Journal of Water Process Engineering 66 (2024) 105974

Contents lists available at ScienceDirect

Journal of Water Process Engineering

journal homepage: www.elsevier.com/locate/jwpe

Assessing the effects of salinity on microbial communities and pollutant removal in urban wastewater treatment plants

Alvaro Javier Moyano Salcedo [a,b,d,*], Miguel Cañedo-Argüelles [a], Sujay S. Kaushal [c], Eva Maria Ciriero-Cebrián [d], Adrià Perez-Blanco [d], Humbert Salvadó [d]

[a] FEHM-Lab (Freshwater Ecology, Hydrology and Management), SHE-2, Institute of Environmental Assessment and Water Research (IDAEA), CSIC, Carrer de Jordi Girona, 18-26, 08034 Barcelona, Spain

[b] Geohazards and Civil Engineering Research Group, Department of Civil Engineering, Saint Thomas Villavicencio University, C/22 No 1a, 500003 Villavicencio, Colombia

[c] Department of Geology & Earth System Science Interdisciplinary Center, University of Maryland, College Park, MD, USA

[d] Department of Evolutive Biology, Ecology and Environmental Sciences, University of Barcelona, 08028 Barcelona, Spain

ARTICLE INFO

Editor: Li Gao

Keywords:
Wastewater treatment plants
Electrical conductivity
Salinity effects
protozoa communities
Pollutant removal efficiency

ABSTRACT

This study assessed the impact of electrical conductivity (EC) on the microeukaryotic community and pollutant removal efficiency in full-scale wastewater treatment plants (WWTPs) in Catalonia, Spain. Monthly samples from seven WWTPs (2010−2021) were collected, with microbial communities identified by microscopy and effluent quality parameters measured. Linear mixed-effects models (LMER), indicator species analysis (IndVal), and structural equation modeling (SEM) were used to evaluate the effects of EC on WWTP operation and microbial communities. EC levels varied widely among WWTPs (800 to 15,000 μS cm^{-1}), with mean removal rates generally low, not exceeding 26 %. EC removal was inversely correlated with organic matter removal ($p < 0.05$). IndVal analysis revealed distinct microbial communities associated with each WWTPs along the EC gradient (e.g., *Beggiatoa* spp. and *Epistylis* sp. were associated with high and low EC, respectively). High EC and peaks negatively affected the abundance of certain microorganisms (e.g., *Acineria uncinata*) ($p < 0.05$). Ciliate genera were most affected by EC peaks, with different species showing different salinity tolerance ranges (e.g. *Holophyra discolor* was affected by EC > 3000 μS cm^{-1}). Seasonal variations did not significantly alter community sensitivity to salinity ($p > 0.05$). LMER and SEM analyses revealed strong adverse effects of high EC and EC peaks on microbial diversity, richness, and the efficiency of organic matter and TKN removal ($p < 0.05$). This highlights the importance of monitoring and controlling EC levels in WWTP influent to maintain optimal treatment performance and the need for effective technologies or biological processes to mitigate saline discharges into rivers.

1. Introduction

Wastewater treatment plants (WWTPs) continuously receive saline wastewater from cities, which can adversely impact their operational conditions and overall functioning [1]. This saline influx can affect physical (e.g., accelerated corrosion), chemical (e.g., coagulation efficiency), and biological processes (e.g., inhibition of microbial communities) within WWTPs [2–4]. For example, the accumulation of saline influent in treatment units (e.g., activated sludge tanks) [5–7] can limit their ability to effectively remove pollutants (e.g., organic matter, nutrients) [8–10]. However, the resistance and resilience of microeukaryotic communities (e.g., protozoan) to increased salinity is still poorly understood, particularly in full-scale WWTPs. Also, the vast majority of experiments simulating activated sludge conditions have used indirect measures, such as the oxygen uptake rate (OUR), to assess community responses (Table S1). Therefore, the direct effects of salt on these communities in a practical operational setting remains unexplored [2,11]. Understanding salinity dynamics within WWTPs is necessary to maintain overall pollutant removal efficiency [12] and safeguard water quality for ecosystems and human consumption [13,14].

Salinity levels in urban wastewater depend not only on domestic activities [15,16] but also on contributions from construction (e.g.,

* Corresponding author at: FEHM-Lab (Freshwater Ecology, Hydrology and Management), SHE-2, Institute of Environmental Assessment and Water Research (IDAEA), CSIC, Carrer de Jordi Girona, 18-26, 08034 Barcelona, Spain.

E-mail address: alvaromoyano@ub.edu (A.J.M. Salcedo).

https://doi.org/10.1016/j.jwpe.2024.105974
Received 12 June 2024; Received in revised form 30 July 2024; Accepted 10 August 2024
Available online 16 August 2024

highway paving and building expansion wastes), transportation (e.g., road de-icers, salts from asphalt wear), and industrial facilities (e.g., food additive and cleaning product industries) [17–20]. The latter occur when treated discharges connect to sewage systems, and ion removal is inefficient (e.g., due to poor regulation and lack of specific salt removal processes) [13,21]. Also, salinity concentrations in the urban environment can vary between regions and seasons. For instance, ion levels in wastewater may increase due to the use of water softeners in areas with hard water [22,23], and the application of salts for ice prevention in municipalities with combined sewage systems can lead to seasonal salinity peaks during winter months [16,19]. In coastal areas, variations in salinity can also occur due to seawater intrusion during high tide seasons [24,25]. Since salt removal efficiency depends on the treatment type [26], the operating conditions, the bacterial communities involved [27], and their adaptation to salinity [28–30], salt removal in WWTPs might require advanced treatments, which are usually lacking in WTTPs located in small and medium size cities [4,31]. Moreover, treatments like reverse osmosis or membrane systems are costly, energy-intensive, and produce by-products (e.g., brines), limiting their adoption [32,33]. Consequently, most urban WWTPs rely on indirect salt removal processes (e.g., conventional physicochemical and biological reactions) and rarely monitor salinity variations and their effects on microbial communities [34,35].

According to laboratory experiments, salinity can negatively impact microbial communities growing in activated sludge, but the salinity tolerance varies among groups, families, genera, and species [2,11,36,37]. However, there are barely no studies testing the response of microbial communities to increased salinity under real conditions (i.e., full-scale WWTPs), especially for microeukaryotic groups (e.g., ciliates, flagellates) [2]. The few available studies show that salinity primarily affects protozoa and metazoa, with less pronounced effects on bacterial activity [38]. Indeed, a strong negative effect of salinity has been observed for some protozoan communities (e.g., rotifers and nematodes), leading to their reduction or even disappearance when salinity exceeds a certain threshold (> 20 g/L NaCl) [2,39,40]. This negative response might depend on the species considered. For example, it has been shown that ciliates such as *Vorticella* spp. and *Opercularia articulata* can survive wide NaCl gradients (from 3 to 40 g/L NaCl) depending on their body size and the exposure time [2]. Understanding the response of protozoans to salinity is important because they play a major role in wastewater treatment and because their mortality has been shown to trigger trophic cascades in other food webs (e.g., reduced ciliate grazing leading to increased bacterial populations and potential effluent quality issues) [41,42].

