

## Environmental parameters that shape zooplankton diversity in coastal wetlands of the Valencian Community, Spain

Bruno G. Chianese-Blanco<sup>a,\*</sup>, Claudia M. Rodríguez-Sierra<sup>a,b</sup> , María Antón-Pardo<sup>a</sup>  and Xavier Armengol<sup>a</sup> 

<sup>a</sup> Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València; Calle Dr. Catedrático José Beltrán 2, 46980 Paterna, Spain.

<sup>b</sup> Surcolombiana University, Huila, Colombia. Avenida Pastrana Borrero Carrera 1ra, 410007 Neiva – Huila, Colombia.

\* Corresponding author: bruchia@alumni.uv.es

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### ABSTRACT

**Environmental parameters that shape zooplankton diversity in coastal wetlands of the Valencian Community, Spain.**

Along the Valencian coastline, numerous coastal wetlands persist as remains of extensive alluvial plains that once dominated the region. Historically, many of these wetlands were drained due to human activity, accelerated by urban development along the Mediterranean coast. Despite this, several larger or strategically located wetlands have endured and are now under protection. These ecosystems encompass diverse aquatic habitats including marshes, springs, canals, and shallow lagoons that support a rich variety of organisms, notably zooplankton, that are essential to aquatic food webs. This research aims to study the diversity ( $\alpha$ ,  $\beta$  and  $\gamma$ ) of zooplankton and to assess how environmental variables influence their composition and diversity. Seasonal samples of zooplankton and water were collected from multiple sites within six selected wetlands: Prat de Cabanes-Torreblanca, Marjal dels Moros, Albufera de Valencia, Marjal Pego-Oliva, Salinas de Santa Pola, and Hondo de Elche. Zooplankton species were identified and quantified, and richness and different diversity metrics were estimated: Shannon and inverse Simpson indices (to estimate  $\alpha$ -diversity), local contribution to beta diversity -LCBD- (for  $\beta$ -diversity), and Chao index (for  $\gamma$ -diversity). Physicochemical parameters, nutrient levels, and pigment concentrations were also measured, and their influence on diversity metrics was evaluated through multiple linear regression. The findings indicated that key factors influencing structure and diversity of the zooplankton community included water conductivity, phosphate concentration, chlorophyll-*a* concentration, seasonal changes, and type of waterbody. Freshwater wetlands showed greater  $\alpha$  and  $\gamma$ -diversity. The Albufera de Valencia sites showed a significantly higher contribution to beta diversity than other sampling sites during all seasons, reflecting consistently unique communities.

**KEY WORDS:** biological diversity; environmental variables; microcrustaceans; rotifers; seasonality.

### RESUMEN

**Parámetros ambientales que condicionan la diversidad del zooplancton en los humedales costeros de la Comunidad Valenciana, España.**

A lo largo de la costa valenciana, diversos humedales costeros persisten como vestigios de las extensas llanuras aluviales que antaño dominaban la región. Muchos de estos humedales fueron drenados debido a la actividad humana, acelerada por el desarrollo urbano en la costa mediterránea. No obstante, algunos humedales más grandes o estratégicamente ubicados han sobrevivido y hoy están protegidos. Estos ecosistemas comprenden distintos hábitats acuáticos, como turberas, marjales,

*surgencias, canales y lagunas, que albergan una rica biodiversidad, especialmente de zooplankton, crucial para las redes tróficas acuáticas. Esta investigación se centra en estudiar la diversidad ( $\alpha$ ,  $\beta$  y  $\gamma$ ) del zooplankton y en evaluar cómo las variables ambientales afectan su composición y diversidad. Se tomaron muestras estacionales de zooplankton y agua en varios sitios de seis humedales: Prat de Cabanes-Torreblanca, Marjal dels Moros, Albufera de Valencia, Marjal Pego-Oliva, Salinas de Santa Pola y Hondo de Elche. Se identificaron y cuantificaron las especies de zooplankton, se estimó la riqueza de especies y diferentes métricas de diversidad: índices de Shannon e inverso de Simpson (para estimar  $\alpha$ -diversidad), contribución local a la diversidad beta -LCBD- (para la  $\beta$ -diversidad) e índice de Chao (para la  $\gamma$ -diversidad). También se midieron parámetros fisicoquímicos y concentraciones de nutrientes y de pigmentos para evaluar su influencia en las métricas de diversidad, mediante regresiones lineales múltiples. Los resultados mostraron que los factores clave que influyen en la estructura y diversidad de la comunidad de zooplankton incluyen la conductividad del agua, la concentración de fosfato, la concentración de clorofila-a, los cambios estacionales y el tipo de hábitat. Los humedales de agua dulce presentaron mayor diversidad  $\alpha$  y  $\gamma$ , y los sitios de la Albufera de Valencia mostraron una contribución más alta a la beta diversidad en todas las estaciones, reflejando sus comunidades únicas.*

**PALABRAS CLAVE:** diversidad biológica; estacionalidad; microcrustáceos; rotíferos; variables ambientales.

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## INTRODUCTION

Anthropogenic activities have led to the alteration or destruction of natural ecosystems, resulting in a global decline in biodiversity in the last centuries (Pimm et al., 1995; Dirzo & Raven, 2003). Wetlands are among the most severely impacted ecosystems, with approximately 87% of their global area lost between 1700 and 2020 (Fluet-Chouinard et al., 2023). Furthermore, the rate of wetland loss and degradation has accelerated over the past three decades (Li et al., 2018). Namely, coastal wetlands, recognized as the most valuable continental ecosystems in terms of the ecosystem services they provide (De Groot et al., 2012), are under severe impacts due to their high productivity and location. Their main threats include overexploitation, habitat loss, introduction of exotic species, and pollution (Hall & Mills, 2000; Dalla-Bona et al., 2015; Kingsford et al., 2016). Since coastal wetlands are considered important biodiversity hotspots, these disturbances pose significant threats to wildlife and compromise the ecosystem services provided by these wetlands (Mitsch et al., 2015), since biological diversity is key to understanding the function and health of aquatic ecosystems.

