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How a constructed wetland within a natural park enhances plankton communities after more than 10 years of operation: Changes over space and time

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ABSTRACT

Constructed wetlands are increasingly used as a solution to treat polluted water in natural environments. Located in the *Albufera de València* Natural Park, a constructed wetland was built in 2009 as a pilot project to act as an intermediary between low-quality waters and the largest protected coastal lagoon in the Iberian Peninsula. With a unique dataset spanning more than a decade (2009–2023), this study assessed changes in plankton communities both spatially (comparing six sampling sites) and temporally (comparing four periods of years). The results show how the constructed wetland, after nearly 15 years of operation, has not only maintained but also improved its capacity to enhance the biological quality of the water which is released into the protected lagoon, thus fulfilling one of the main aims of its construction. During the last period (2020–2023) of the time series, the constructed wetland outlets had significantly higher zooplankton biomass, particularly filter-feeding cladocerans, compared to the inlets. This clear improvement in the plankton community was due to management interventions (*e.g.*, drying sectors of the constructed wetland during the summers since 2019) and the rise in temperature. These circumstances promoted earlier hatching of cladoceran diapause eggs from the sediments compared to previous years, maintaining their presence throughout all seasons. Consequently, the outlets of the constructed wetland had significantly lower phytoplankton abundance and sestonic chlorophyll-*a* concentrations than in the past, nearly oligotrophic states, and a reduced biovolume of potentially toxic cyanobacteria in the released waters.

1. Introduction

To mitigate the degradation of wetlands, mainly due to human activities (Verhoeven, 2014), artificial or constructed wetlands (hereafter CWs) have been increasingly used to restore the ecosystem services provided by wetlands, and nowadays they are being created worldwide (Scholz and Lee, 2007; Moshiri, 2020). Due to their green infrastructure, CWs are used not only for treating urban wastewater (Verhoeven and Meuleman, 1999; Ávila et al., 2013; Vymazal, 2022; Zeng et al., 2024), but they have also been implemented in natural environments with eutrophic waters (He et al., 2007; Zhang et al., 2023; Borgström et al., 2024); particularly the surface-flow type (Rodrigo et al., 2018; Rodrigo and Segura, 2020; Rochera et al., 2024), which resemble more natural conditions and allow for plankton development. Eutrophication (*i.e.,* increased nutrient concentration) results in a disproportionate growth of phytoplankton with significant changes in ecosystem functioning, such as the dominance of potentially toxic species (Dodds et al., 2009), or even the disappearance of the aquatic macrophytes (Rodrigo et al., 2018). Therefore, the enhancement of biological water quality, in terms of a reduction in phytoplankton biovolume and an increase in zooplankton biomass (particularly cladocerans as efficient microalgae filterers; Rodrigo et al., 2013a; Rodrigo and Segura, 2020) is one of the

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main objectives of CWs (Guo et al., 2016; Li et al., 2014), since these systems are playing a key role in counteracting the eutrophication process (Jung et al., 2009). At the same time, CWs also aim to transform the composition of plankton communities towards a higher diversity (Declerck et al., 1997; Rojo et al., 2010), which allows for an efficient transfer of energy and matter as well as higher stability in the food web leading to an improvement in ecosystem services (Puche et al., 2021).

Plankton communities within the CWs depend on biological, physical and chemical factors, hence they are important indicators of operational conditions (Amengual-Morro et al., 2012; Zhang et al., 2014). As CWs are human-operated systems, environmental management decisions could have an effect on plankton communities (Ghosh and Biswas, 2015; Liu et al., 2024). Previous studies have pointed out that due to the short generation times of plankton, these organisms rapidly track changes in environmental conditions (Neukermans et al., 2018). Therefore, the evaluation of variations in plankton communities has been seen as a promising approach for long-term, effective-treatment system operation (Neukermans et al., 2018). Despite this, there is little information on the changes occurring in planktonic communities, including both phytoplankton and zooplankton, as the water flows within and through the different sectors that CWs are commonly composed of (Chen et al., 2011; Calero et al., 2015; Rodrigo et al., 2013a; Travaini-Lima et al., 2016; Rodrigo and Segura, 2020; Carabal et al., 2024). Additionally, none of these studies analysed more than four years of data-sets, thus limiting long-term comparisons over time. Such long-term comparisons are crucial due to ongoing global change, since climate gradients are inherent in many large-scale datasets and are among the most important predictors of plankton abundance and community structure (Gyllström et al., 2005).

These changes inside CWs are of special relevance when they act as intermediary systems between low-quality waters and protected wetlands. This is the case of Tancat de la Pipa (TP-CW hereafter), a CW built in 2009 to meet the requirements of the European Water Framework Directive (2000/60/CE) in the *Albufera de València* Natural Park (AVNP hereafter). The AVNP is a nationally and internationally recognised wetland due to its cultural and natural singularity, which includes the largest coastal lagoon in the Iberian Peninsula, the hypertrophic *Albufera de València* lagoon (AVL hereafter) affected by a strong cultural eutrophication process since the 1970s (Dafauce, 1975). Moreover, TP-CW is located within the Mediterranean area, one of the climate-change hotspots (Lionello and Scarascia, 2018; IPCC, 2023). In Mediterranean wetlands, the acute rise in air and water temperature is accompanied by an increase in phytoplankton biomass (particularly cyanobacteria; Taylor et al., 2021). During the early years of operation (2009–2015), the different sectors into which TP-CW is divided were shown to improve water quality in terms of nutrient reduction (Martín et al., 2013; Rodrigo et al., 2013a; Hernández-Crespo et al., 2017) as well as plankton community enhancement (Calero et al., 2015; Rodrigo and Segura, 2020). However, all of these studies focused on the early years of operation, and most of them only on the inner sectors of TP-CW, hindering the assessment of how the different management interventions (particularly those implemented in recent years) have affected plankton communities, paying special attention to those developed in the waters that will be finally discharged into the Natural Park. In this context, monitoring planktonic communities becomes indispensable for the successful operation of CWs. More in-depth research should focus on the last operational years of the TP-CW, given that this stage is always significant for long-term applications of these systems, allowing for an evaluation of its useful life.

Therefore, with almost 15 years of plankton data (2009–2023), one of the longest plankton data series obtained for a CW, this system provides the perfect scenario to make comparisons between sampling sites and years, allowing the assessment of whether TP-CW has continued to meet the objective of improving biological water quality as previously reported. In this paper, we have analysed phytoplankton and zooplankton data from the inlet, middle sites, and especially the outlets of TP-CW (*i.e.,* water which is discharged into the protected AVL) in the 14-year data series. We hypothesise that after the water has passed through TP-CW: (i) the phytoplankton biovolume will continue to be reduced and the zooplankton biomass will continue to be greater, (ii) the planktonic composition will be enhanced at the outlets, following the various management actions that have been implemented, towards a community with a higher capacity in resource use and presumable top-down phytoplankton control and (iii) due to the general temperature increase, and the actions implemented by the managers in specific sectors, the spatial effect will be stronger than the seasonal effect in structuring plankton communities.