Overall, there is little information on how salinity can affect the structure and seasonal dynamics of microbial communities involved in water treatment [43–47]. For example, sudden saline water inflows during storm events lead to temporary salinity peaks that can alter the structure of microbial communities [16,25]. At the same time, the response of the microbial communities to increased salinity might depend on the time of the year at which the event occurs. For example, seasonal temperature variations can cause shifts in microbial community composition, with certain taxa becoming more dominant in warmer months while others thrive in cooler conditions [46–48].

Understanding how microbial communities are modulated by EC is important because it can affect pollutant removal, although the available studies provide conflicting information (Table S1). It has been reported that pollutant removal efficiency is reduced under high saline conditions [1,49–51] due to inhibition of microbial enzyme activity or the mortality of microorganisms [52–55]. Conversely, some studies have not observed significant effects of saline wastewater on pollutant removal [56,57], provided that there is no impact on the colonization of microeukaryotic species (e.g., yeast *Meyerozyma*) associated with efficient contaminant removal [8,58]. Moreover, the vast majority of the studies addressing the effects of salinity on WWTPs employed pilot systems simulating high NaCl levels (30–60 g/L) with advanced treatments (e.g., MBBR) [59,60]. Thus, the typical salinity of full-scale conventional plants (< 20 g/L NaCl) [49], which can vary between cities and climates, has been overlooked [4,13,61].

In this study, we focused on the protozoa community due to its crucial role as a filtering community responsible for the elimination of suspended solids, as well as a bioindicator used to monitor effluent quality [36,62–66]. Also, the loss of protozoa can affect the entire microbial community through cascade effects, negatively impacting the wastewater treatment process [38,42,65,66]. We assessed the electrical conductivity (EC, used as a proxy for salinity) dynamics within seven urban WWTPs and their effects on the protozoa communities, with a special emphasis on salinity peaks and their implications for pollutant removal efficiency. The specific objectives of this study were to: (i) assess the effects of salinity on protozoan diversity and richness in full-scale urban WWTPs; (ii) identify the impact of EC peaks on microbial abundance and community dynamics; and (iii) evaluate the effect of increased salinity and salinity peaks on pollutant removal efficiency within WWTPs.

2. Materials and methods

2.1. Description and operating conditions of WWTPs

The study included seven WWTPs located in the Mediterranean region of Catalonia, Spain. These WWTPs, specifically located in the municipalities of Roses (WWTPRSS), Llançà (WWTPLLN), Castelló d'Empúries (WWTPCES), Reus (WWTPRUS), Amposta (WWTPAMP), Les Cases d'Alcanar (WWTPALC) and Sant Carles de la Ràpita (WWTPSCR), were selected for their local relevance, data availability, accessibility, and the use of biological systems for the removal of organic matter and, in some cases, nutrients. A detailed description of each WWTP is shown in Table S2 [67]. During the study period (2010–2021) samples were collected monthly from the WWTP biological treatment processes. These samples were analyzed for the identification of microeukaryotic and filamentous communities. Also, a comprehensive dataset of operational parameters and effluent quality measurements was compiled monthly for the specified study period. An approach of profiling each WWTP is presented (Table S2), based on site visits and data collection from the Catalan Water Agency [67], to show the main design and operating conditions.

2.2. Physical and chemical wastewater conditions

Influent and effluent quality parameters such as EC, pH, temperature, dissolved oxygen (DO) in the aeration tank, organic matter (biochemical oxygen demand, BOD_5, chemical oxygen demand, COD), nitrogen (total nitrogen (TN), Total Kjeldahl Nitrogen (TKN), ammonium, nitrate, and nitrite) and total phosphorus (TP) were measured for each WWTP during monthly sampling days. The EC values used were taken directly from the activated sludge process. All laboratory analyses were performed using sensors (EC, pH, temperature,DO) and following the methodology prescribed in the Standard Methods (BOD_5, COD, TN, TKN, ammonium, nitrate, nitrite and TP) [68]. These analyses were performed and reported by each WWTP. The microbiological community in the activated sludge tanks of the WWTPs was identified under stable operating conditions on the monthly days throughout the period of this study. The mean and standard deviation of the physicochemical characteristics of the effluent in the secondary treatment (i.e., the biological process) of each WWTP are presented in Table S3. Moreover, the variations in water quality parameters in the activated sludge tank of the WWTPs were evaluated using the coefficient of variation (CV) [69].

2.3. Microeukaryotic and filamentous microorganisms sampling, counts and identification

Activated sludge samples from each WWTP were used to identify the microeukaryotic and filamentous bacterial communities. Monthly visits were made to each WWTP during the study period to collect activated sludge process samples. The activated sludge tank sampling protocol was the same at each plant. Samples were collected from the well mixed areas of the tanks. Sterile 0.5 L bottles were filled to 50 % capacity to avoid rapid depletion of DO during transport. Samples were transported to the University of Barcelona laboratory except for those from WWTPRSS, WWTPLLN and WWTPCES which were counted and identified within each WWTP following the same protocol as used in the university laboratory. Each sample was cooled, and protected from direct sunlight, where they were stored under refrigerated conditions (4 °C) until analysis within 2 h of arrival. Then, using optical microscopy (Zeiss Axioskop 40 microscope), microorganisms were sorted, identified, and counted every sample day at the family and genus/species levels, depending on the specific microeukaryotic and filamentous groups. Abundance of filamentous microorganisms was measured at 400× following Salvadó [70]. Counts of microeukaryotes larger than 20 μm were conducted following the method described by Madoni [71], which involved analyzing three 25 μL replicates at 100× magnification. For microeukaryotes smaller than 20 μm (such as small flagellates and amoebae), counts were performed at 400× magnification. Specifically, 15 microscopic fields on the coverslip (20 × 20 mm) were analyzed for each replicate. All counts were conducted in vivo using well-homogenized samples.

Filamentous microorganisms were identified at the morphotype level using the guidelines provided by Eikelboom [72] and Jenkins et al. [73]. Species-level determination of ciliates was carried out according to the methods outlined by Curds et al. [62] and Foissner et al. [74], using the ammoniacal silver carbonate impregnation [75] and dry silver nitrate techniques for accurate identification of morphologically similar species [76]. Also, based on the recommendations of Foissner et al. [77], certain species of peritrich ciliates were identified. Flagellated protists were identified following the protocols described by Jeuck and Arndt [78] and Lee et al. [79]. Amoebae were categorized based on size into small (<20 μm) and large (>20 μm) categories. Taxonomic classification of microeukaryotes followed the guidelines outlined by Adl et al. [80]. However, it is important to note that the terms 'flagellates' and 'amoebae' are not formal taxonomic ranks but are used to describe organisms possessing conspicuous flagella or pseudopodia, respectively, as commonly employed in bioindication analyses.

2.4. Microbial biodiversity indices

Four key indices were calculated to assess microbial diversity in activated sludge from wastewater treatment plants. These indices were calculated for both the total microbial community and specifically for Ciliates, allowing for a more focused analysis at genus/species resolution of this particular group. Richness was determined by counting the species present using the apply() function in R. The Shannon index was calculated considering the abundance and evenness of the species using the diversity() function from the "vegan" package. The Margalef index was calculated based on species richness and total abundance according to Margalef [81]. Heip's Evenness (HeipE) was evaluated for evenness using the equations proposed by Heip [82]. These indices provided a comprehensive understanding of the diversity and structure of microbial communities in WWTPs.

2.5. Electrical conductivity measurements

The effect of EC on the microbial community was determined using the monthly EC data for the study period for each WWTP. EC peaks were identified using the "findpeaks" function in the time series data. The monthly average EC values and EC peaks for each WWTP were used to assess the effect of EC on pollutant removal and the seasonal salinity effects on the communities.