The Mediterranean region is recognized as a crucial biodiversity hotspot (Myers et al., 2000; Cuttelod et al., 2009), especially hosting numerous valuable coastal wetlands. These ecosystems are characterized by considerable spatial and temporal environmental heterogeneity, holding

a diverse array of natural and artificial habitats such as canals, temporary marshes, coastal lagoons, ponds, or water springs (Blondel & Aronson, 1999). The environmental heterogeneity of patches can favor high values of the different components of biodiversity at the different spatial scales at which it is measured: alpha ( $\alpha$ ), beta ( $\beta$ ) and gamma ( $\gamma$ ) diversity. The  $\alpha$ -diversity refers to the diversity at a local scale (e.g., a site), the  $\beta$ -diversity indicates species turnover between sites (i.e., the rate with which species replace each other from site to site), and the diversity at regional scales (i.e., across a group of local habitats) is the  $\gamma$ -diversity (Whittaker, 1972; Baselga & Gómez-Rodríguez, 2019). Despite their importance, Mediterranean wetlands have traditionally received less scientific attention compared to their temperate counterparts (Álvarez-Cobelas et al., 2005; Downing, 2010), resulting in knowledge gaps regarding their ecological importance. Zooplankton have been used as indicators of water quality or eutrophication, because of their fast response to environmental changes and the negative impacts of human disturbances on some taxa (Jeppesen et al., 2011; García-Chicote et al., 2018; 2019). Therefore, their sensitivity to variations in environmental conditions can create differences in biodiversity patterns (spatially and temporally), and this is why some authors have proposed the composition and structure of the zooplankton community as a criterion to consider for wetland conservation (Jeppesen et al., 2011; Gilbert et al., 2014).

Many studies have been conducted to identify the most relevant stressors that affect zooplankton diversity, which have shown that both high salinity and eutrophication result in a reduction in zooplankton diversity, especially cladocerans (Antón-Pardo & Armengol, 2012; García-Chicote et al., 2018; 2019; Vilas-Boas et al., 2021). On the other hand, some zooplanktivorous fish can give a competitive advantage to small size zooplankters, such as rotifers, through the predation of larger zooplankton. In fact, the reduction of efficient competitors, such as cladocerans (Gilbert, 1989), or predators, such as copepods (Brandl, 2005), leads to higher densities and richness of rotifers (Conde-Porcuna et al., 2004). Finally, some environmental parameters, such as food availability, can increase zooplankton diversity (Braghin et al., 2021). Zooplankton communities are characterized by their seasonal dynamics and short generation times. These features make seasonal monitoring necessary to accurately include this temporal variability in biodiversity measures. This is particularly important in the global change scenario, as the environment of many wetlands is changing. The possibility to disentangling and predicting the impact of these variations on aquatic communities can help to make appropriate decisions to mitigate them and provide tools to protect and manage aquatic biodiversity.

The present study aims to investigate the biodiversity patterns of the zooplankton communities located in six coastal wetlands in the Valencian region (Eastern Iberian Peninsula), presenting a wide range of environmental conditions, and to identify the spatial and seasonal trends of the diversity components ( $\alpha$ ,  $\beta$  and  $\gamma$ -diversity) and their relationship with environmental variables.