2. Materials and methods

2.1. Study site

TP-CW (39°22′04"N; 0°20′46"W) is located within the AVNP (Spain; Fig. 1). This Mediterranean coastal Natural Park (Hernández-Crespo et al., 2017) is a Ramsar and Natura 2000 site (Council Directive, 92/43/EEC; Directive, 2009/147/EC; MITECO, 2021) and hosts the hypertrophic AVL with a current annual mean chlorophyll-*a* concentration of approximately 150 μg L^{-1} (IZONASH, 2023); it has suffered from high agricultural, urban, and industrial pressure for many years. Situated on the north border of the AVL, TP-CW, belonging to the Water Authorities (*Confederación Hidrográfica del Júcar*) is managed by two non-governmental organizations (*Acció Ecologista Agró* and SEO-BirdLife), and it was built as a pilot project within the area to improve water quality and species and habitat diversity.

TP-CW was a former rice field transformed *via* ecological engineering to receive water and release it into the AVL, acting as a buffer between low-quality waters and the protected AVNP. The incoming water is a mixture of recirculated water from the AVL and water collected from different agricultural and urban discharges (Fig. 1). Water mixing at the inlet depends on the water level of the AVL, which varies mainly due to agricultural demands for rice cultivation *via* flow management through the opening and closing of floodgates (Soria, 2006). In TP-CW the water depth is controlled by vertical sluice gates at the entrance and the exit. During operation, water flows through TP-CW and is finally released into the AVL. The water flow rates (WFR) were not constant during the study period (Fig. 2; Hernández-Crespo et al., 2017). TP-CW covers an area of 40 ha, and it is divided into different sectors: a free-water surface flow sector (water mean depth of 0.2 m; Fig. 2), which is divided into subsectors and planted with emergent vegetation (*Phragmites australis*, *Typha angustifolia*, *Sparganium erectum* and *Iris pseudacorus*) and two shallow lagoons (called the Reserve and Educative lagoons) located at the end of the system (water depth ranging from 0.3 to 0.7 m), with a surrounding fringe of helophytic vegetation and with occasional occurrences of submerged vegetation meadows (mainly *Chara vulgaris* and *Tolypella glomerata;* Rodrigo et al., 2023).

2.2. Sample collection and analyses

Plankton was sampled at six sites: the General Inlet and Middle Site from 2009 to 2015, the Inlet and Outlet of the Reserve Lagoon from 2009 to 2023, and the Inlet and Outlet of the Educative Lagoon from 2009 to 2012, and from 2017 to 2023. In total, 81 sampling campaigns were carried out during the whole study. Due to the large number of samplings, we decided to analyse data in periods spanning several years. Thus, four periods were established (Fig. 2). The first one ranged from April 2009 to August 2012, spanning the early years after the construction of TP-CW and carrying out 39 samplings in each site (8–13 samplings per year). The second one was established from January 2014 to October 2015, within the framework of a "science-based governance" LIFE project (LIFE12 ENV/ES/000685), with a total of 6 samplings each year. The third period, from March 2017 to June 2019, was marked by the decision of the TP-CW managers to harvest the emergent vegetation

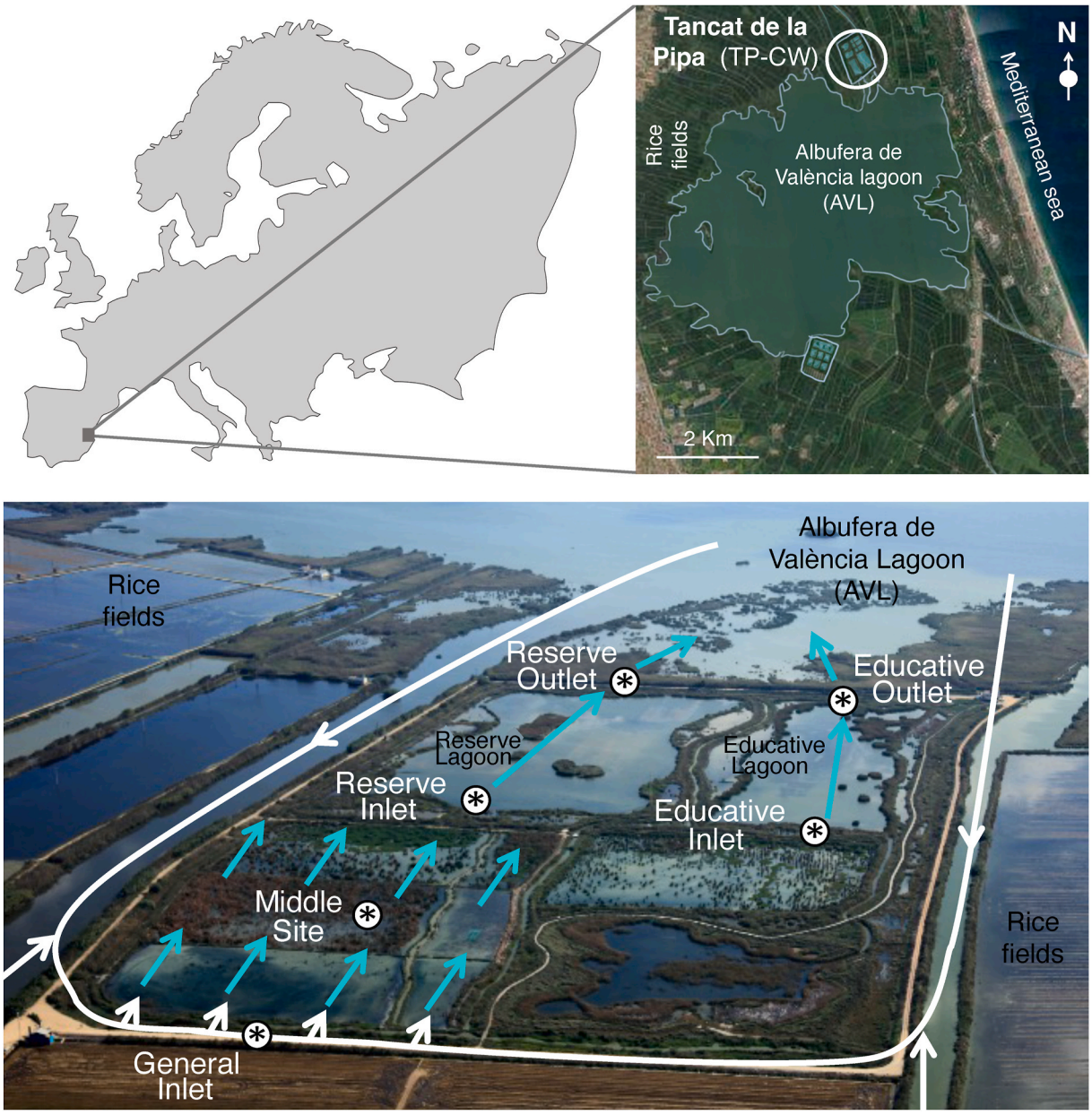

Fig. 1. Location of the studied constructed wetland, Tancat de la Pipa (TP-CW), in the *Albufera de València* Natural Park (AVNP). Its structure, the water flux and the sampling sites (white circles with asterisks) are depicted. The surface water flow from the outside area to the TP-CW inlets is marked with white arrows, and once inside, with blue arrows.

within the Middle Site annually and the vegetation surrounding both lagoons biennially, accompanied by the removal of part of the filamentous algae within both lagoons. During this period, 13 samplings were performed in each site (4–5 samplings per year). Since the end of 2019, a systematic drying of the Middle Site and both lagoons was implemented for several weeks each summer, defining the fourth period, which extends from January 2020 to June 2023. Dryings were also implemented, but only in the Educative Lagoon, in 2012 for maintenance works within the lagoon, and in 2018, following the first outbreak of botulism in TP-CW (Fig. 2; data provided by the TP-CW managers). Moreover, during Period 4, it was decided to increase the water flow in the inlets during the summer season, to reduce the water retention time and decrease phytoplankton proliferation within the lagoons. During this last period, 17 samplings were conducted in each site: 7 in 2020, 3 in 2021, 4 in 2022 and 3 in 2023.