2.6. Data analysis

All statistical analyses were performed in R Core Team [83], and the nomenclature proposed by Muff et al. [84] was used to report our results in the language of evidence. One-way Kruskal-Wallis tests were performed for each sampling month to assess variation in richness, Margalef, Shannon, and HeipE indices, and physicochemical parameters of effluent across WWTPs. When significant differences were detected following the Kruskal-Wallis test (p value < 0.05), post hoc comparisons were conducted using Mann-Whitney U test (p value < 0.05). Linear mixed-effects models (lmer) were constructed using the 'lme4' package to examine the relationship between EC concentrations and protozoan diversity and richness indices for each WWTP (included as a random factor) [85]. These models allowed us to assess both fixed effects (EC concentrations) and random effects (variance associated with each WWTP) on protozoan diversity and richness. Bacterial and protozoan indices were calculated using the "vegan" package [86]. Furthermore, Spearman correlation analyses were conducted to assess the relationships between EC and each diversity index (richness, Shannon, Margalef, Simpson, and HeipE), as well as environmental and water quality parameters. We interpreted the Spearman correlation as follows: (0 to 0.19) Very Weak or None, (0.20 to 0.39) Weak, (0.40 to 0.59) Moderate, (0.60 to 0.79) Strong, (0.80 to 1.0) Very Strong [87]. Indicator species analysis (IndVal) [88] was performed to identify indicator taxa for each WWTP using the 'labdsv' package [89]. These analyses were used to determine species according to each WWTP condition and EC level. Variance Inflation Factors (VIF) were used to determine collinearity between EC and environmental and water quality parameters [90].

The 'findpeaks' function from the 'pracma' package was used to identify EC peaks [91]. Significant peaks were defined as those exceeding the minimum detected peak value, capturing extreme variations in EC observed at each WWTP. The impact of these EC peaks on microbial species was assessed through pairwise comparisons between each EC peak and the immediately preceding non-peak value, using a binary flag system. Microorganisms were flagged as either 1 or 0 based on the presence or absence of EC peaks. These comparisons were conducted separately for each pair of groups (i.e., 0, 1), with each group consisting of two samples: one corresponding to a value of 0 and the other to a value of 1, as determined by the temporal variability of EC. The Mann-Whitney U test was then used to evaluate if there was a significant difference in microbial community abundance between samples associated with EC peaks and non-peaks. Subsequently, a Bonferroni correction was applied to mitigate Type I errors due to multiple testing. This approach accounted for the temporal proximity of the data, comparing months or days where data were available (e.g., samples taken monthly during periods of high or low EC, such as January - no EC peak, February - EC peak). The temporal variability of EC was also assessed in relation to the Margalef index over the year, examining the relationship between these two variables through a Spearman correlation analysis. Seasonal diversity associated with EC peaks and non-peaks was separately analyzed for WWTPRSS, WWTPLLN, and WWTPRUS. These plants were selected to represent WWTPs with high, intermediate, and low EC levels, respectively, and also had sufficient seasonal data to correlate the Margalef index with EC peaks per season.

Finally, a structural equation model (SEM) was built to assess the interactions between salinity, bacterial and protozoan communities, and pollutant removal efficiency using the "lavaan" package [92]. SEM is based on the variance-covariance matrices between predictor and response variables and interactively assesses direct and indirect causal pathways using correlations between these variables and their statistical significance [93]. The global model contained 305 sampling units which included all WWTP samples (i.e., WWTPRSS: 59 samples; WWTPLLN: 52 samples; WWTPCES: 52 samples; WWTPRUS 86 samples; WWTPAMP: 19 samples; WWTPALC: 9 samples; WWTPSCR: 27 samples) and variables (EC, percent removal of COD, BOD_5, NTK, NO_3^- and TP), as well as the abundance, richness, Margalef and Shannon indices of bacterial and protozoan communities. Also, a global SEM was computed specifically for EC peak samples identified (i.e., WWTPRSS: 19 samples; WWTPLLN: 14 samples; WWTPCES: 13 samples; WWTPRUS: 18 samples; WWTPAMP: 4 samples; WWTPSCR: 10 samples), along with individual SEM models calculated for each WWTP. Before building the models, variables with a Spearman correlation higher than 0.9 were excluded [94]. Salinity was set as the predictor variable. Similar SEM models were computed individually for each WWTP.

3. Results

3.1. EC levels and operational conditions among WWTPs

Strong differences in EC were observed among the WWTPs evaluated. These differences were very strong between WWTPRSS and WWTPRUS, and between WWTPRSCR and WWTPRUS (Kruskal-Wallis *p* value <0.05, Table S3, Table S4, Table S5). WWTPRSS had the highest mean EC compared to the other WWTPs, followed by WWTPSCR and WWTPCES, while WWTPLLN and WWTPALC had intermediate to low EC values. Conversely, WWTPRUS had the lowest mean EC, followed by WWTPAMP (Table S3, Fig. 1).

Based on the CV and the range of water quality parameters in the activated sludge tank, variations were low to moderate (Table S3). The highest CVs for EC were observed in WWTPLLN (41 %) and WWTPSCR (45 %), followed by WWTPALC (39 %) and WWTPCES (30 %); and the lowest in WWTPRSS (21 %) and WWPTRUS (16 %). For DO, CVs were below 37 %, with WWTPRSS showing the lowest variation (20 %). COD and BOD_5 CVs ranged from 16 % to 44 %, with WWTPLLN having the highest CVs (COD = 39 %, BOD_5 = 44 %). For TN, CVs were highest in WWTPLLN (45 %), followed by WWTPRSS (39 %) and WWTPCES (37 %). The Kruskal-Wallis test showed no evidence of strong changes in physicochemical variables (EC, pH, temperature, DO, COD, BOD_5, TN, TP) during the operational period (*p*-value >0.05, Tables S6).

3.2. Microbial community composition and taxa associated with WWTP EC levels

Microbial community composition among WWTPs showed strong similarity (Fig. S1, NMDS analyses), dominated by different groups (Table S7). WWTPRSS showed the lowest values for the Shannon, Margalef, Richness, and HeipE indices, followed by WWTPALC and WWTPSCR. Conversely, WWTPRUS exhibited the highest values for the Shannon, Margalef, and Richness indices (Fig. S2). IndVal analysis (Table S8) identified five taxa associated with WWTPs with contrasting EC values (i.e., WWTPRSS and WWTPSCR, which have the highest average EC, and WWTPRUS, which has the lowest average EC). *Beggiatoa* spp. and *Choanoflagellates*, were found exclusively in WWTPRSS, while *Arcella* sp. was strongly associated with WWTPSCR. Finally, *Vorticella infusionum*, and *Epistylis* sp. were associated with WWTPRUS.