## MATERIAL AND METHODS

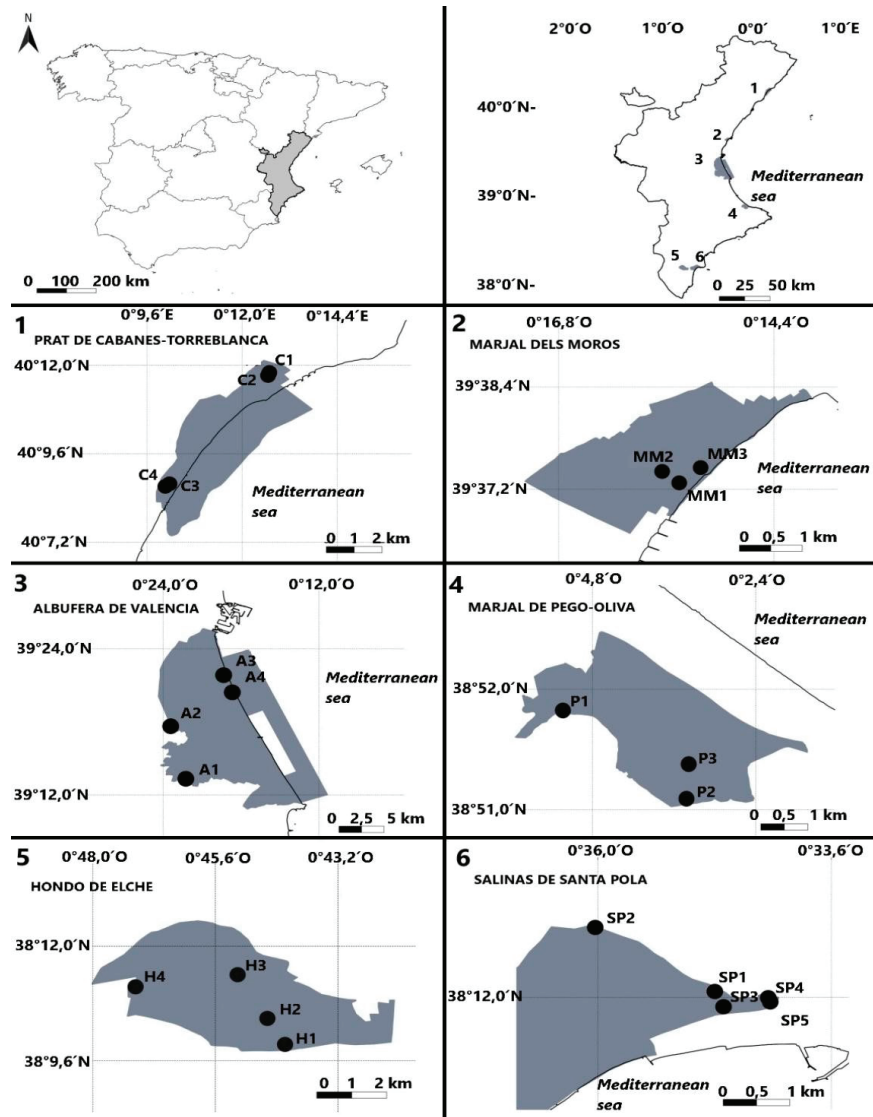
### Study area

Six coastal wetlands from the Valencian Region (Eastern Iberian Peninsula) were studied (Fig. 1): Prat de Cabanes-Torreblanca, Marjal dels Moros, Albufera de Valencia, Marjal de Pego-Oliva, Hondo de Elche and Salinas de Santa Pola. All these wetlands are ZEPA (zone of special protection for birds) and Ramsar sites, and all, ex-

cept Marjal dels Moros, are included in Natural Parks. They cover a wide range of environmental features (such as surface, salinity, nutrients, water transparency...), presenting different types of waterbodies and a great variety and intensity of anthropogenic impacts. From each wetland, samples were taken in different types of waterbodies, such as canals, ponds (including a shallow lagoon in El Hondo, dug peatlands in Prat de Cabanes-Torreblanca and dune slacks, locally known as *malladas*, in the Albufera de Valencia) and limnocrenes (groundwater springs, locally named *ullals*, where the water is generally of good quality; Soria, 1989). We chose 22 sites distributed among these wetlands as follows: four sites in Prat de Cabanes-Torreblanca (C1-C4), Albufera de Valencia (A1-A4), Hondo de Elche (H1-H4), and Salinas de Santa Pola (SP1-SP4); and three sites in Marjal dels Moros (MM1-MM3) and in Pego-Oliva (P1-P3). All of these sites harbored populations of the invasive fish *Gambusia holbrooki* Girard, 1859 (Table 1).

### Sampling

Sampling was carried out seasonally between March 2021 and February 2022, except for some sites that were not sampled in autumn (C1, P2, SP4, H1 and H2; see Table 1), or in summer (SP4) because they were dry. Physicochemical parameters were measured at each site and season: conductivity (Hanna Instruments HI 98311), pH (Hanna Instruments HI98128), dissolved oxygen concentration and water temperature (both with WTW MultiLine 3430). Depth was measured with a graduated stick, and water transparency was measured with a Snell tube (Van de Meutter et al., 2006), an opaque tube 60 cm long and 10 cm in diameter, where a small Secchi disk was inserted and the depth at which it was not seen was noted. Water samples were also taken at each site and filtered through Whatman GF/F filters for measuring the concentrations of dissolved nutrients (nitrate, nitrite, ammonium, and phosphates; APHA, 1980) by spectrophotometry. The filters were used for measuring chlorophyll-*a* concentration, through the extraction of the pigment with acetone 90% and determining the concentration by spectrophotometry following the equations



**Figure 1.** Location of sampling sites in the Valencian region. *Localización de los sitios de muestreo en la Comunidad Valenciana.*

of Jeffrey and Humphrey (1975). Annual average values of chlorophyll-*a* concentrations were used to classify each sampling site following their trophic status (OCDE, 1982; see Table 1).

Zooplankton samples were taken using a 20 cm diameter plankton net with a mesh size of 63  $\mu$ m. The net was towed along several transects, keeping a similar distance in the different sites, and covering the different microhabitats within each site (littoral, open waters, among the vegetation, etc.). The retained organisms were collected and fixed with 70% ethanol. Organisms were

identified and counted in the laboratory using an Olympus CK40 inverted optical microscope. By using different identification keys (Dussart, 1967; Dussart, 1969; Koste, 1978; Segers, 1995; Alonso, 1996, and Bledzki & Rybak, 2016), taxa were classified to the species level, if possible, and their abundances were estimated.

### Zooplankton diversity

After calculating the total species richness in each sample,  $\alpha$ -diversity was estimated consid-

**Table 1.** Sampling sites within each wetland, type of waterbody, area, trophic status (following mean chlorophyll-*a*; OCDE, 1982), and seasons when each site was sampled. *Lugares de muestreo dentro de cada humedal, tipo de cuerpo de agua, área, estado trófico (según la media de la clorofila a; OCDE 1982) y estaciones en las que se muestreó cada sitio.*