Both phytoplankton and zooplankton samples were taken from the shore of each site at a depth of approximately 25 cm with a handmade sampler designed for shallow water environments. It consisted of a long-handled jug (1.5 m) connected to a 1.5-L jar, which allowed us to collect water samples preventing the resuspension of the sediment. The samplings were always conducted during the morning, from 9 a.m. to 11 a.m. We have included in our "plankton" analyses all the species found in the samples including the benthic organisms, which were also present in these kinds of samples since the wetland is a shallow system with a high connection between the water column and the sediment, and because they are important members of the aquatic network (Puche et al., 2021). Phytoplankton samples (250 mL), fixed with Lugol and preserved in darkened bottles, were counted in Utermöhl chambers with an inverted microscope (Olympus CK2) at 100 and 400 magnifications to obtain the density. At least 400 individuals of the most abundant population were counted, implying a 10% error (Lund et al., 1958). Each species was taxonomically identified to the lowest possible taxonomic level by a

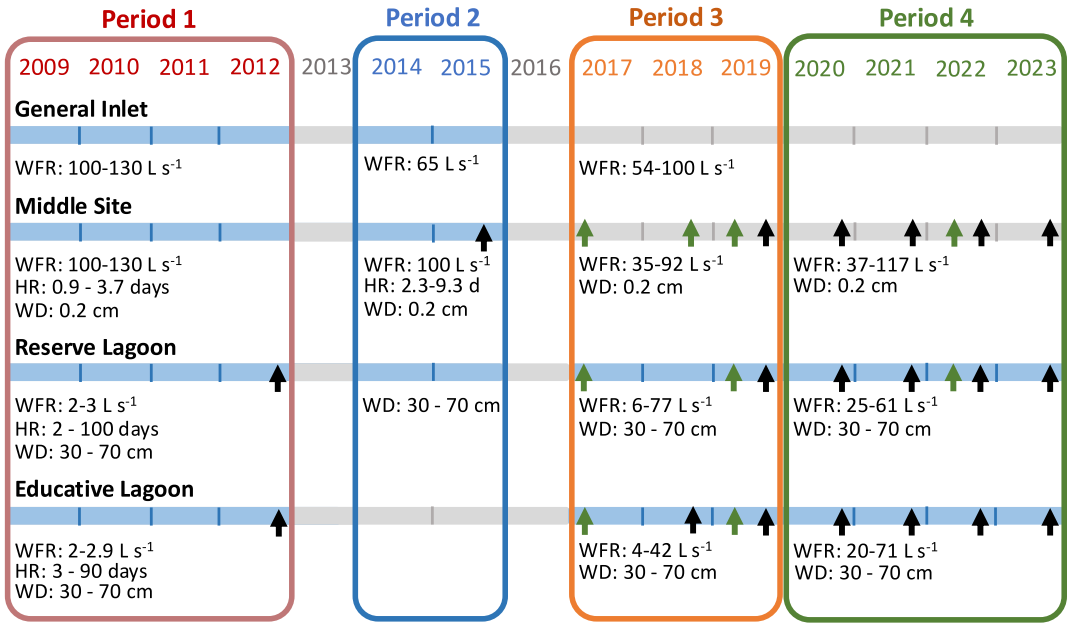

Fig. 2. Sampling periods (1, 2, 3 and 4) established during the study years (from 2009 to 2023; in 2013 and 2016 no monitoring could be performed) according to the management actions carried out within TP-CW during the plankton samplings. The black arrows indicate the systematic dryings implemented by the TP-CW managers, and the green ones denote the harvest times of the emergent vegetation. The water flow rate (WFR), hydraulic retention (HR) and water depth (WD) ranges (maximum and minimum values for each period at the different sites of TP-CW) are also indicated.

qualified expert. Algal biovolume (μm^3) was calculated from cell densities and cell volumes, measuring sizes of, at least, 20 individuals (Rott, 1981; Hillebrand et al., 1999). For zooplankton sampling, between 6 and 10 L of water were collected using the sampler described above and later filtered through 45 μm Nytal mesh and preserved in a glass tube with a formalin solution (4% final concentration). Abundance (population density as ind L^{-1}) was calculated by counting settled samples with an inverted microscope (Olympus CK2) at 40 and 100 magnifications. Taxonomic identification was obtained following the manuals of Dussart (1967), Koste (1978), Segers (1995), Einsle (1996), Orlova--Bienkowskaja (2001) and Nogrady and Segers (2002). For biomass determination (μgDW L^{-1}), at least 20 individuals of each species were measured. Rotifer and ostracod biovolumes were calculated assimilating body shapes to geometrical bodies. Biovolume was converted to biomass, assuming a body density of 1 g cm^{-3}. Crustacean biomass was obtained with length-dry weight regressions and a 1/10 proportion for dry/wet weight.

At each sampling campaign and site, physical and chemical variables were also measured *in situ*, including water temperature (∘C), pH, dissolved oxygen (mg L^{-1}) and conductivity (μS cm^{-1}). Additionally, water samples were taken to laboratory analysis of turbidity (NTU), chemical oxygen demand (mg L^{-1}), dissolved inorganic nitrogen (N-NH_4^+, N-NO_2^- and N-NO_3^-, -mg L^{-1}-) and phosphates (mg L^{-1}), using a Spectroquant® Analysis System from Merck (Martín et al., 2013; Hernández-Crespo et al., 2017). Further details on sampling method and analysis procedures can be found in Martín et al. (2013). Sestonic chlorophyll-*a* (μg L^{-1}) was determined in the lab by extraction of photosynthetic pigments, filtering a known volume of water through a glass microfiber filter (Whatman GF/F, 0.7 μm pore size) and using acetone 90% as a solvent. Absorbance values were determined with a spectrophotometer (Thermo Scientific Genesys 10S UV–VIS) and the equations published by Jeffrey and Humphrey (1975) were used for concentration calculations.