3.3. Effects of EC on microbial diversity and richness indices

The linear mixed effects model showed a very strong negative effect of EC on the richness (*p* value <0.05, Table S9), Shannon (p value <0.05, Table S10), and Margalef (p value <0.05, Table S11) indices for ciliates (Fig. 2). The global linear mixed effects model showed a similar strong

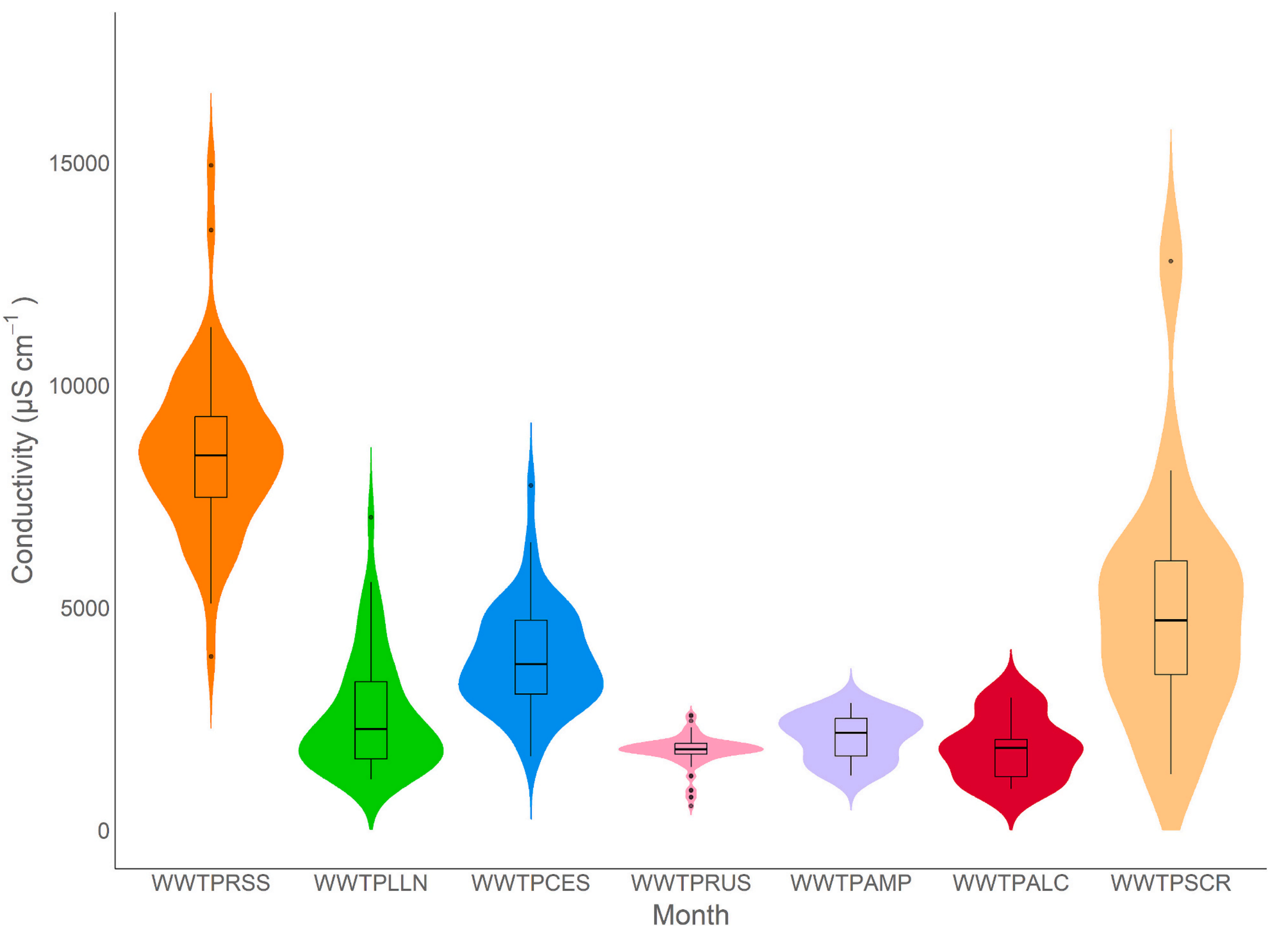

Fig. 1. Violin plots grouping monthly conductivity values by WWTP. WWTPRSS: Roses wastewater treatment plant. WWTPLLN: Llançà wastewater treatment plant. WWTPCES: Castelló d'Empúries wastewater treatment plant. WWTPRUS: Reus wastewater treatment plant. WWTPAMP: Amposta Wastewater Treatment Plant. WWTPALC: Les Cases d'Alcanar Wastewater Treatment Plant. WWTPSCR: Sant Carles de la Ràpita Wastewater Treatment Plant.

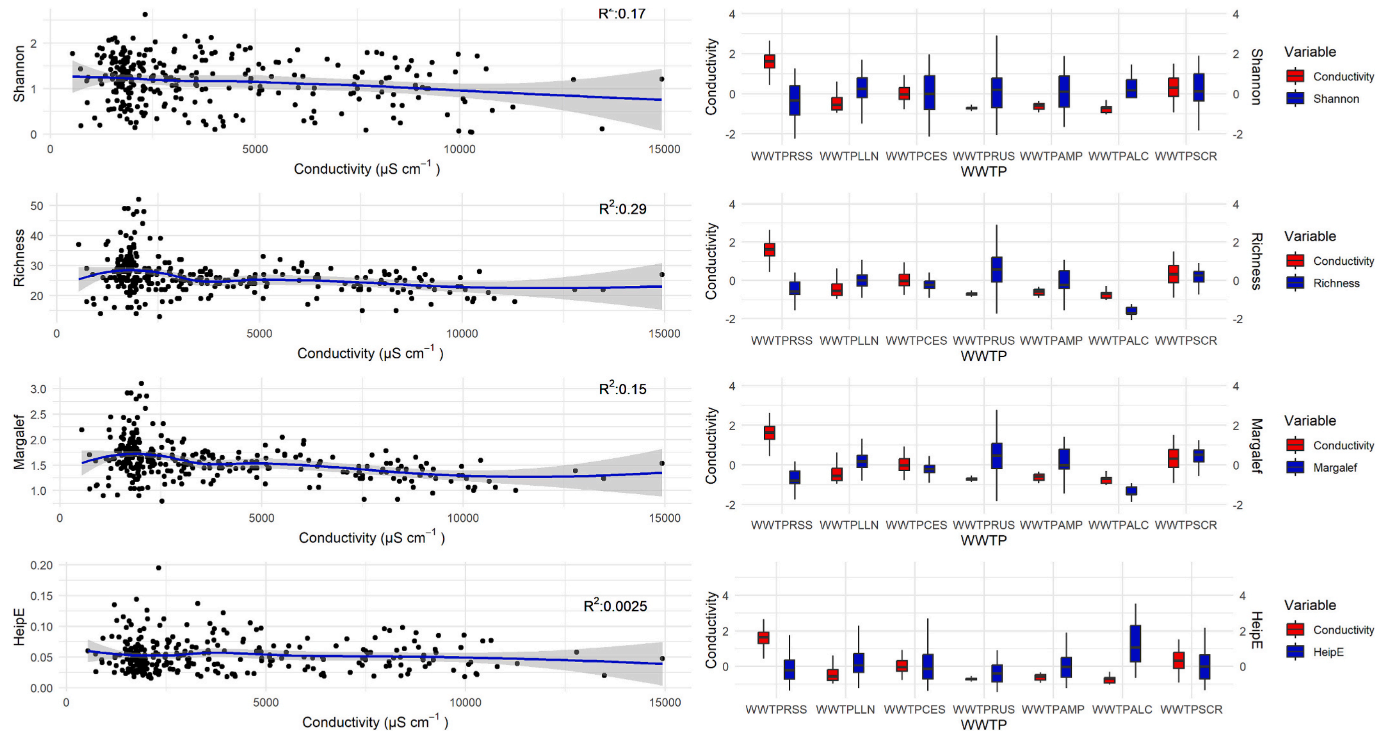

Fig. 2. On the left: linear mixed models of Shannon, richness, Margalef and HeipE indices for ciliates as a function of conductivity for each WWTP. On the right: box plot comparing conductivity and biodiversity indices for each WWTP. WWTPRSS: Roses wastewater treatment plant. WWTPLLN: Llançà wastewater treatment plant. WWTPCES: Castelló d'Empúries wastewater treatment plant. WWTPRUS: Reus wastewater treatment plant. WWTPAMP: Amposta Wastewater Treatment Plant. WWTPALC: Les Cases d'Alcanar Wastewater Treatment Plant WWTPSCR: Sant Carles de la Ràpita Wastewater Treatment Plant.

negative effect of EC on richness, Shannon, and Margalef indices for the total microbial community (Fig. S3).