Wetland	Sampling site	Type of waterbody	Area (m <sup>2</sup> )	Trophic status (based on chlorophyll- <i>a</i> )	Sampling period			
					Spring 21	Summer 21	Autumn 21	Winter 22
Prat de Cabanes-Tor-reblanca	C1	Peatland pond	77580	Ultraoligotrophic	X	X	-	X
	C2	Peatland pond	55412	Oligotrophic	X	X	X	X
	C3	Canal	58	Mesotrophic	X	X	X	X
	C4	Pond	261	Mesotrophic	X	X	X	X
Marjal dels Moros	MM1	Canal	13078	Hypereutrophic	X	X	X	X
	MM2	Pond	2883	Hypereutrophic	X	X	X	X
	MM3	Pond	810	Mesotrophic	X	X	X	X
Albufera de Valencia	A1	Ullal	1712	Ultraoligotrophic	X	X	X	X
	A2	Ullal	3047	Ultraoligotrophic	X	X	X	X
	A3	Mallada	1753	Mesotrophic	X	X	X	X
	A4	Mallada	4387	Oligotrophic	X	X	X	X
Marjal de Pego-Oliva	P1	Ullal	335	Oligotrophic	X	X	X	X
	P2	Ullal	2609	Oligotrophic	X	X	-	X
	P3	Canal	711	Oligotrophic	X	X	X	X
Hondo de Elche	H1	Pond	235933	Hypereutrophic	X	X	-	X
	H2	Shallow lagoon	3270	Hypereutrophic	X	X	-	X
	H3	Pond	98440	Oligotrophic	X	X	X	X
	H4	Canal	72211	Mesotrophic	X	X	X	X
Salinas de Santa Pola	SP1	Canal	115	Oligotrophic	X	X	X	X
	SP2	Canal	179	Ultraoligotrophic	X	X	X	X
	SP3	Pond	33 289	Mesotrophic	X	X	X	X
	SP4	Pond	31 950	Mesotrophic	X	-	-	X

ering two different levels (Chao et al., 2012): Shannon-Wiener index, which provides information on the evenness of the community, and the inverse of the Simpson index, which considers species dominance.

In a Hellinger-transformed abundance matrix,  $\beta$ -diversity was obtained for every season with the estimation proposed by Legendre & De Cáceres (2013), where this value is obtained as the total variance of the community composition matrix. This value varies between 0 (high similarity) and 1 (low similarity). Furthermore, this value was divided into the local contribution of each site to beta diversity (LCBD), which can be used as an indicator of the unique conditions of each site in terms of community composition. This was done using the *beta.div* function of the

*adespatial* package (Dray et al., 2023), using R 4.3.2 software (R Core Team, 2023). Finally,  $\gamma$ -diversity was estimated as the total species richness in each studied wetland, and also as the Chao index (Chao, 1987). The latter was calculated using PAST software (Hammer et al., 2001).

## Data analysis

To analyze the most relevant drivers (environmental variables, seasonality, and type of waterbody) for species richness,  $\alpha$ -diversity indices (Shannon and inverse Simpson), and the partition of beta diversity (LCBD), multiple linear regressions (MLR) were performed with the function *lm* of the stats package (R Core Team, 2023). The requirements of this analysis (homoscedasticity



and normality) were visually checked (with the *plot* function), and in the only case in which the assumptions were not met (richness), this parameter was logarithmically transformed. In each model, a selection of variables was performed with the progressive introduction method (forward selection), selecting those models with the lowest value of AIC (Akaike Information Criterion). This was done using the *stepAIC* function of the *MASS* package (Ripley et al, 2024). When the season, which corresponds to the sampling time, was selected and significant, pairwise comparisons were made by changing the reference season in the MLRs.

RESULTS

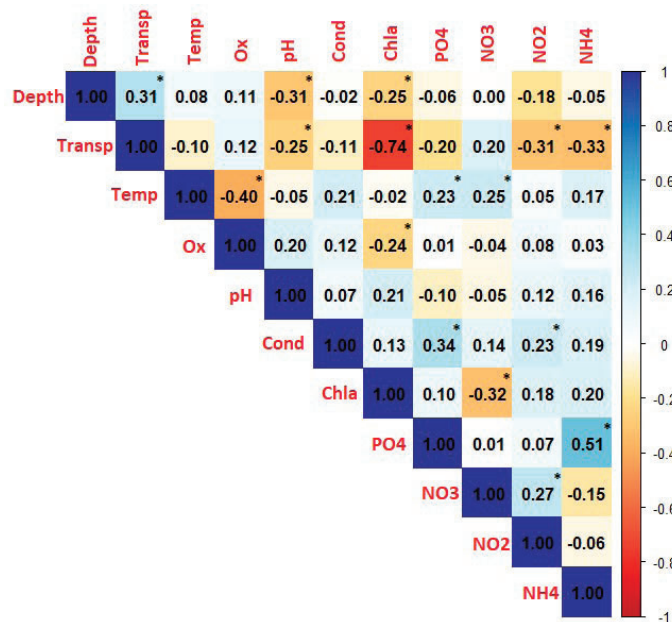
Environmental variables

The measured environmental variables showed considerable variation among wetlands, within each wetland and among seasons. The highest average values of conductivity were observed in Salinas de Santa Pola, Prat de Cabanes-Torreblanca, and Hondo de Elche. A high chlorophyll-*a*

concentration was reached in Marjal dels Moros and Hondo de Elche and exhibited wide variability in all wetlands (Table 2).

Nutrient concentrations were high in most wetlands, especially in Santa Pola, with the highest values of phosphate and nitrate, and Hondo de Elche, with the highest values of nitrite and ammonium. The average depth ranged from 56 cm (Santa Pola) to 107 cm (Pego-Oliva). The latter wetland presented high values of water transparency (shared with Albufera de Valencia) and dissolved oxygen (shared with Cabanes-Torreblanca). Mean pH values ranged from 7.0 (Cabanes) to 7.7 (Santa Pola); minimum average dissolved oxygen was measured in Marjal dels Moros, and the maximum in Cabanes-Torreblanca and Pego-Oliva.

