwater-saltwater interfaces as stated by Valiente et al. (2022). This can help for the attenuation of eutrophication process by nutrient recycling and pollutant removal. Thus, the limited water exchange

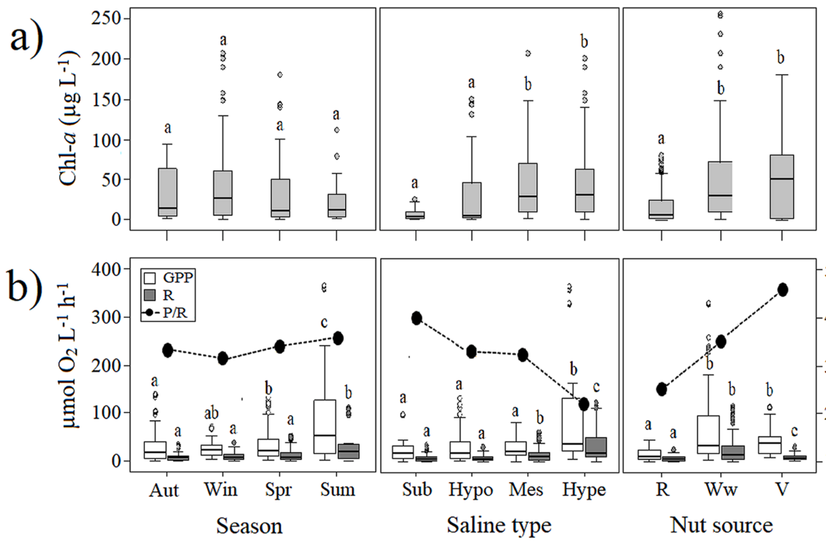



**Fig. 6.** Planktonic algal biomass and metabolic rates in the lakes based on the factors explored in the MANOVA analysis. a) Chlorophyll a concentration (Chl-a), b) gross photosynthetic production (GPP), respiration rates (R) and production/respiration ratio (P/R) of the plankton of studied lakes. Data are grouped based on the factors explored in the MANOVA analysis: Season (Aut: autumn, Win: winter, Spr: spring, Sum: summer), Saline type of lakes (Sub. Subsaline, Hypo: hyposaline, Mes: mesosaline, Hype: hypersaline) and Nutrient source (R: run-off, Ww: wastewater, V: volcanic substrate). The box plot shows the median (bold horizontal line), 25–75th interquartile range (box), 10–90th interquartile range (whiskers) and outlier points (dots). Letters above the boxes indicate post-hoc groups of Tukey HSD tests. Accordingly, the absence of a letter in common denotes significant differences ($p < 0.05$) between subgroups.

because the high salinity may act as natural filters against pollutants, added to the microbial turnover of nutrients.

*Ecosystem functioning through metabolic patterns*

The multivariate PCA analysis illustrates the evolving eutrophication processes taking place in these lakes. Samples distribution along the first component correlates with growing point-source pollution impact, while the second component highlights the inherent endorheic nature of these lakes, which leads to a natural and gradual nutrient buildup. The absence of wastewaters reveals then the progressive rise in nitrogen and organic carbon concentrations, paralleled by prolonged water retention times. The metabolism of the planktonic compartment behaves according to the described trophic scenarios, as evidenced by the correlations between causal factors (PCA components) and response variables (metabolic rates).

The PCA shows GPP and R rates being closely linked, suggesting that autochthonous photosynthetic activity fuels respiration via the release of fresh and labile DOM. Nonetheless, a partial mismatch persists, especially during winter, likely due to contributions of allochthonous organic matter inputs associated with lakes recharge in this period. The higher TOC:TNw and TOC:TPw ratios observed during winter support this idea, decreasing as the hydroperiod advances and water residence time increases. This seasonal dynamic, where the input of low-quality organic matter initially drives metabolic processes, followed by a shift to more autochthonous nutrient cycling, mirrors patterns observed in other studies of endorheic lake systems, such as those reported by Zagarese et al. (2017) in Patagonia's shallow lakes and by Huang et al. (2018) in the endorheic lakes of the Tibetan Plateau. Furthermore, Kritzberg et al. (2006) and Berggren et al. (2015) also highlighted similar trends in boreal and temperate lake systems, where the influx of terrestrial organic material during specific periods significantly alters the lake's metabolic balance before transitioning to more locally driven processes as the season progresses