2.3. Data analysis

The data were analysed in two steps. Firstly, to understand the site-effect (General Inlet, Middle Site, Inlet and Outlet of the Reserve and Educative lagoons), the differences between the plankton communities of the different sampling sites were assessed, separating the four periods indicated above. One-way ANOVA tests (or non-parametric Kruskal-Wallis tests if normality and homoscedasticity were not met) were performed to compare total phytoplankton biovolume and zooplankton biomass between sites. Then, t-tests (or non-parametric Mann-Whitney *U* test) were also carried out to evaluate the differences in the biovolume or biomass of the main plankton groups between inlets and outlets of both lagoons. To assess the association between plankton species and the different sampling sites in each period, the indicator value of species was calculated (Dufrêne and Legendre, 1997; De Cáceres et al., 2010). Due to the large number of plankton species detected during the whole period, for this analysis, only those that, at some study sites, exceeded 5% of the total biovolume or biomass were taken into account. The removal efficiencies of potentially toxic cyanobacteria between the inlets and outlets of both lagoons were also determined by assessing the difference in biovolume, using the value of the Inlet as a reference, and expressed as a percentage of biovolume reduction. A Two-way cluster analysis was performed to identify similarities in distribution between plankton functional groups using season and site categories and the Bray-Curtis dissimilarity index as a measure of distance (based on abundance data; Bray and Curtis, 1957). To do this, phytoplankton was grouped into 31 functional groups using the criteria and acronyms given by Salmaso and Padisák (2007). Zooplankton was grouped into seven functional groups (decided according to the species found and the objectives of the study): herbivorous and carnivorous rotifers (HerbRoti and CarnRoti), omnivorous and herbivorous copepods (OmniCope and HerbCope), grazers and filter-feeding cladocerans (GraClado and FiltClado) and ostracods (Ostra). Before the analyses, biovolume and biomass data were normalised by applying a min-max scaling to each functional group. The results were visualised in a heatmap.

Secondly, we assessed changes in plankton communities over time. One-way ANOVA tests (or non-parametric Kruskal-Wallis tests) were performed to compare the total phytoplankton biovolume and zooplankton biomass of the inlets of the four periods among them and the outlets among them. To assess the effect of the environmental variables on plankton functional groups, a distance-based redundancy analysis (dbRDA) was performed based on Bray-Curtis dissimilarity matrices. All the environmental variables were transformed to *z*-score.

The RDA was chosen because it was the best-constrained ordination method according to the detrended correspondence analysis (DCA) (Ter Braak and Prentice, 1988). Before analysis, a Hellinger transformation was applied to the plankton functional groups dataset, as Legendre and Gallagher (2001) suggested on community composition data containing many zeros and used in the statistical analyses. ANOVAs with 999 permutations were performed to assess the significance of constrained axes. Given the results of this last analysis, Pearson correlation coefficients were determined between cladoceran biomass and sestonic chlorophyll-*a* concentrations in the outlets of both lagoons. The averages of sestonic chlorophyll-*a* concentration and the reduction efficiencies between the inlets and outlets were also calculated.

Phytoplankton biovolume can be used as an indicator to assess water quality due to the rapid response to environmental condition changes, the phytoplankton's primary role in the food web and their impact on other organisms (Willén, 2001), However, since the European Water Framework Directive (2000/60/CE) metrics for estimating water quality, based on plankton, were specially designed for lakes and reservoirs, these metrics cannot be suitably applied in our constructed shallow system. Alternatively, and following Willén (2000), we have used the annual means of phytoplankton biovolume to evaluate how the trophic state and ecological status changed as the water flowed through TP-CW, and over time. We can assume, therefore, it properly reflects the effectiveness of TP-CW in this sense.

All analyses were performed in R software version 4.2.2 (R Core Team, 2022). We applied the *anova* and t.*test* functions to determine significant differences between biovolume and biomass, considering statistically significant differences at a probability p-value <0.05. To obtain the indicator value of the species, the *multipatt* function from the *indicspecies* package was used (De Cáceres et al., 2020). A Two-way cluster analysis was performed using the *hclust* function from the *factoextra* package and, *pheatmap* from the *pheatmap* package to visualise

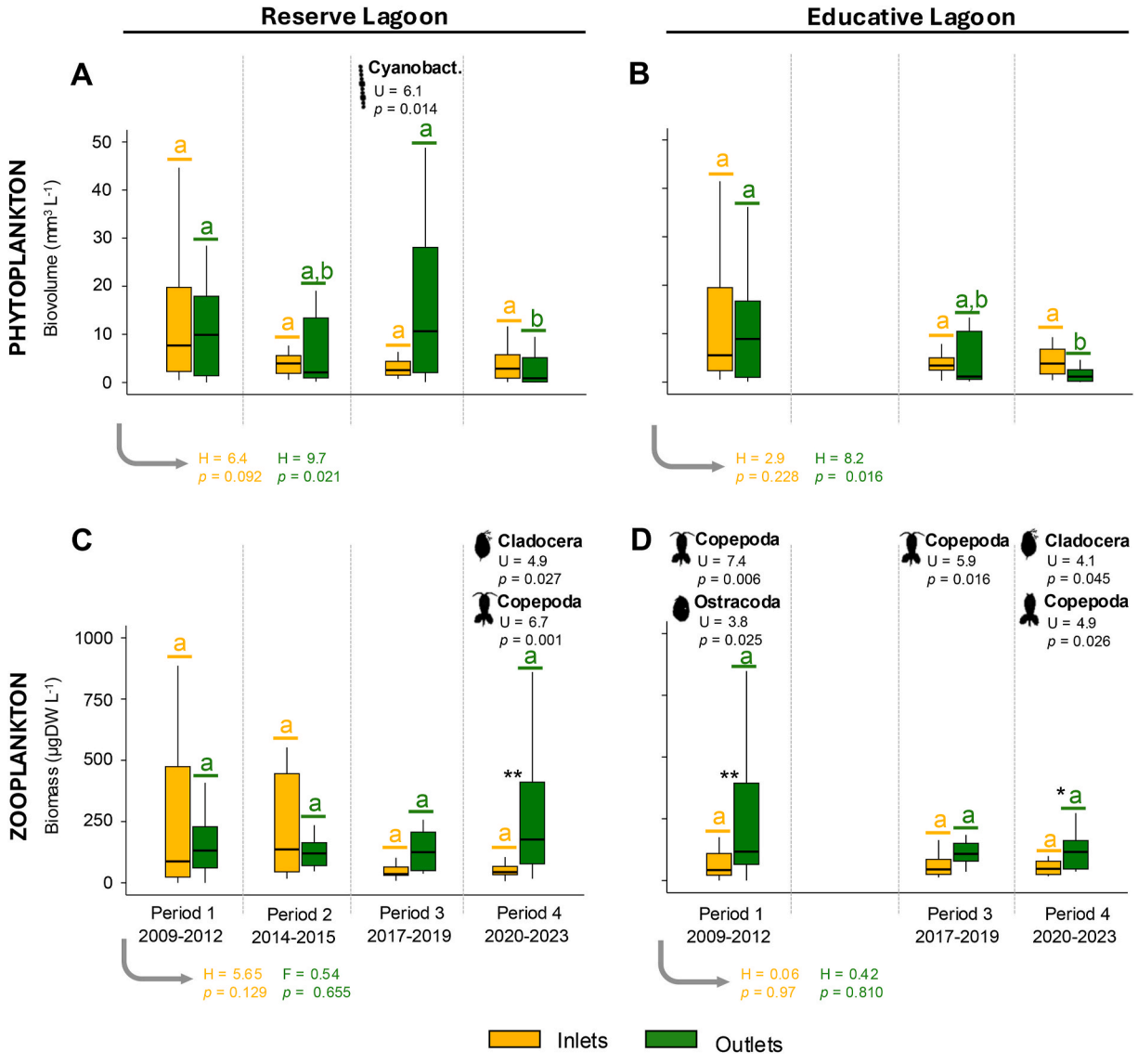

Fig. 3. Box plots of total biovolume of phytoplankton (graphs A and B, in $mm^3\ L^{-1}$) and total biomass of zooplankton (graphs C and D, in $\mu gDW\ L^{-1}$) in the inlets (in yellow) and outlets (in green) of the Reserve Lagoon (left part) and the Educative Lagoon (right part) for each period. The box plot shows the median (black line inside the box), minimum and maximum (thin lines), and first and third quartiles (lower and upper box boundaries). The results of the One-way ANOVA tests or non-parametric Kruskal-Wallis (F/H and p-value) comparing just the inlets (in yellow), and then just the outlets (in green) are shown below each graph. The yellow and green lines above the bars indicate the results of the consequent post-hoc tests (Tukey or Mann-Whitney pairwise tests), showing the differences ($p < 0.05$) or lack of them with small caps ($p > 0.05$). Post-hoc results of the significant One-way ANOVA or non-parametric test comparing sites between them (detailed in Fig. S1) are also indicated (*: *p*-value <0.05; **: *p*-value <0.005). Significant results of *t*-test or non-parametric Mann-Whitney *U* test (U and p-values <0.05) comparing the main plankton groups between sites are indicated for each period.