The analysis of environmental variables revealed predominantly positive correlations, with a subset of these being statistically significant (Fig. 2). Depth showed significant positive correlation with transparency, and negative correlation with pH and chlorophyll-*a* concentration. Transparency, in turn, had a significant negative correlation with pH, chlorophyll-*a*, nitrite, and ammonium



**Figure 2.** Correlations between environmental variables. Significant correlations ( $p < 0.05$ ) are highlighted with “\*”. Abbreviations as in Table 2. *Correlaciones entre las variables ambientales. Las correlaciones significativas ( $p < 0.05$ ) están destacadas con “\*”. Abreviaturas como en la Tabla 2.*

**Table 2.** Average values ( $\pm$  standard deviation) of the environmental variables measured at all sites from each wetland and in all seasons. *Valores promedio ( $\pm$  desviación estándar) de las variables ambientales medidas en todos los sitios de cada humedal y en todas las estaciones.* Transp: water transparency (Snell tube); Temp: temperature; Ox: dissolved oxygen; Cond: conductivity; Chl-*a*: chlorophyll-*a* concentration; PO<sub>4</sub>: phosphate; NO<sub>3</sub>: nitrate; NO<sub>2</sub>: nitrite; NH<sub>4</sub>: ammonium

Wetland	Depth (cm)	Transp Snell (cm)	Temp (°C)	Ox (mg/l)	pH	Cond (mS/cm)	Chl- <i>a</i> (µg/l)	PO <sub>4</sub> (mg/l)	NO <sub>3</sub> (mg/l)	NO <sub>2</sub> (mg/l)	NH <sub>4</sub> (mg/l)
Prat de Cabanes-Torreblanca	96 $\pm$ 46	40 $\pm$ 17	20.1 $\pm$ 6.5	7.9 $\pm$ 4.5	7.0 $\pm$ 0.9	16.9 $\pm$ 12.4	9.67 $\pm$ 10.87	0.34 $\pm$ 0.29	52.55 $\pm$ 54.58	0.09 $\pm$ 0.09	0.91 $\pm$ 0.89
Marjal dels Moros	57 $\pm$ 23	26 $\pm$ 7	19.0 $\pm$ 5.3	5.6 $\pm$ 3.4	7.5 $\pm$ 0.5	4.2 $\pm$ 2.5	34.08 $\pm$ 33.19	0.27 $\pm$ 0.25	22.80 $\pm$ 11.26	0.08 $\pm$ 0.04	0.73 $\pm$ 0.43
Albufera de Valencia	64 $\pm$ 20	43 $\pm$ 10	18.3 $\pm$ 5.7	5.9 $\pm$ 2.9	7.4 $\pm$ 0.5	1.6 $\pm$ 0.4	5.07 $\pm$ 8.45	0.13 $\pm$ 0.08	80.93 $\pm$ 93.85	0.10 $\pm$ 0.09	0.48 $\pm$ 0.28
Marjal de Pego-Oliva	107 $\pm$ 45	43 $\pm$ 15	18.8 $\pm$ 4.6	7.9 $\pm$ 1.5	7.3 $\pm$ 0.6	3.8 $\pm$ 2.4	5.30 $\pm$ 4.49	0.26 $\pm$ 0.22	40.60 $\pm$ 28.82	0.09 $\pm$ 0.05	0.50 $\pm$ 0.31
Hondo de Elche	73 $\pm$ 16	24 $\pm$ 12	21.4 $\pm$ 5.6	6.9 $\pm$ 2.9	7.6 $\pm$ 0.4	10.7 $\pm$ 3.6	45.18 $\pm$ 59.99	0.29 $\pm$ 0.19	33.78 $\pm$ 27.01	0.36 $\pm$ 0.38	1.20 $\pm$ 0.85
Salinas de Santa Pola	56 $\pm$ 19	41 $\pm$ 17	20.4 $\pm$ 5.1	7.4 $\pm$ 2.4	7.7 $\pm$ 0.4	18.1 $\pm$ 11.4	8.99 $\pm$ 9.10	0.41 $\pm$ 0.42	151.77 $\pm$ 168.71	0.19 $\pm$ 0.15	0.91 $\pm$ 0.96

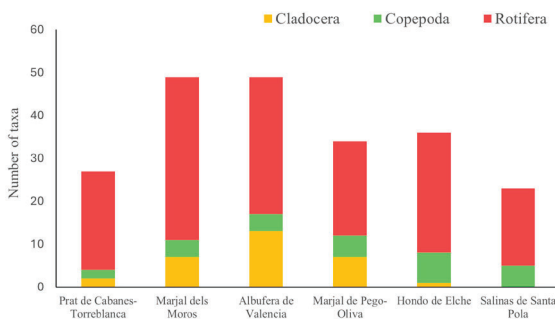
concentrations. The temperature exhibited significant negative correlation with dissolved oxygen and positive correlations with both phosphate and nitrate levels. Dissolved oxygen was significantly and negatively correlated with chlorophyll-*a* concentration, while conductivity showed significant positive correlations with phosphate and nitrite concentrations. Chlorophyll-*a* concentration was significantly and negatively correlated with nitrate levels. Additionally, phosphate concentrations had a positive and significant correlation

with ammonium levels, and nitrate showed a significant positive correlation with nitrite concentrations.