The hypersaline subgroup of lakes show a significant reduction in the P/R ratio compared to others. There are different processes that, either individually or mutually, could explain this decrease in the ratios. Elevated salinity influences the photodegradation of DOM, with chloride and other ions intensifying the photo-bleaching process on water surfaces exposed to sunlight (Schafer et al., 2021). In the presence of light, these ions can facilitate the generation of reactive oxygen species, which can then initiate oxidation processes. Also, an additional oxygen consumption could be favored by the solubilization of organic material accumulated in sediments, which may occur due to the enhancement of clay dispersion and OM mobilization caused by the Na-organic linkages (Sumner et al., 1998; Rengasamy et al., 2016). The primary objective of our metabolic survey was to outline the accumulation and mineralization of carbon within the lakes. However, certain processes described previously may encompass abiotic chemical oxidation, so that an increase of R might not necessarily correspond to an increase in the respiration rates. There are some studies showing that photobleaching might otherwise undergo a decay at high water ionic strength (Minor et al., 2006; Song et al., 2017; Zhu et al., 2018), which apparently contradicts our previous argumentation. However, this is primarily associated with the photodegradation of allochthonous DOM, which is more prone to undergoing this process and plays a minor role in the hypersaline lakes of this study.

The second component of the PCA signifies both a P deficiency and a drop of metabolic activities. This is evident for the well-preserved lakes arranged based on this component (e.g., Alcahozo, Tirez, Peñahueca, Salicor). In these lakes, concentrations of TOC (~80 % as dissolved organic carbon; DOC) are substantially elevated, falling within the range reported for saline lakes (Boros et al., 2017; Butturini et al., 2022; Osburn et al., 2011). The TOC concentrations increase proportionally more than the other nutrients as the salinity and the water retention time do. A buildup of uncolored DOC, likely recalcitrant, apparently occurs in these well-preserved lakes. This aligns with observations made in other steppe lakes (Osburn et al., 2011; Torremorell et al., 2015; Waiser and Robarts, 2000) and is likely responsible for the reduced respiration rates measured in those lakes. Increased solar UV radiation, compounded by extended water retention times, has been proposed as a potential explanation for the buildup of colorless DOM (Osburn et al., 2011; Torremorell et al., 2015). This accumulation of low biodegradable DOM has major implications in C cycling, as it leads to a substantial reservoir of organic matter that remains unmineralized. Under good ecological condition, this is expected to promote the C sink role of these lakes, a conclusion also supported by findings in other studies (Camacho et al., 2017; Morant et al., 2020).