Spearman rank correlation showed no evidence of strong relationships between EC and the other measured environmental and water quality variables (pH, DO, temperature, COD, BOD_5, TN, TP) within the evaluated WWTPs (Fig. S4). This suggests that EC levels in WWTPs did not exhibit strong collinearity with these parameters and independently influenced WWTP microbial community dynamics. Furthermore, VIF analysis for EC in relation to pH, DO, temperature, COD, BOD_5, TN, and PT were all within acceptable limits (ranging from 1.04 to 2.95, Fig. S5), indicating no substantial multicollinearity issues.

3.4. Impact of EC peaks on microbial communities and seasonal diversity response

EC peaks were identified in each of the WWTPs except WWTPALC (Table S12), which was not considered for this analysis due to its low number of samples. The temporal trend of EC and Margalef index by WWTP is shown in Fig. 3. The highest range in EC peaks was observed in WWTPRSS (i.e., EC from 6500 to 15,000 μS cm^{-1}) and WWTPSCR (EC from 3400 to 13,000 μS cm^{-1}), followed by WWTPCES (i.e., from EC 3700 to 8000 μS cm^{-1}) and WWTPLLN (i.e., EC from 1500 to 7000 μS cm^{-1}), which had moderately higher EC peaks (Table S12). In contrast, the conductivity in WWTPRUS (i.e., EC from 1800 to 2600 μS cm^{-1}) and WWTPAMP (i.e., EC from 2400 to 2700 μS cm^{-1}) remained fairly stable throughout the study period, with few peaks when compared to the other WWTPs (Table S12, Fig. 3).

Strong evidence of changes in total abundance of microorganisms in response to EC peaks was observed only in WWTPRSS and WWTPSCR (Kruskal-Wallis *p* value <0.05, Table S13). The microbial taxa that showed strong responses to EC peaks is shown in Table 1 (Mann-Whitney, p value <0.05, Table S14). Among them, *Acineria uncinata* and *Holophyra discolor* were the most sensitive. Moreover, a moderate negative correlation between EC and the Margalef index (Spearman, *p*-value <0.05) was found in WWTPRSS and WWTPSCR (Table S15, Fig. 3). Finally, Kruskal-Wallis analysis showed no evidence of seasonal changes (i.e., no clear differences in EC levels and community diversity between seasons) in the evaluated WWTPs (i.e., WWTPRSS, Fig. S6; WWTPLLN, Fig. S7; and WWTPRUS, Fig. S8; Table S16).

3.5. EC removal rates in urban WWTPs and salinity effects on pollutant removal efficiency

A relatively low mean EC removal, ranging from 9 to 26 %, was observed in all WWTPs (Fig. S9). We found strong evidence of an inverse relationship between EC removal and organic matter removal (COD, BOD_5, Fig. S10, *P* value <0.05, Table S17), but no evidence of a relationship between EC removal and nutrient removal (TN, TP, Fig. S11, *P* value >0.05, Table S17). EC removal reached a maximum of 60 % in WWTPSCR, but generally remained below 45 %. During the periods of worst efficiency in EC removal, all WWTPs had efficiencies below 5 %, implying high salinity discharges into the environment.

Furthermore, lmer models showed a negative effect of EC on pollutant removal efficiency (COD, BOD_5, TKN, NO_3^-, TP) (Fig. S12, lmer, Table S18 to Table S22). For BOD_5, COD and TKN, a strong inverse relationship with EC was observed (lmer, *P* value <0.05), indicating that removal efficiency of these pollutants decreased with increasing EC (Fig. S12, lmer, Table S18, Table S19, Table S20). Conversely, we found no strong negative effect of EC on nitrate and TP removal efficiency (lmer, P value <0.05, Fig. S12, Table S21, Table S22). These findings remained consistent across individual plants when analyzed separately using simple linear models (Fig. S13).

The global SEM model provided further evidence for EC as a primary driver of microbial abundance and community composition, thereby affecting pollutant removal (Fig. S14, Table S23 provides a summary of the global SEM). This finding was observed both for the overall microbial community and the ciliate community indices (Fig. S15). Strong negative regression coefficients show that EC can strongly affect