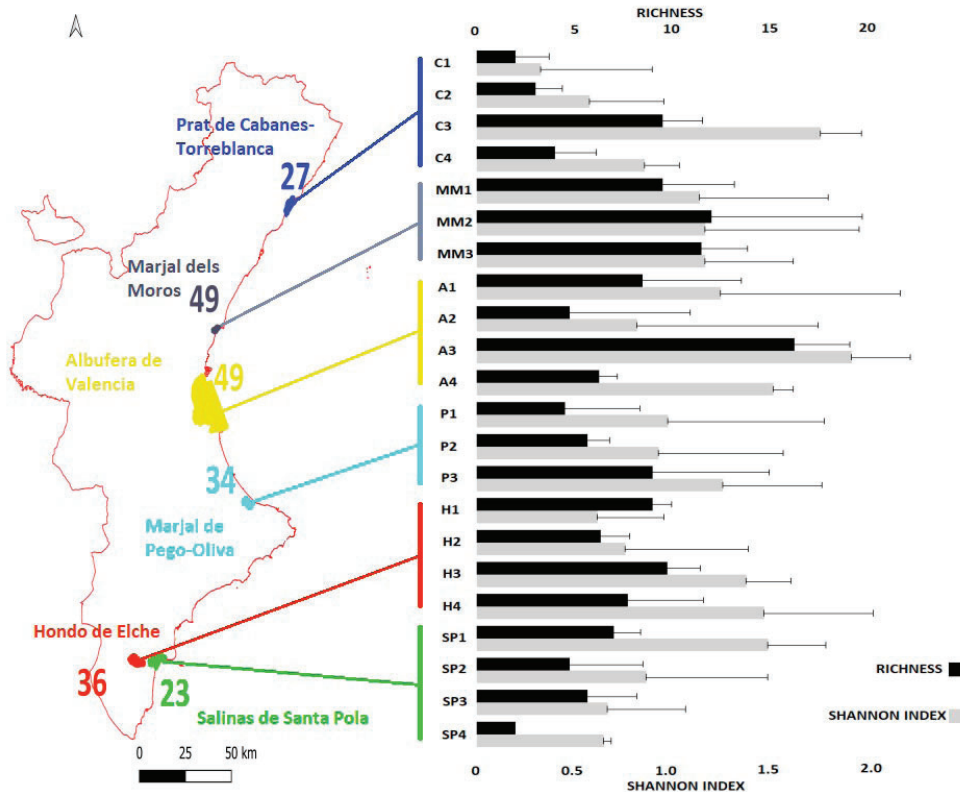
### Zooplankton diversity

A total of 85 zooplankton taxa were identified across the studied wetlands and seasons, comprising 54 rotifers, 16 cladocerans, and 15 copepods, being the most common species of each group *Brachionus plicatilis*, *Chydorus sphaericus* and *Cletocamptus confluentis* respectively (Table S1, supplementary information, available at <https://www.limnetica.net/en/limnetica>). Rotifers had the highest richness values in all wetlands (Fig. 3). On the other hand, copepods were found in all wetlands, showing higher richness than cladocerans in Hondo de Elche and Santa Pola. Finally, cladocerans were not observed in Santa Pola, but showed higher richness than copepods in Marjal dels Moros, Pego-Oliva and Albufera de Valencia, where this group presented the highest richness.

Species richness varied among sampling sites and seasons, ranging from an average of 3 to 34 species per site throughout the year ( $\bar{X} \pm \text{sd} = 16.2 \pm 8.8$ ). A higher mean species richness (Fig. 4) was found in freshwater sites: site A3 from Al-



**Figure 3.** Number of taxa of the main groups of zooplankton found in all sampling sites from each wetland and in all seasons. *Número de taxones de los principales grupos de zooplankton encontrados en todos los sitios de muestreo de cada humedal y a lo largo de todas las estaciones.*



**Figure 4.** Mean richness and Shannon index with their standard deviation at each sampling site. The colored number at each location shows the total richness in each wetland. *Riqueza media e índice de Shannon con su desviación estándar en cada punto de muestreo. El número de color en cada ubicación muestra la riqueza total en cada humedal.*

bufera de Valencia ( $\bar{x} \pm sd = 16.3 \pm 2.9$ ) and site MM2 from Marjal dels Moros ( $\bar{x} \pm sd = 12.0 \pm 7.8$ ). On the contrary, a lower average species richness was reported in brackish sites: site C1 from Prat de Cabanes-Torreblanca ( $\bar{x} \pm sd = 2.0 \pm 1.7$ ), and site SP4 from Salinas de Santa Pola ( $\bar{x} \pm sd = 2.0 \pm 0.0$ ).

Shannon diversity index (Fig. 4) varied considerably across the study sites, ranging from 0.3 to 1.9. In general, the inverse Simpson index (results not shown) revealed a pattern of diversity among the sampling sites that was consistent with the Shannon index. The highest value of these indices was observed at sites from Albufera, while the lowest values were recorded at sites from Cabanes-Torreblanca and Santa Pola.

The value of  $\beta$ -diversity calculated from all study sites showed slight seasonal fluctuations: it ranged from 0.64 (summer) to 0.72 (spring).

These values revealed differences in the composition of the zooplankton community among the studied sites throughout the year analyzed. On the other hand, the LCBD values (Table 3) exhibited spatial and temporal variations in most wetlands and sampling points, ranging from 0.021 (C1 in spring) to 0.110 (A2 in autumn). Sites from Albufera de Valencia showed relatively high LCBD values throughout the year at most of its sampling points, reflecting a comparatively unique and stable community.

The value of species richness on the regional scale revealed variations among the studied areas. Two wetlands, Albufera de Valencia and Marjal dels Moros, exhibited the highest  $\gamma$ -diversity, each supporting 49 zooplankton species. On the contrary, Prat de Cabanes-Torreblanca and Salinas de Santa Pola showed the lowest values of  $\gamma$ -diversity, with 27 and 23 species, respectively. Comple-



menting this observation, the Chao index estimated a potential total of  $109 \pm 13$  species in the study area, in contrast to the 85 observed species.

### Parameters influencing diversity

The results of the multiple linear regressions (MLR; Table 4) revealed that chlorophyll-*a*, conductivity, and  $\text{PO}_4$  were the significant variables most directly related to species richness, explaining 33.0 % of the variance. Conductivity remained a significant variable both for the Shannon and Simpson indices, also including in the selected models the type of waterbody (increasing values in canals), and seasonality, with significantly higher values in summer compared to winter, spring, and autumn. Additionally, chlorophyll-*a* also had a significant and positive effect on the Shannon index. Finally, the LCB<sub>D</sub> values were only significantly affected by conductivity, which explained 15.1 % of the variability.

### DISCUSSION

The results highlight the wide range of environmental conditions that can be found in coastal Mediterranean wetlands, which in turn allows for high levels of zooplankton diversity found at the different spatial scales:  $\alpha$ ,  $\beta$  and  $\gamma$ -diversity.