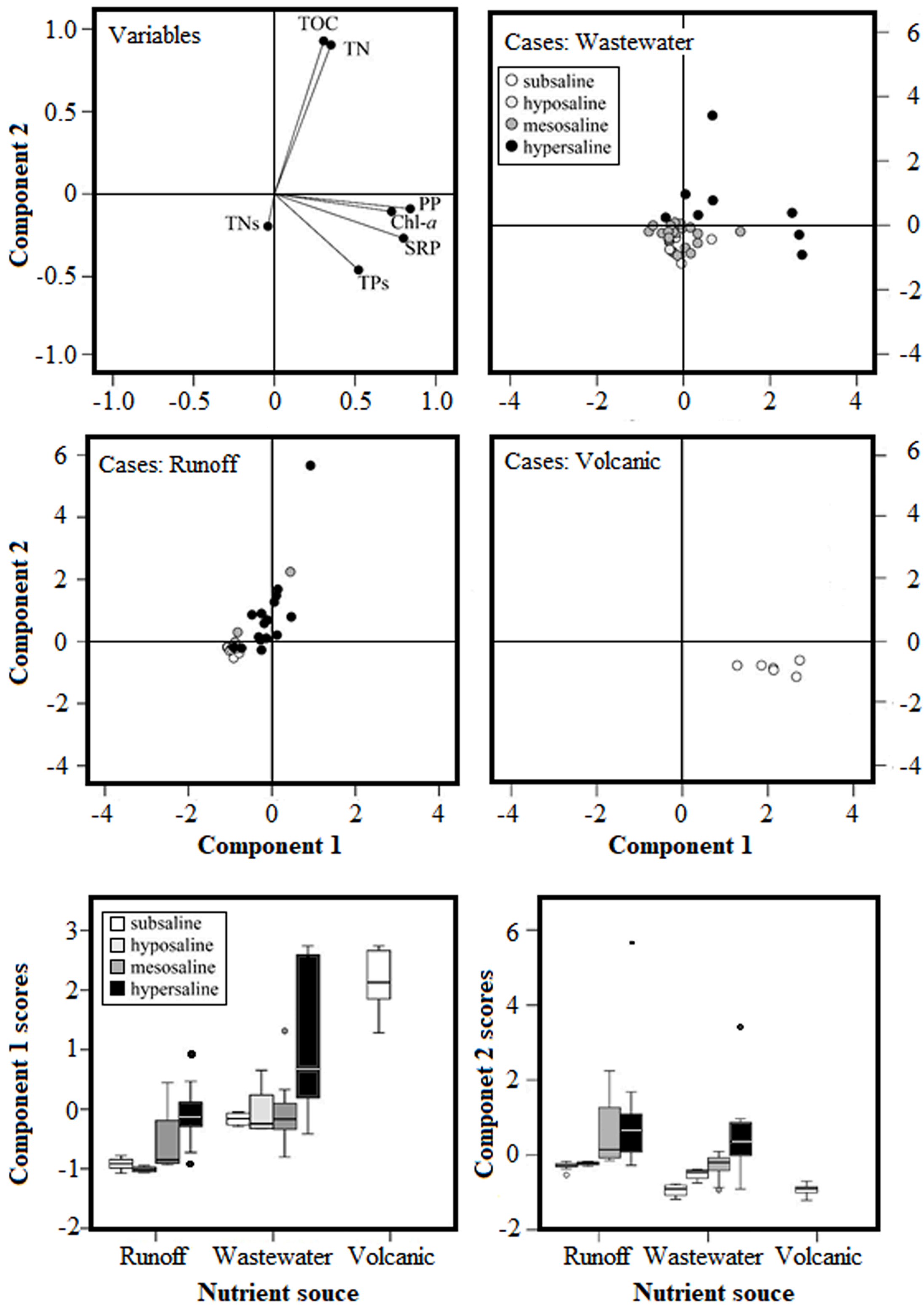



**Fig. 7.** Principal components analysis based on the trophic variables of the studied lakes. Biplots for the first and second components of the PCA are represented separately based on the Nutrient factor (Runoff, Wastewater and Volcanic). Colors of the circle symbols and boxplots are based on the Salinity factor (subsaline, hyposaline, mesosaline and hypersaline) as indicated in the legend.

A major deviation from the patterns described previously is observed in Lake Almodovar, which represents the volcanic region of Campo de Calatrava. It shows a catchment substrate containing alkali basalts (Cebriá and López-Ruiz, 1995), which is characterized by an important content of P (Porder and Ramachandran, 2013) and a limited capacity to adsorb the excess of this P. This leads to the high release of SRP observed in Lake Almodovar, emphasizing the susceptibility of these volcanic lakes to potential eutrophication if concurrent N inputs also occur. However, the elevated turbidity, which is also a characteristic feature of these volcanic lakes (Fernández et al., 2009), results in a significant

**Table 1**
Spearman correlation coefficients for the relationships between the studied variables in the lakes. Bold type indicates significant relationships (* $p < 0.05$; ** $p < 0.01$). Letters W and S as subscript indicate water and sediment samples, respectively.

| | EC | SRP | $TP_w$ | DOC | TOC | TDN | $TN_w$ | $TP_s$ | $TN_s$ | Chl-*a* |
|---|---|---|---|---|---|---|---|---|---|---|
| Depth | −0,48** | −0,10 | −0,32** | −0,49** | −0,49** | −0,33** | −0,33** | 0,27** | 0,09 | −0,22** |
| EC | | 0,21** | 0,58** | 0,83** | 0,85** | 0,74** | 0,79** | −0,13 | −0,12 | 0,45** |
| SRP | | | 0,70** | 0,29** | 0,31** | 0,33** | 0,34** | 0,42** | −0,00 | 0,31** |
| $TP_w$ | | | | 0,70** | 0,71** | 0,69** | 0,74** | 0,30** | −0,09 | 0,53** |
| DOC | | | | | 0,98** | 0,85** | 0,88** | −0,05 | −0,01 | 0,49** |
| TOC | | | | | | 0,87** | 0,89** | −0,01 | 0,00 | 0,50** |
| DTN | | | | | | | 0,94** | 0,09 | 0,04 | 0,45** |
| $TN_w$ | | | | | | | | 0,11 | 0,06 | 0,52** |
| $TP_s$ | | | | | | | | | 0,53** | 0,40** |
| $TN_s$ | | | | | | | | | | −0,09 |

reduction of light penetration, consequently constraining primary production. This would account for the moderate phytoplankton biomass and photosynthetic activity measured in Lake Almodovar, even in the presence of high nutrient availability. For the other type of lakes, further inputs of nutrients, whether N or P, may add to the surplus of the other nutrient, which has implications for the C cycling. Our results indicate that the secondary production of plankton, which represents an important part of the potential C export from the system, is mainly fueled by autochthonous primary production, which is ultimately regulated by non-natural inputs of nutrients. This holds relevance in lakes from this region where plankton outweighs the role of benthic organisms (Camacho et al., 2017).