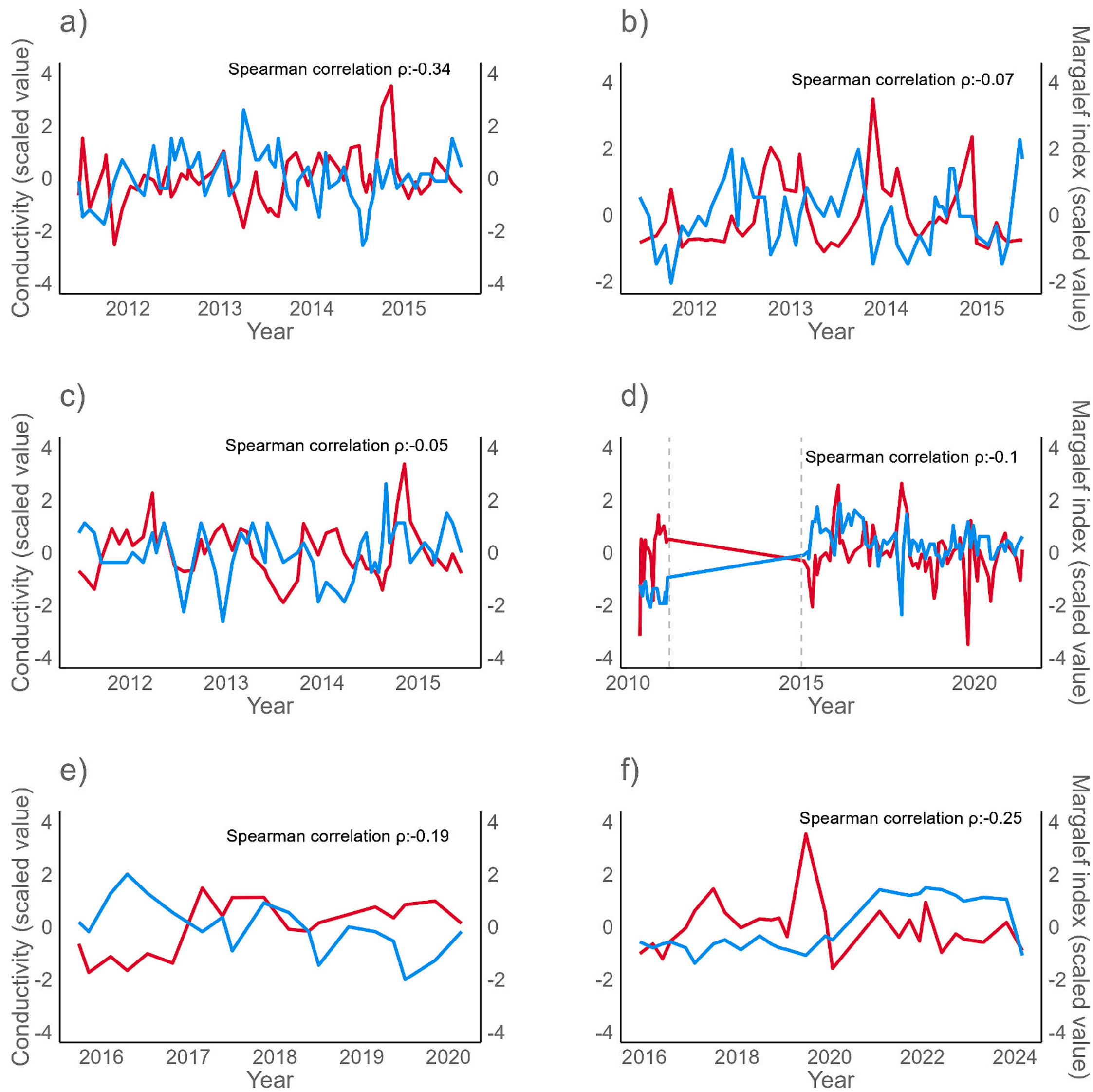

Fig. 3. Temporal variations in electrical conductivity (μS cm^{-1}) and Margalef index by WWTP. The red line represents electrical conductivity, and the blue line represents the Margalef index. In section c), the interval delimited by dashed lines represents a period for which there is no data a) WWTPRSS: Roses wastewater treatment plant. b) WWTPLLN: Llançà wastewater treatment plant. c). WWTPCES: Castelló d'Empúries wastewater treatment plant. d) WWTPRUS: Reus wastewater treatment plant. e) WWTPAMP: Amposta Wastewater Treatment Plant. f) WWTPSCR: Sant Carles de la Ràpita Wastewater Treatment Plant. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

richness (*p* Value <0.001), the Margalef index (*p* value <0.001), the Shannon index (p Value <0.05) and the percentage of BOD_5 removal (p Value <0.001). We also found moderate negative effects of EC on TKN and nitrate, and no evidence of effects on the percentage of TP removal (p Value >0.05). Strong covariances were also observed between the latent richness variables, Margalef and Shannon, indicating a positive association between these diversity measures. When the global SEM model was run with only the EC peaks using ciliates abundance and diversity indices, it revealed an increased effect of EC on the measured variables in the WWTPs (Fig. 4, Table S24). This was particularly evident for the richness and Margalef indices (Fig. 4), accompanied by the intensification of the negative relationship on BOD_5 and TKN, resulting in decreased removal efficiencies associated with EC peaks (Fig. S16).

Finally, when the SEM analysis was individually built for each plant, we found strong evidence that EC can affect the microbial community when it reaches a certain level (Fig. S17). WWTPs with higher EC levels showed a stronger negative effect of EC on the microbial community. There was considerable variability in the correlation between EC and pollutant removal among WWTPs, revealing specific effects for each WWTP that also appeared to be influenced by EC levels. Although BOD_5 and COD removal was affected by EC at most sites, these relationships varied among WWTPs. For instance, a positive relationship was observed between EC and the removal of COD, BOD_5, and TP in WWTPRUS (which had the lowest EC values).

4. Discussion

Overall, the effects of EC on microbial communities varied between WWTPs, although specific taxa were associated with different EC levels. Microbial diversity and abundance strongly decrease along EC gradients in WWTPs with moderate to high EC ranges. In contrast, WWTPs with low EC levels showed weak to negligible response of the microbial communities to changes in EC. Ciliate abundance was strongly reduced by EC peaks, which also caused a moderate reduction in ciliate diversity. All these effects were consistent across seasons and EC removal rates remained low (they ranged between 10 % and 26 %) across WWTPs, showing no correlation with nutrient removal rates. The efficiency of

Table 1
Effect of EC peaks on the abundance of microorganisms in WWTPs.

WWTP	Genus/ Species	EC Peaks effects	EC peak intervals	Reference EC values of salinity tolerance (Foissner, 1995)
WWTPRSS	*Acineria uncinata*	Strongly Reduced	Min: 6435; Max: 14935 μS cm^{-1}	0–400 mg L^{-1} Cl^{-}
	Chilodonella uncinata	Strongly Reduced		433–54,000 μS cm^{-1}
	Holophyra discolor	Strongly Reduced		0–5000 mg L^{-1} Cl-
	Metacineta sp.	Strongly Reduced		570–23,000 μS cm^{-1}
	Trochilia minuta	Moderately Reduced		405–1700 μS cm^{-1}
	Tokophrya sp.	Moderately Reduced		0–800 mg L^{-1} Cl^{-}
	Vorticella aquadulcis	Moderately Reduced		395–1100 μS cm^{-1}
WWTPSCR	*Acineta* sp.	Strongly Reduced	Min: 3370; Max: 12780 μS cm^{-1}	0–800 mg L^{-1} Cl^{-}
	Acineria uncinata	Strongly Reduced		0–400 mg L^{-1} Cl^{-}
	Holophyra discolor	Moderately Reduced		0–5000 mg L^{-1} Cl^{-}
	Opercularia sp.	Moderately Reduced		0–400 mg L^{-1} Cl^{-}

Strongly Reduced and Moderately Reduced categorize the impact of EC peaks on microorganisms abundance. This impact was determined by the difference in average abundance between peak and non-peak periods (Mann-Whitney test, Table S17). 'Strongly Reduced' indicates a highly significant decrease ($p < 0.001$), while 'Moderately Reduced' indicates a significant decrease ($p < 0.05$).

organic matter and nitrogen removal was affected at high EC levels, potentially driven by disruptions in both biological interactions and physicochemical processes.

4.1. Specific taxa responses to EC

The community of protozoa and filamentous bacteria associated with WWTPs with high EC, such as WWTPRSS and WWTPSCR, was dominated by *Beggiatoa* sp., *choanoflagellates*, and *Arcella* sp. (as indicated by IndVal analysis), aligning with findings from previous studies [95–99]. For example, *Beggiatoa* sp. is known to be resilient to environmental changes in extreme aquatic environments, including hypersaline lakes such as Chiprana in Spain, being present in effluents rich in sulfide and nitrate, anoxic conditions, and even in the absence of oxygen [95,100,101]. Similarly, several species of *choanoflagellates* such as *Salpingoeca crinita* have adapted to the salt flats of the Atacama Desert in Chile [97–99]. Higher salinity has also been shown to increase *choanoflagellate* abundance in WWTPs [11]. Moreover, Roe and Patterson [102] reported a strong association between species within the *Arcella sp*, particularly *Arcella vulgaris*, and lakes affected by salt runoff from road deicing and agricultural areas (i.e., fertilizer and pesticide runoff with elevated salt and nutrients). Therefore, the abundance of these species in both aquatic environments and WWTPs, as reported in our study, suggest that they could be used as bioindicators of salinization, not only in these areas, but also in wastewater treatment processes [11,97,102].