Habitats varied from low salinity and oligotrophic wetlands (particularly ullals in Albufera de Valencia and Marjal de Pego-Oliva) to saline and some mesotrophic-eutrophic sampling sites (in Hondo de Elche, Salinas de Santa Pola, and Prat de Cabanes-Torreblanca). It should be noted that in Albufera de Valencia the main lagoon was not studied. This lagoon that covers a great proportion of the natural park presents a hypertrophic state approximately from 1970 onwards (Vicente & Miracle, 1992; Soria, 2006; Soria-Perpinyà et al., 2019). Instead, this study sampled two permanent interdunal ponds (*malladas*) and ground-water springs (*ullals*), which have better water quality (Antón-Pardo & Armengol 2010; Rueda et al., 2013). In addition to spatial variability, all the wetlands had great temporal variations in their environmental conditions. Generally, conductivity, chlorophyll-*a*, and water temperature were higher during the spring and summer months;

while transparency and oxygen concentrations reached their peaks during autumn and winter.

Regarding the zooplankton assemblages found in these wetlands, the majority of taxa in all sites were rotifers (63.5%), followed by cladocerans (18.8%) and copepods (17.6%). A study conducted three decades ago in similar sites within the same wetlands also reported rotifer dominance in most cases (Oltra & Armengol, 1999). The marked dominance of rotifers may be related to the presence of the invasive fish *Gambusia holbrooki* at all sites, since zooplanktivorous fish could benefit rotifers. This fish preferentially feeds on large zooplankton, decreasing its density directly by predation. This interaction results in a reduction of the competition of cladocerans and rotifers, and the decrease of predation pressure of copepods upon rotifers, increasing indirectly the density and richness of the last group (Gilbert, 1989; Cabral et al., 1998; Conde-Porcuna et al., 2004; Brandl, 2005).

The sampling points in Albufera and Marjal dels Moros presented the highest number of species, both at the individual site level -local- and at the wetland level -regional-. In contrast, Prat de Cabanes-Torreblanca and Salinas de Santa Pola had the fewest species. These comparisons regarding richness should be interpreted with caution, because, although at all sampling sites we sampled a similar volume of water, a great variability in organism abundances was found (data not shown), so we cannot discard a sampling effect related to these differences. Both biodiversity indices (Shannon and the inverse Simpson) showed a similar pattern compared to species richness, but they further reflect that species abundances were more equitable at sites of Albufera de Valencia and Marjal dels Moros. On the contrary, in the brackish wetlands, the values of these indices were lower, which can be attributed to a high salt concentration that only allows a few species typical of these brackish habitats to present high densities and be dominant. This is the case of several species of the genus *Brachionus*, typical of brackish waters (Miracle et al., 1987; Anton-Pardo & Armengol 2014), which were dominant in many of the brackish wetlands studied. Indeed, this negative effect of salinity on diversity is evident in the results obtained from

**Table 3.**  $\beta$ -diversity estimated for each season and its partition in the Local Contribution to Beta Diversity (LCBD) for each sampling site. Significant LCBD values are highlighted in bold.  *$\beta$ -diversidad estimada para cada estación y su partición en la Contribución Local a la Diversidad Beta (LCBD) para cada sitio de muestreo. Los valores significativos de LCBD están resaltados en negra.*

Wetland	Sampling site	LCBD VALUES			
		Spring	Summer	Autumn	Winter
Prat de Cabanes-Torreblanca	C1	0.021	0.042	-	<b>0.083</b>
	C2	<b>0.071</b>	0.042	0.035	0.029
	C3	0.037	0.034	0.036	0.030
	C4	0.031	0.028	0.058	0.036
Marjal dels Moros	MM1	0.038	0.048	<b>0.097</b>	0.048
	MM2	<b>0.083</b>	0.037	0.046	0.035
	MM3	0.045	0.034	0.079	0.031
Albufera de Valencia	A1	<b>0.069</b>	<b>0.068</b>	<b>0.093</b>	<b>0.070</b>
	A2	<b>0.082</b>	<b>0.061</b>	<b>0.110</b>	0.033
	A3	0.046	0.057	<b>0.087</b>	<b>0.069</b>
	A4	0.043	0.046	0.065	<b>0.066</b>
Marjal de Pego-Oliva	P1	0.048	0.048	0.031	0.038
	P2	0.040	<b>0.061</b>	-	0.025
	P3	0.066	0.036	0.033	0.031
Hondo de Elche	H1	0.028	0.048	-	0.053
	H2	0.029	<b>0.064</b>	-	<b>0.063</b>
	H3	0.026	0.054	0.039	0.030
	H4	0.039	0.040	0.060	0.039
Salinas de Santa Pola	SP1	0.041	0.030	0.040	0.033
	SP2	0.033	0.035	0.028	0.030
	SP3	0.037	0.045	0.063	0.059
	SP4	0.048	-	-	<b>0.070</b>
$\beta$ -diversity		0.72	0.64	0.69	0.70

multiple linear regression models, as conductivity negatively influenced richness and all  $\alpha$ -diversity parameters (Shannon and Simpson indices). It is well known that salinity is a stressor that prevents the presence of species that cannot tolerate high salt concentrations, especially cladocerans (e.g., Boronat et al., 2001; Boix et al., 2010; Anton-Pardo & Armengol, 2012).