the results. To obtain Bray-Curtis dissimilarity values, *vegdIist* from the *vegan* package was applied. For dbRDA, we used the *decorana*, *decostand* and *dbrda* functions from the *vegan* package and the *anova* function to verify the axis significance.

3. Results

3.1. Between-site changes in plankton assemblages

For total phytoplankton biovolume, no significant differences were observed between sampling sites considering periods separately (One-way ANOVA, Table S1). Overall, the lowest values were detected in the outlets during Period 4 (2020–2023), even though, from the beginning, the inlets of both lagoons have remained the same (Table S1; Fig. 3). The composition of dominant phytoplankton groups varied through sites and periods, but with a strong dominance of diatoms and cryptophytes during the whole study (Fig. S1). Euglenophytes accounted for a high percentage of the total biovolume during Period 1, and in the inlets of the lagoons in all the other periods (Fig. S1). Significant differences from the *t*-test were found only for cyanobacteria in Period 3 (2017–2019), which were higher at the Outlet compared to the Inlet of the Reserve Lagoon (Fig. 3).

Total zooplankton biomass varied throughout sampling sites during the study period (One-way ANOVA, Table S1). Significant differences were observed between the Inlet and Outlet of the Educative Lagoon in Period 1 (2009–2012), and also between the inlets and outlets of both lagoons during Period 4 (Table S1; Fig. 3). However, comparing the inlets among them and outlets among them, no differences were observed (One-way ANOVA, Fig. 3). The dominance of rotifers in total biomass occurred during all periods and sampling sites except for the outlets of both lagoons during Period 4 (Fig. S2). During this last period, the outlets had significantly greater numbers of cladocerans and copepods (*t*-test, Fig. 3). In the Educative Lagoon, a significantly greater number of copepods was also observed in Period 1 (along with ostracods) and Period 3 (*t*-test, Fig. 3).

A total of 343 phytoplankton taxa and 153 zooplankton taxa were identified in TP-CW throughout the studied period (2009–2023; Table S2). However, only 149 taxa for phytoplankton and 59 for zooplankton were considered as main descriptors of the phytoplankton and zooplankton communities (*i.e.*, representing at least five per cent of each taxon in relation to total phytoplankton biovolume or zooplankton biomass). The analysis of the indicator value of species revealed distinct patterns across the study period. During Period 1 (2009–2012), species of potentially toxic cyanobacteria were detected as indicators exclusively at the Outlet of the Reserve Lagoon (*e.g., Cylindrospermum* sp.), but not at the inlets (Table S3). This observation persisted during Period 3 (2017–2019), but also with potentially toxic cyanobacteria as indicators at the inlets of both lagoons (*Anabaenopsis circularis*, *Microcystis aeruginosa*, etc.). In Period 4 (2020–2023), no potentially toxic cyanobacteria were detected at any of the sampling sites. During Periods 3 and 4, a mixotroph species of cryptophytes (*Chroomonas* sp.) and a sessile euglenophyte species (*Colacium* sp.) were indicator species at the outlets. Until Period 4, filter-feeding cladocerans (*Daphina magna*) were not detected as indicators at the outlets. On the other hand, in Periods 1 and 3, almost all zooplankton indicator species in both outlets were rotifers (*Alona rectangula, Asplanchna brightwellii, Lecane bulla*, *Polyarthra dolichoptera,* etc.) (Table S3).

In contrast to Periods 1, 2 and 3, in which the removal efficiencies of potentially toxic cyanobacteria between the inlets and outlets of both lagoons did not occur in more than 25% of the samplings, in Period 4 this percentage rose to more than 50% in both lagoons (Fig. S3). In fact, during Period 4, in approximately 50% of the cases, these reductions resulted in the total elimination of the potentially toxic cyanobacteria biovolume, and there was only an increase in two of the samplings, these being ones of the lowest accumulations throughout the study period (Fig. S3).

A total of 25 functional groups for phytoplankton and seven for zooplankton were identified in TP-CW throughout the studied period. Two-way cluster analyses showed how functional groups during Periods 1 (2009–2012), 2 (2014–2015) and 3 (2017–2017), are separated seasonally, by winter-spring and summer-autumn (Fig. 4). The biovolume of phytoplankton increased rapidly during the summers and autumns, and was mainly dominated by cyanobacteria functional groups (Nostocales, UnicCyano, LargeVacC, SmallChroo and FilaCyano), and large *Euglena* species (LargeEugl). In terms of zooplankton, rotifers dominated (HerbRoti and CarnRoti). The opposite trend could be observed during the winters and springs of these periods, but with the presence of diatoms (LargeCent and SmallPenn) and omnivorous copepods (OmniCope). During Period 4 (2020–2023), functional groups were more grouped by sampling sites than by seasons. The inlets of both lagoons had greater amounts of cyanobacteria (FilaCyano, SmallChroo, UnicCyano and Nostocales), euglenas (SmallEugl and LargeEugl) and small phytoplankton species (SmallCent, SmallPenn and SmallChry1) than the outlets. However, the outlets of TP-CW were related to zooplankton functional groups, mainly cladocerans (FiltClado and GraClado), herbivorous rotifers (HerbRoti), ostracods (Ostrac). Chlorophytes (NakeChlor and GelaChlor) and large pennate diatoms (LargePenn) were abundant throughout the sites and seasons (Fig. 4).

3.2. Between-periods changes in plankton assemblages and relationships with environmental variables

The results of the distance-based ordination analysis (dbRDA) demonstrated temporal differences for all six sampling sites, separating each period of years (Fig. 5). The highest value of R-square was observed when we analysed functional groups in the Outlet of the Educative Lagoon and environmental variables (R-square = 0.39); all the rest, shown in Fig. 5, also had an R-square higher than 0.30.