Among the ciliate protozoa, peritrich ciliates such as *Vorticella infusionum* were associated with WWTPRUS (i.e., the WWTP with the lowest EC). Concordantly, Salvadó et al. [2] found that the abundance of *Vorticella infusionum* was reduced at high salt concentrations. Also, *Epistylis* sp. seemed to be very sensitive to salinity according to our results. This aligns with Foissner [74], who showed that *Epistylis* spp. was associated with low EC ranges (i.e., between 500 and 1500 μS cm^{-1}). Moreover, other studies showed that its abundance declines at high salinities (i.e., > 5 g/L) in both experimental setups and natural aquatic environments [2,103,104]. These responses appear to depend on factors such as the duration of the salinity exposure, acclimation to different salinities, specific species traits (e.g., size, feeding), and interactions among

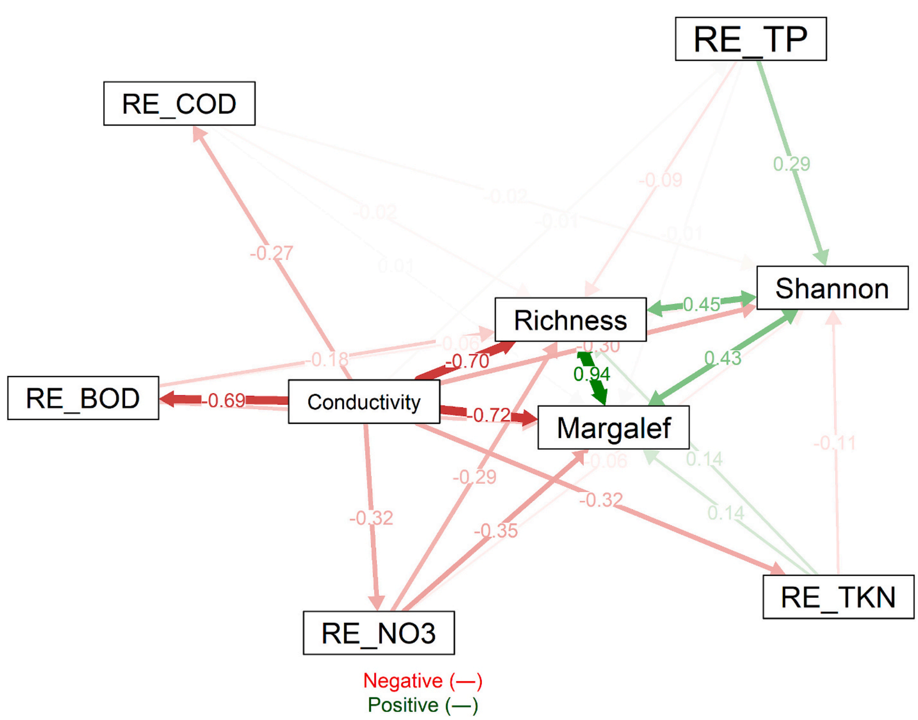

Fig. 4. Structural equation model showing the effects of electrical conductivity peaks on protozoan community indices for ciliates and percent pollutant removal. Conductivity: conductivity (μS cm^{-1}); RE_BOD: biochemical oxygen demand removal percentage; RE_COD: chemical oxygen demand removal percentage; RE_TKN: nitrogen total Kjeldahl removal percentage; RE_NO_3^-: nitrate removal percentage; RE_TP: total phosphorus removal percentage; Richness: Taxa richness of ciliates in the activated sludge process; Shannon: Shannon diversity of ciliates in the activated sludge process. Margalef: Margalef richness of ciliates in the activated sludge process. Red and green lines indicate negative and positive relationships, respectively. Model fit indices were set at CFI ≥ 0.90 and RMSEA ≤0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

protozoa within assemblages [40,104,105]. For example, Jones et al. [104] found that gradual acclimation to salinity strongly improved the survival of *Epistylis* sp. under laboratory conditions.

4.2. EC effects on the protozoa communities

The increase in EC was mainly responsible for the negative effects on community diversity and abundance indices. These findings are consistent with previous studies that have reported negative effects of high EC on aquatic communities not only in freshwater [106–110] but also in microorganisms from activated sludge experiments [2,111,112] (Table S1). This could be explained by the influence of EC on factors such as nutrient availability, osmolarity, and environmental toxicity, thereby potentially modulating the activity and composition of microbial communities [113–115]. In our WWTPs, the response of microorganisms appears to be codependent on EC concentration (i.e., as EC increases, biodiversity indices decrease). However, other factors, such as microbial adaptation to high salinity in activated sludge [5,116], operational factors (e.g., low COD and high salinity), environmental factors [46,117], and species interactions [118,119], also might play important roles in their response to salinity.

Although establishing links between resilience to toxic EC levels (e.g., at the species level), community interactions (e.g., individually, and collectively), and the resulting impact on pollutant removal efficiency is challenging [2,111,120], especially when analyzing data at a real scale (i.e., under uncontrolled conditions). It is important to consider the constant decrease in microbial diversity and richness indices at elevated EC concentrations, which could result in the loss of taxa crucial for WWTP processes and the disruption of community interactions. For example, it has been reported that interactions between protozoa such as *Paramecium* sp. *Vorticella* sp. *Epistylis* sp. and *Opercularia* sp. have been shown to increase their collective ability to degrade pollutants (e.g., COD, petroleum hydrocarbons) and better withstand adverse conditions compared to when they act individually [105,121,122]. This synergy among protozoa in a consortium may be a key factor in their efficiency to remove contaminants.

4.3. EC peaks effects on the ciliate communities

It is important to note that in our study the ciliate group was most negatively affected by EC peaks. Species such as *Acineria uncinata*, along with other species negatively correlated with EC (*Trochilia minuta*, *Opercularia sp*), may indicate not only the potential importance of ciliates as salinity indicators in WWTPs, but also that the changes in the structure of their assemblages may potentially affect pollutant removal [41,65,71]. We hypothesize that the moderate decrease in BOD_5 removal efficiency obtained in our study may be related to the negative effects of increased EC on *Acineria uncinata* and other ciliates (*Trochilia minuta*, *Vorticella* spp., *Opercularia* spp.). This aligns with several studies that have linked crawling ciliates, such as *Acineria uncinata*, with organic matter removal, not only individually but also acting in consortia with other communities [105,123,124]. Also, *Acineria uncinata* is considered an indicator of deficient sludge settlement conditions, playing a crucial role in the identification of disruptions in WWTP [66]. However, regression models only showed that EC primarily affected both ciliate species and pollutant removal efficiency separately. A clear relationship between ciliate group abundance and effects on COD and BOD_5 removal was not found. Furthermore, we ruled out any direct or indirect effects on N removal by species such as *Acineria uncinata*, in agreement with other studies that found no evidence of a relationship between ciliates such as *Acineria* spp. and N removal [64,66,125]. However, this is not always the case within the ciliate group, as other ciliates, like *Trochilia minuta*, have been associated with nitrifying conditions [126].