Other variables influencing richness and  $\alpha$ -diversity were related to eutrophication, although with two contrasting effects. On the one hand, phosphate had a negative effect on richness, as it has been found in other studies (Jeppesen et al., 2000; Antón-Pardo & Armengol, 2012). On the other hand, chlorophyll-*a* increased richness and Shannon index. Considering that most zooplank-

ton species found are filter-feeders, the increase in the availability of its main resource -phytoplankton- can influence the presence of a higher number of species and prevent the dominance of a few taxa caused by competition (Hessen et al., 2006). In Albufera de Valencia and Marjal dels Moros, the low conductivity and low trophic state allowed the presence of a greater number of cladoceran species (Boronat et al., 2001; Conde-Porcuna et al., 2004). Meanwhile, in the more eutrophic and brackish sites analyzed, the number of species in this group was scarce or non-existent. Furthermore, rotifers also tend to dominate in eutrophic systems (Conde-Porcuna et al., 2004; García Chicote et al., 2018; 2019), as is the case in many of the sampling points. Therefore, this

**Table 4.** Results of the Multiple Linear Regressions of the different diversity parameters, showing the selected variables in the model with the lowest AIC, the estimates and the p-values for each variable, and the p-value of the model and their explained variance ( $R^2$ ). n.s.: non-significant. *Resultados de las Regresiones Lineales Múltiples de los diferentes parámetros de diversidad, mostrando las variables seleccionadas en el modelo con el AIC más bajo, las estimaciones y los p-valores para cada variable, así como el p-valor del modelo y su varianza explicada ( $R^2$ ). n.s.: no significativo.*

Diversity measures	Selected variables	Estimate	p-value	Model p-value	$R^2$ (%)
Richness	Chlorophyll- <i>a</i>	0.24	$p < 0.001$	$p < 0.001$	33.0
	Conductivity	-0.24	0.001		
	Phosphate	-0.68	0.040		
	Nitrite	0.73	n.s.		
Shannon	Conductivity	-0.61	$p < 0.001$	$p < 0.001$	26.1
	Chlorophyll- <i>a</i>	0.45	0.013		
	Waterbody (no canal)	-0.40	0.003		
	Summer-Winter	0.53	0.003		
	Summer-Spring	0.60	0.001		
	Summer-Autumn	0.56	0.007		
	Transparency	0.81	n.s.		
	Oxygen concentration	0.50	n.s.		
Inverse Simpson	Conductivity	-1.62	$p < 0.001$	$p < 0.001$	25.7
	Waterbody (no canal)	-1.07	0.005		
	Summer-Winter	1.20	0.006		
	Summer-Spring	1.51	0.002		
	Summer-Autumn	1.36	0.005		
LCBD	Conductivity	-0.01	0.015	$p < 0.001$	15.1
	Waterbody (no canal)	0.01	n.s.		
	Temperature	-0.03	n.s.		

could explain the specific composition of the sampled wetlands and the dominance of rotifers over the other groups.

In addition, the MLR analyses revealed that seasonality had a significant influence on the Shannon and Simpson indices, with higher values in summer compared to other seasons. These temporal variations may be attributed to certain environmental conditions that prevent the dominance of a few species, such as greater food availability in summer, primarily in the form of phytoplankton, and higher temperatures (Brugnano et al., 2011; Panwar & Malik, 2016).

Finally, the type of waterbody had an influence on  $\alpha$ -diversity: higher diversity values were found in canals compared to other habitats, including ponds, shallow lagoons, springs and peat bogs. As canals were usually inflows from or outflows of lentic water bodies and considering that

the water flow was moderate in all cases, its higher diversity values could reflect their function that favors connectivity among other water bodies, which act as species sources in these intermediate habitats (Zhao et al., 2018).

Regarding  $\beta$ -diversity, the total value did not vary considerably throughout the year, reflecting that the sites presented consistently different communities during the four seasons. However, LCBD values highly fluctuated at most of the sampling points throughout the year, showing that the uniqueness of their communities varied greatly. Probably, seasonal variations in the environmental variables allowed the presence of rare and nonshared species in certain sites. The highest LCBD values were reached at sites from Albufera de Valencia throughout all seasons, probably related to their higher species richness, which can increase the number of unique species (espe-

cially cladocerans) and therefore their dissimilarity values. The negative influence of conductivity supports the results observed for  $\alpha$ -diversity: high salinity constrains the presence of nontolerant species and promotes homogenization of communities.

Finally,  $\gamma$ -diversity in each wetland (cumulative species richness) was closely related to the average  $\alpha$ -diversity in its local sites, showing the same response to conductivity and eutrophication. Although there was relatively high habitat heterogeneity within each wetland (temporal and spatial), which may have a positive effect on regional diversity (Stein *et al.*, 2014; Ortega *et al.*, 2018), stressors are likely able to constrain species richness at the harshest sites and limit the regional species pool that could colonize the other water bodies. Additionally, the Chao index yielded a value considerably higher than the total number of recorded species, indicating that there is still a high percentage of species that have not been reported. This result may reveal the presence of rare species in the studied systems, suggesting that diversity must be higher at certain sites, at least in terms of richness and dissimilarity.

To conclude, our study highlights the great environmental variability (temporal and spatial) in the studied wetlands, which resulted in high zooplankton diversity values, considering the type of studied waterbodies and the fish pressure. The different levels of diversity ( $\alpha$ ,  $\beta$  and  $\gamma$ ) were affected by a similar set of variables. Firstly, conductivity, which excludes a high number of species that cannot tolerate high salt concentrations (especially cladocerans), can homogenize zooplankton assemblages, and thus, decrease regional species pool. And secondly, eutrophication, seasonality, and the type of habitat also influenced  $\alpha$ -diversity. These obtained results should be considered in management actions to promote high aquatic diversity in Mediterranean coastal wetlands.

## AUTHOR CONTRIBUTIONS

B.C.: Data curation, formal analyses, research, methodology, writing – original draft; C.M.R.S.: Conceptualization, research, methodology; M.A.P.: Supervision, research, writing: revision and edition; X.A.: Conceptualization, supervi-

sion, research, writing: revision and edition.

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