Water temperature and dissolved oxygen (Temp and DO) were the environmental variables that influenced most plankton assemblages, followed by the chemical demand for oxygen and the chlorophyll-*a* concentration (COD and Chl) (Fig. 5). The General Inlet and Middle Site showed that Period 1 (2009–2012) was related to temperature and associated with herbivorous rotifers (HerbRoti) (Fig. 5). The inlets of both lagoons showed that Period 1 was related to chlorophyll-*a* and associated with cryptophytes (Crypto) and filter-feeding cladocerans (FiltClado), particularly in the Educative one. Period 4 (2020–2023) was related to temperature and associated with unicellular cyanobacteria (UnicCyano), herbivore zooplankton (HerbCope and HerbRoti) and small euglenophytes (SmallEugl). However, the outlets of both lagoons in Period 4 were negatively related to chlorophyll-*a*), turbidity (Turb) and temperature, and associated with cladocerans (FiltClado and GraClado), especially filter-feeding ones. Period 1 was related to the concentration of chlorophyll-*a* and associated with cryptophytes, cyanobacteria (Nostocales, FilaCyano and UnicCyano) and small phytoplankton species (SmallDino, SmallChlor, CmallChry2, SmallEugl, etc.). Compared with temperature, dissolved oxygen had the opposite dynamic and chemical oxygen demand had the same dynamic. Nutrients (ammonium, nitrate, nitrite and phosphate) were not significant environmental variables in most sampling sites.

There was a statistically significant and inverse correlation between the dynamics of cladoceran biomass and the concentration of chlorophyll-*a* in the outlets of both lagoons (Reserve Lagoon: $r = -0.29$, $p = 0.010$, Educative Lagoon: $r = -0.27$, $p = 0.031$; Fig. S4). Both lagoons facilitated reductions in sestonic chlorophyll-*a* concentrations in the water during Periods 1 (2009–2012, only in the Reserve Lagoon), 2 (2014–2015) and 4 (2020–2023) (Fig. S5). The highest reductions occurred during Period 4, with over 20% and 50% of mass removal in the Reserve and Educative lagoons, respectively (Fig. S6). According to the results of the trophic state following Willén (2000), the oligotrophic state was reached in the outlets of both lagoons only in Period 4 (Fig. S7). From the beginning of Period 4, no hypertrophic states were

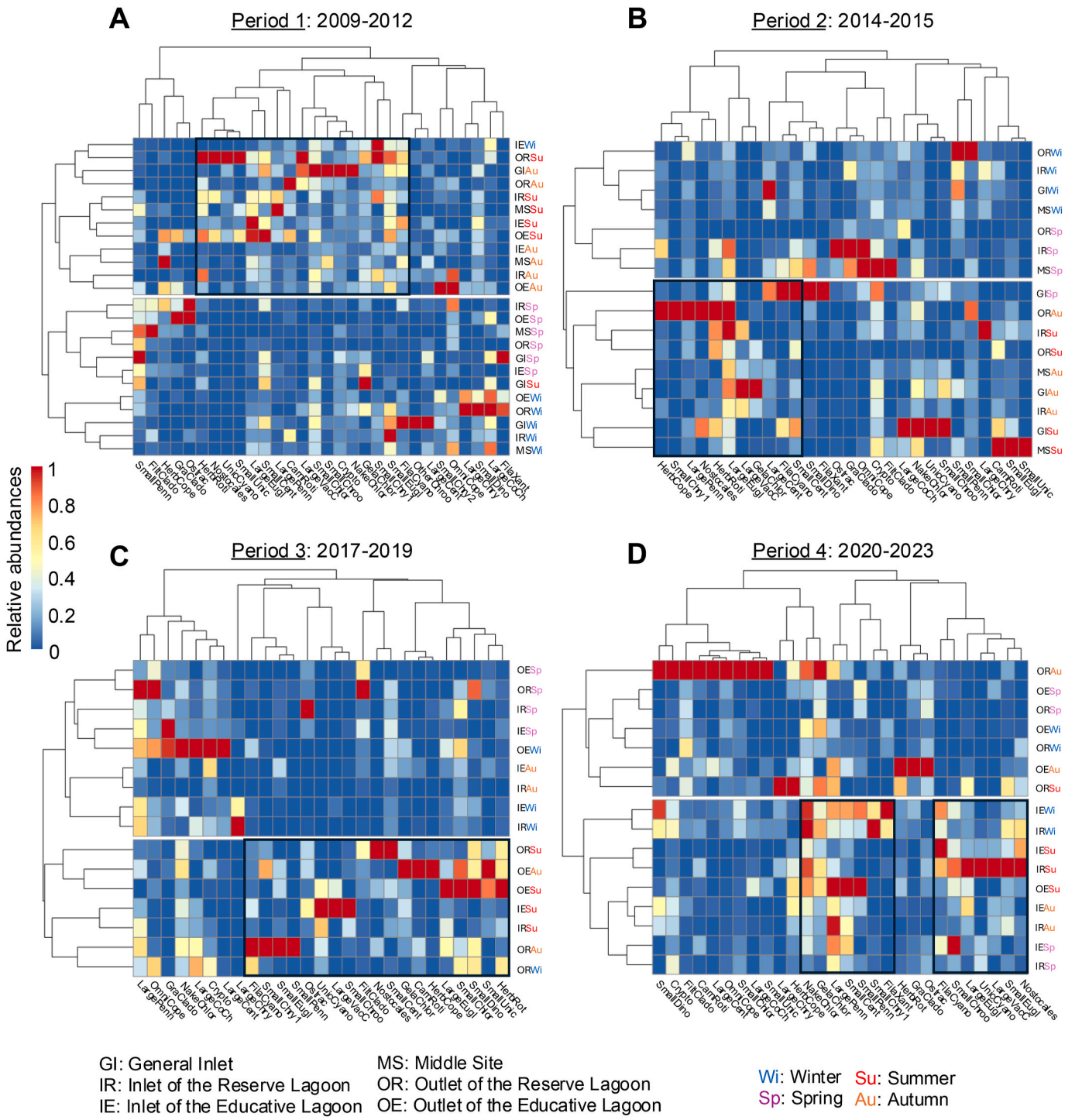

Fig. 4. Heatmap showing the results of the relative abundance of functional groups in the different sampling sites (General Inlet, Middle Site and Inlet and Outlet of the Reserve and Educative lagoons) and seasons in the established periods (Period 1, 2, 3 and 4, corresponding to graphs A, B, C and D, respectively). Two-way cluster dendrograms of the community structure are also shown. Phytoplankton functional groups and acronyms as suggested by Salmaso and Padisák (2007); the zooplankton ones are indicated in the "Material and Methods" section.

detected again (Fig. S7).

4. Discussion

After nearly 15 years of operation, TP-CW has not only maintained but it has also improved its capacity to enhance the biological quality of the water, one of the main reasons for its construction, thus, supporting our first and second hypotheses. The significant rise in air temperature detected in TP-CW from 2009 to 2023 (Pearson's $r = 0.7$; $p = 0.003$, see Fig. S4; AVAMET, 2023), and consequently in the water, should have stimulated microalgal growth (Kholssi et al., 2023; Dory et al., 2024). However, the total phytoplankton biovolume at the outlets of both lagoons was significantly lower in the last period (2020–2023) compared to the others. A greater top-down control may have caused this (Jeppesen et al., 2011), since the zooplankton biomass was significantly greater in the outlets of both lagoons compared to the inlets in Period 4.