Comparisons between samples associated with EC peaks and non-peaks were influenced by both the magnitude of the peak and the stability of EC levels within WWTPs [2,127,128]. WWTPs with lower EC levels and greater EC stability (e.g., WWTPRUS) exhibit higher abundance and diversity of microbial communities, which are distinctly separated from WWTPs characterized by higher EC concentrations and variability (e.g., WWTPRSS) [2,127]. Consequently, WWTPs with higher EC levels also tend to experience higher EC peaks (i.e., WWTPRSS), resulting in pronounced effects not only on species diversity, as indicated by the negative correlation between EC peaks and the Margalef index (Fig. 3), but also on specific species such as *Holophyra discolor and Metacineta* sp. These effects extended to other diversity indices such as richness and Shannon diversity (according to EC peak SEM model, Fig. 4). However, the impact of salinity on community dynamics did not vary with the seasons. This could be explained by the lack of a strong correlation between salinity and temperature (i.e., salinity did not consistently and predictably align with seasonal changes in community dynamics). Finally, it has been reported that salt peaks negatively impact several parameters of activated sludge and contribute to the corrosion of equipment, including a reduction in floc size by approximately two-thirds, which affects the activity of this process in WWTPs [127–129]. This trend is particularly evident in the context of COD and BOD_5 removal efficiency, where a stronger negative interaction is observed between EC peaks and the efficiency of organic matter removal, as shown in the comparisons between SEM models.

4.4. EC removal in WWTPs and salinity effects on pollutant removal efficiency

A notable finding of our study is that we observed a relatively low EC removal, with an average never exceeding 26 % across all WWTPs evaluated. Furthermore, for these percentages of EC removal in WWTPs, we found evidence of a relationship with organic matter removal and no evidence of a relationship with nutrient removal (i.e., WWTPs with N removal by nitrification and denitrification). This positive association suggests that the processes involved in removing organic matter also contribute to reducing EC. However, a high elimination of organic matter does not ensure a high removal of EC. This observation could be explained by the decomposition of organic matter, which can produce organic acids and soluble salts (e.g., chloride, sulfate, nitrate) as byproducts of the removal process [130–132], thereby increasing the concentration of dissolved ions in the effluent. Also, the decomposition of organic matter can consume dissolved oxygen in the biological process, leading to anaerobic conditions and the production of ions through chemical reactions [133–135]. The absence of a relationship with nutrient elimination may suggest that, while some salinity is likely utilized in processes converting nitrogen from wastewater to gaseous nitrogen, the portion of EC removed as ammonium and alkalinity (e.g., estimated between 14 and 33 % of total EC) may not constitute a significant fraction of the total EC [136,137]. This could potentially explain the lack of a noticeable reduction in conductivity attributed to nitrogen removal processes. It is likely that the majority of EC was eliminated through physical processes (e.g., filtration due to adsorption of the cations on the colloids negatively charged) and chemical processes (e.g., flocculation, coagulation), as well as biological treatment (i.e., communities utilizing dissolved ions in the effluent to some extent) in the evaluated WWTPs [138–140].

BOD_5 and TKN removal efficiencies showed a strong negative response to elevated EC levels (lmer model), but we found no compelling evidence for changes in NO_3^- and TP removal efficiencies (individual lmer for each plant as well as the global lmer). This is consistent with numerous studies focused on WWTP exposed to extremely high salinity concentrations (e.g., 60 g/L NaCl) [9,47,124] (Table S1). However, a few studies have established correlations between low to moderate salinities (0.1 to 5 g/L NaCl) and reductions in contaminant removal (e.g., BOD_5, COD) due to the inhibition of microbial communities [7,38] (Table S1). According to our results, this negative effect of EC on the removal of organic matter and TKN could be related to the sensitivity to salinity of certain communities responsible for this process. The alteration of microeukaryotic communities, such as ciliates, may have significant repercussions on the functioning of the treatment system [41,65,141,142]. For example, ciliates play a crucial role in regulating bacterial populations through predation and the release of essential nutrients [141,142]. If the ciliate population is affected, this could disturb the biological balance of the system (i.e., cascade effects), which in turn could impact the ability of ammonium-oxidizing (AOB) and denitrifying bacteria to effectively carry out their functions [65,142]. This disruption in microbial interactions could have serious implications for the overall efficiency of wastewater treatment in WWTPs.

Although we did not observe strong effects on nitrate and TP removal, our results (lmer and SEM), suggest that nitrate removal could be reduced during EC peaks. We hypothesize that in WWTPs with higher EC conditions (e.g., $>$ 15,000), nitrate and TP removal may be more affected. These results are also consistent with previous studies, which highlight the variability in nutrient removal reductions depending on EC levels and the type of wastewater treatment system used (Table S1). Therefore, although EC might not be the main determinant of wastewater treatment efficiency, the effects of elevated EC levels and EC peaks on wastewater treatment processes should be monitored and controlled, especially in municipal WWTPs with salt-rich influents or salt intrusion [24,25,143]. Moreover, as we have highlighted, the relationship between EC and the biological processes involved in wastewater treatment can strongly vary from one WWTP to another and deserve further research.

5. Conclusions

This study is the first to analyze EC dynamics in WWTPs at a real scale and their effects on microeukaryotic communities and pollutant removal. We found strong evidence of negative effects of high EC levels and EC peaks on WWTP microbial communities, particularly affecting the ciliate group, as well as inverse relationships with organic matter and TKN removal. These effects are consistent across seasons and are evident at high concentrations and peaks of EC (i.e., EC levels to which both communities and WWTP processes are not acclimated). The response of microorganisms is related to EC concentration, although it is difficult to determine clear responses at the genus and species level. WWTPs with high EC levels harbor microbial communities dominated by species resistant to saline environments, such as *Beggiatoa* sp., *choanoflagellates*, and *Arcella* sp., which could serve as bioindicators of salinization in WWTPs. Disruption of ciliate communities could have significant implications for organic matter removal and overall WWTP performance. EC removal rates in conventional WWTPs, which lack advanced treatments, are relatively low, with a maximum mean observed removal of 26 %, and are not significantly correlated with nutrient removal efficiency. In summary, although EC is not the sole determinant of WWTP efficiency, its effects on WWTP functioning must be considered in the design of effective monitoring and management strategies to mitigate the adverse effects of EC fluctuations and ensure optimal wastewater treatment performance.

Funding

This work was supported by a doctoral grant from the Ministerio de Ciencia, Tecnología e innovación y Colfuturo (Colombia) and IDAEA-CSIC contract associated to Ramón y Cajal (RYC2020-029829-I) for Alvaro Moyano.

CRediT authorship contribution statement

Alvaro Javier Moyano Salcedo: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Miguel Cañedo-Argüelles:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Sujay S. Kaushal:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Eva Maria Ciriero-Cebrián:** Methodology, Investigation, Formal analysis, Conceptualization. **Adrià Perez-Blanco:** Methodology, Investigation, Formal analysis, Conceptualization. **Humbert Salvadó:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, 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.

Data availability

Data will be made available on request.

Acknowledgements

We thank Consorci d'aigües Costa Brava Girona, Empresa Mixta d'Aigües de la Costa Brava S.A, EMACBSA- Roses WWTP, especially Anna Maria Huguet, Consell Comarcal del Montsià, Acciona Agua, and Aigües de Catalunya (the current entity managing the WWTP operations in the South Ebro Delta), and Aigües de Reus for their support in providing access to treatment plants, samples, and information. We also thank Oriol Canals for his general support during the process of sample collection and identification.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jwpe.2024.105974.

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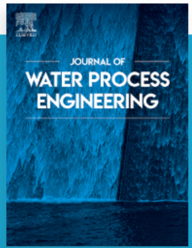

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