The mediation analysis performed sheds some light on the relationships between physical lake characteristics, nutrient dynamics, and their downstream effects on ecosystem function. It indicates that nitrogen and phosphorus processes are key to the ecological dynamics of the saline lakes. While depth appears to influence dissolved organic carbon through nitrogen, the mediation strength suggests an important link, though it is not statistically significant. Soluble reactive phosphorus, however, has a clear effect on pH, highlighting its role in regulating water chemistry. Chlorophyll-a played a minor role, pointing to some involvement in productivity regulation, albeit limited. The connection between lake surface area, phosphorus in sediments, and nitrogen accumulation further emphasizes the intricate links between nutrient cycling and physical characteristics. These results underscore the need for targeted phosphorus management to preserve water quality and ecosystem function, as previously suggested for these lakes (Corrales-González et al., 2019).

### *Management and restoration approaches*

Bayley et al. (2013) emphasize the critical role of submerged aquatic vegetation in controlling eutrophication processes and providing transparency to the water column, as this type of vegetation can absorb excess nutrients and stabilize sediments. However, in La Mancha Húmeda, these submerged communities, even though originally characteristic of these ecosystems, are largely absent due to ongoing degradation processes, thereby exacerbating eutrophication. Where they are currently present, they typically occur in low densities, particularly in the less threatened and highly saline systems, where their ability to mitigate nutrient imbalances is diminished. Given this context, the restoration and recovery of submerged aquatic vegetation should be a key focus in restoration programs. However, in volcanic lakes, such as those in the Campo de Calatrava region, high turbidity occurs naturally and significantly limits light penetration, which not only hinders plankton development, as demonstrated in this study, but also the development of submerged vegetation. This reduces the ecosystem's capacity to regulate nutrient levels naturally. Consequently, the typical strategies for restoration in clearer waters may be less effective in this case, necessitating alternative approaches that address both turbidity and nutrient management in these volcanic environments.

Maintaining permanent hydroperiods artificially in lakes from La Mancha Humeda is relatively rare. Therefore, certain lakes impacted by wastewater discharges (e.g., Longar or Manjavacas) continue to dry out during the summer, resulting in a hydrological pattern that closely resembles their natural cycle. This helps these lakes to preserve many of their ecosystem services without excessive disruptions. On the other hand, the presence of permanent lakes, even during the warmest periods, can lead to additional challenges related to an excessive population of waterfowl. In this context, flamingos have been observed to regulate the availability of dissolved nutrients by contributing guano inputs and enhancing sedimentary P mobilization through bioturbation (Batanero et al., 2017). This release of internal P loads is expected to be significant in the present case, as inferred from a previous P-fractionation study conducted in lakes from La Mancha Humeda (Corrales-González et al., 2019).

The presence of waterfowl during warm periods in flooded lakes can also raise concerns about public health. This is linked to the potential occurrence of Clostridium perfringens and Clostridium botulinum when wastewater inputs persist during warmer seasons (Anza et al., 2014). These researchers noted the presence of C. botulinum in bird feces from Lake Veguilla, indicating the role of waterfowl as carriers and emphasizing the risk of botulinum toxin production, which could lead to avian botulism outbreaks.

## Conclusions

This study offers key insights into nutrient dynamics and the functioning of shallow saline lakes in the partially explored region of La Mancha Húmeda. These lakes, due to their enclosed nature, are highly sensitive to both environmental and human-induced disturbances, which can disrupt nutrient balances and carbon processes. The research provides a foundation for assessing ecological status under various scenarios, including pollution, natural eutrophication, and the increasing impact of artificial desalination, which exacerbates salinity fluctuations and further threatens nutrient cycling. Effective management should focus on controlling nutrient inputs from point sources, particularly wastewater, as this has a greater impact on lake degradation than agricultural practices. Moreover, reducing wastewater inputs is more cost-effective compared to land-use changes. Conservation strategies must also account for the vulnerability of volcanic lakes and the growing challenge of desalination to maintain ecological balance.

## CRediT authorship contribution statement

**Maykoll Corrales-González:** Writing – original draft, Investigation, Formal analysis. **Carlos Rochera:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Antonio Picazo:** Methodology, Investigation, Formal analysis. **Antonio Camacho:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2024.122830.

## Data availability

The authors do not have permission to share data.

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