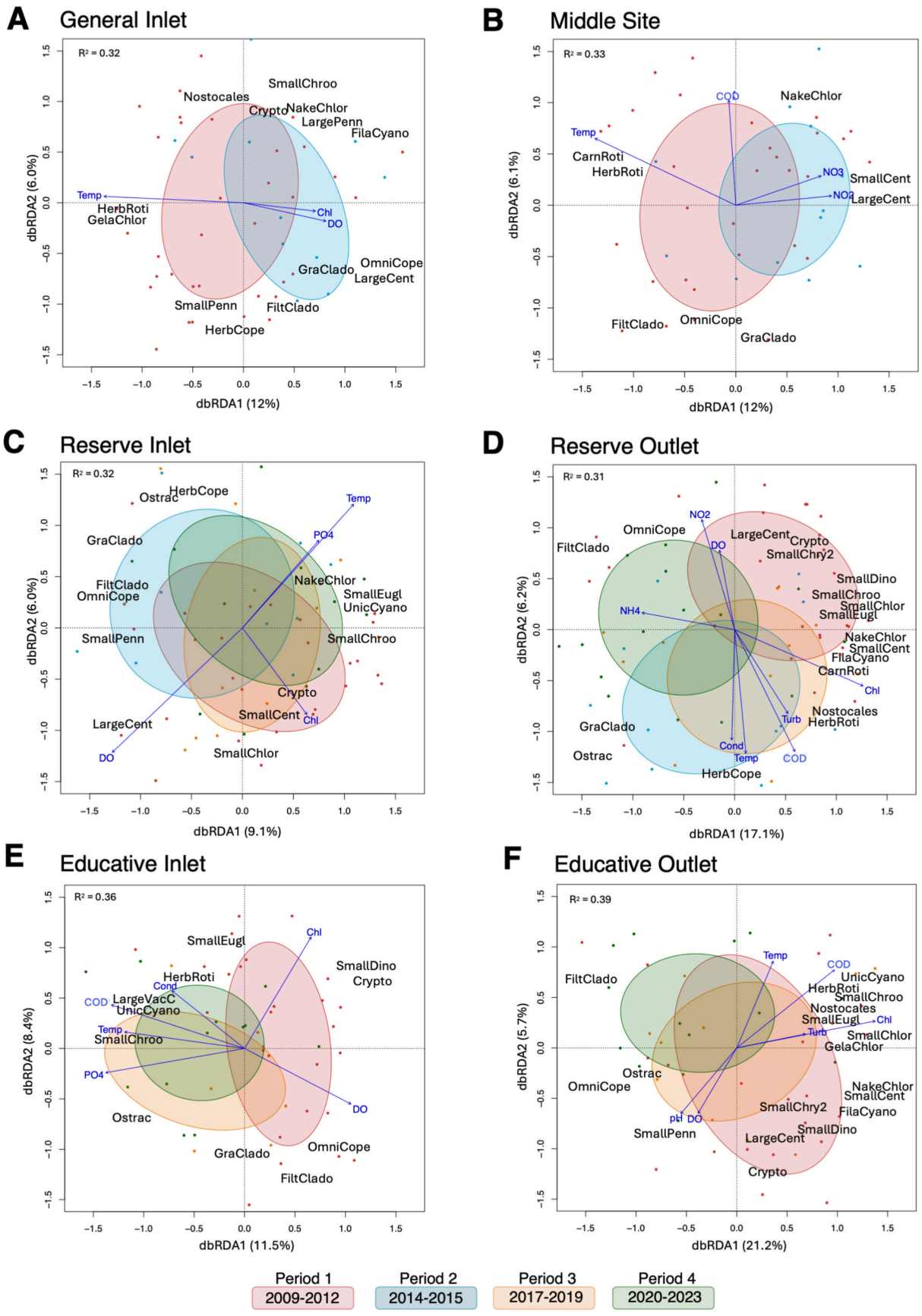

Fig. 5. The dbRDA ordination of plankton functional groups and environmental variables at the six sampling sites (General Inlet, Middle Site, Inlets and Outlets of the Reserve and Educative lagoons, corresponding to graphs A, B, C, D, E and F respectively) for each established period (Period 1, 2, 3 and 4). Phytoplankton functional groups and acronyms as suggested by Salmaso and Padisák (2007); the zooplankton ones are indicated in the "Material and Methods" section.

This clear improvement in biological water quality in both outlets during Period 4 became especially relevant when most of the zooplankton was composed of filter-feeding cladocerans. The significant increase in air-water temperature coupled with the systematic drying implemented in the lagoons, followed by the corresponding re-inundation, promoted the earlier hatching of diapause eggs, mainly those from cladocerans such as *Daphnia magna*, which had previously been found in high densities in the sediment of TP-CW (more than 30 ephippia g DW sediment^{-1}; Rodrigo et al., 2021). This fact stresses the relevant internal contribution of cladocerans from the ephippia sediment bank in TP-CW. Once in the water column, the herbivory of these organisms reduced the water turbidity by reducing phytoplankton biomass, allowing light to penetrate to the sediment and promoting the germination of charophytes (Scheffer et al., 1993; Rodrigo et al., 2023) from the bank of oospores present in the sediment of both lagoons (Alonso-Guillén, 2011; Rodrigo et al., 2013b). The aquatic vegetation can also positively affect zooplankton communities by acting as a refuge from predators for larger, mainly pelagic zooplankton species, such as *Daphnia*, and also by expanding the habitat for benthic macrophyte-associated species (Jeppesen et al., 1997; Rodrigo et al., 2018). In turn, charophytes consume nutrients (bottom-up control), and with their allelopathic effects outcompete phytoplankton (Rodrigo et al., 2007; Rojo et al., 2013). Since 2020, in TP-CW there have been repeated phases of totally transparent water (less than 1 μg Chl-a L^{-1} and less than 5 NTU) with spontaneous growth of charophytes (mainly *Tolypella glomerata* and *Chara vulgaris*) in these lagoons, reaching their maximum historical coverage in 2023 with an extension of 3.75 ha (Rodrigo et al., 2023). The systematic drying implemented in TP-CW since 2019 was always initiated with partial drainage which reduced the water level, attracting herons (*Ardea cineresa* and *A. purpurea*) to feed on the exposed fish (mainly *Cyprinus carpio* and *Lepomis* sp.) (Ferris, D. personal communication). Subsequently, the lagoons were completely dried out, facilitating the manual removal, by the managers, of any remaining fish as well as filamentous algae biomass, which also developed in the lagoons (overgrowth that they tried to control by increasing the water flow), and the beginning of diapause egg formation by zooplankton. This practice effectively reduced the predation of planktivorous fish (such as *Gambusia hoolbroki*, also inevitably present in TP-CW) and fry of other fish, on filter-feeding cladocerans once hatched from the sediment and minimised herbivory and mechanical disturbance on submerged vegetation during the whole year (Torn et al., 2010; Zhang et al., 2014; Li et al., 2024). At the same time, complete drying also allowed the atmospheric oxygen to oxidise the sediment surface and thus decrease the phosphorus for the next year (Wu et al., 2024).

Despite the fact that comparisons in mean phytoplankton biovolume did not show significant differences between the inlets and outlets due to great data variability (which partially refutes our first hypothesis regarding the planktonic primary producers), in 2023, for the first time, oligotrophic states (according to Willén, 2000) were achieved in both outlets, together with a low representation of small-size phytoplankton, due to the effect of filter-feeding cladocerans on edible phytoplankton (Sommer and Sommer, 2006). Moreover, the lowest sestonic chlorophyll-*a* concentration was reached in the outlets in Period 4 (2020–2023), both when comparing these outlets in other periods, as well as comparing the outlets and inlets during the same period. Through the characterisation of the sampling sites with the indicator value of the species, *Daphnia magna* appeared as dominant in the Outlet of the Reserve Lagoon. However, the presence of other, not-so-large filter-feeding cladocerans (such as *Macrothrix laticornis*) implies a wide variety of predators and, with that, a wider grazing spectrum over phytoplankton (Sommer and Sommer, 2006) having a strong structuring power on the planktonic community by selective feeding (Lampert, 1974; DeMott, 1981). Indeed, the maximum reduction for potentially toxic cyanobacteria was achieved at the outlets throughout Period 4. The concentrations of these problematic taxa found within the lagoons during all the periods were similar to the ones found in other inner sites of TP-CW (Rodrigo et al., 2013a; Calero et al., 2015), but during Period 4, in all the samplings, the measured concentrations were below the toxicity limit of 2 mm^3 L^{-1} established for the AVL (Romo et al., 2013).

Plankton communities in TP-CW differed between seasons, as has also been observed in other CWs (Travaini-Lima et al., 2016; Latinopoulos et al., 2020). However, the environmental management interventions (helophyte harvesting, drying and variations in water flow rate) along with the increase in temperature in recent years, seem to have diminished the seasonal effect on structuring plankton communities in Period 4 (2020–2023), making the "site effect" more pronounced (and supporting our third hypothesis). During the first three periods (from 2009 to 2019), as observed in other Mediterranean wetlands, rotifer biomass fluctuated from low values in winter-spring to maximum biomass in summer-autumn. Copepods, on the other hand, mainly peaked in winter and spring in TP-CW, as has also been observed in other wetlands (Ortega-Mayagoitia et al., 2000). Phytoplankton, particularly cyanobacteria, decreased in spring when cladocerans appeared (Gyllström and Hansson, 2004). As the rice fields of the surroundings of TP-CW have the appropriate conditions to favour the hatching of cladoceran diapause eggs (Rodrigues et al., 2011), cladoceran individuals were carried to TP-CW when, from January to March, the rice farmers released their excess irrigation water into the gullies from which water enters TP-CW (Romo et al., 2005), possibly explaining the lack of significant differences in the biomass of cladocerans between the inlets and outlets of the lagoons during the first three periods, because a large part of them might have come from outside. In the springs and winters, an increase in diatoms was also observed. Numerous species of cyanobacteria, such as *Dolichospermum* spp. and *Microcystis* spp. were described as potentially toxic (Sant'anna & Azevedo, 2000; Jakubowska et al., 2013) and may be responsible for inhibiting the growth of other algae groups such as diatoms (Keating, 1978). These patterns were also observed in Period 4, however, the presence of cladocerans (mainly filter-feeding ones) was maintained in both outlets throughout all the seasons, favoured by all that has been mentioned above. In contrast to the outlets, the inlets during Period 4, as expected by the subsequent top-down control within the lagoons, had greater amounts of small phytoplankton species and cyanobacteria.

The results from TP-CW align with the findings from other CWs and similar systems. CWs have been widely recognised for their capacity to improve water quality and control phytoplankton through the regulation of biological interactions. Research on fish removal (Zhang et al., 2014), supports the strategy carried out in TP-CW to control planktivorous fish populations, promoting the growth of macrophytes and large-body cladocerans like *Daphnia*, improving the overall ecosystem features. Vymazal (2014, 2022) highlights the importance of promoting biological filtration by the zooplankton in similar systems, consistent with the reduction of phytoplankton observed in TP-CW. Studies by Jeppesen et al. (1997, 2011) and Moshiri (2020) demonstrate that the management of CWs through the integration of hydrological control and biotic factors can lead to more stable plankton communities and oligotrophic conditions, as has occurred in TP-CW. These comparisons emphasize the importance of adaptive management practices in CWs to optimize their ecological functioning over time.

5. Final remarks and conclusions

Our results confirm that TP-CW management actions have been effective in coping with the effects of increased temperature, and that TP-CW is increasingly efficient in enhancing the planktonic community, improving the biological quality of the water over more than 10 years of operation. The drying of parts of TP-CW, which was initially designed as a measure to curb botulism outbreaks common in areas like this (high temperature, high bird densities, shallow waters, sporadic anoxic conditions; Rocke and Bollinger, 2007), has played a crucial role. This management practice has not only prevented such diseases, but has also enhanced the ecological functioning of the CW, leading to the ecosystem

service of improving water quality and promoting the development of more stable plankton communities. Nevertheless, TP-CW is currently facing a new challenge posed by climate change. Since 2020, a significant increase in the number of flamingos (*Phoenicopterus roseus*) has been reported within the AVNP (eBird, 2023). Since the start of monitoring, the greatest number of flamingos within TP-CW was reported for 2023 (in particular, more than 500 individuals on the same day within the Reserve Lagoon; Ferris, D. personal communication), whereas, in previous periods (Periods 1, 2 or 3), their numbers never exceeded 100 individuals. The poor conservation state (mainly lack of water) of the really suitable wetlands for this species, such as *Doñana* National Park (in southern Spain), forced the flamingos to move to other places in search of water, shelter and food availability (Donnelly et al., 2020; Qiu et al., 2024), arriving in large number at the AVNP. Such a high abundance of flamingos has a strong impact on wetlands, since they trample submerged vegetation and sediment, causing resuspensions and increasing water turbidity. Moreover, the contribution of guano by flamingos to the water column increases the nutrients that favour the presence of phytoplankton (Batanero et al., 2017), thereby altering the aquatic ecosystem. In fact, in 2024 the number of flamingos has continued to increase, and the charophyte meadows in the TP-CW lagoons were less extensive than in previous years. All this makes evident new challenges for environmental management in CWs.

As a final remark, and through the results of this study, we advocate for long-term research which reveals the dynamics of CW functioning, not only in terms of physical and chemical variables, but also considering the crucial role of biological factors, such as plankton communities. Understanding the interplay between these elements is essential to establish effective management measures in the current context of global change.

CRediT authorship contribution statement

Nuria Carabal: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Luciana S. Cardoso:** Writing – review & editing, Supervision, Software, Methodology, Formal analysis, Conceptualization. **Judit Padisák:** Writing – review & editing, Supervision, Methodology. **Géza B. Selmeczy:** Writing – review & editing, Supervision, Software, Methodology. **Eric Puche:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **María A. Rodrigo:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Nuria Carabal de Antonio reports financial support was provided by University of Valencia Cavanilles Institute of Biodiversity and Evolutionary Biology. Nuria Carabal reports financial support was provided by Generalitat Valenciana. Judit Padisak reports financial support was provided by Hungarian National Research, Development and Innovation Office, Hungary. Judit Padisak reports was provided by National Laboratory for Water Science and Water Safety program, Hungary. Geza B. Selmeczy reports financial support was provided by Hungarian National Research, Development and Innovation Office, Hungary. Geza B. Selmeczy reports was provided by National Laboratory for Water Science and Water Safety program, Hungary. Eric Puche reports financial support was provided by University of Valencia Cavanilles Institute of Biodiversity and Evolutionary Biology. Eric Puche reports financial support was provided by Government of Spain Ministry of Universities. Maria. A. Rodrigo reports financial support was provided by University of Valencia Cavanilles Institute of Biodiversity and Evolutionary Biology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be available in the institutional repository of the Universitat de València (Roderic).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envres.2024.120114.

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