Topics of limnological research in Mexico

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This book is dedicated to
Dr. Singaraju Sri Subrahmanya Sarma,
in gratitude for all his teachings in the world of limnology.

Index

Seasonal and Diel Influence of Environmental Factors on the Parameters of a Zooplankton Community in a Tropical Coastal Lagoon

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Abstract

Zooplankton communities show seasonal and diel changes mainly associated with the variability of abiotic and biotic factors. Community parameters are good descriptors for evaluating these changes. The study's objective was to analyze the seasonal and diel variation of the parameters of a zooplanktonic community in the La Mancha Lagoon (Veracruz state, Mexico), and the influence exerted by environmental factors. For a year, a 24-h cycle was completed each month, sampling zooplankton every 4 h during a new moon. Abiotic and biotic variables were recorded simultaneously. Univariate permutational analysis of variance, canonical correspondence analysis, and simple correlation analysis were used to analyze the data. Species richness, diversity, and dominance showed significant differences at the seasonal and diel levels. Seasonally, diversity and species richness showed their highest values in November-December and April, and low values in May, while dominance presented a completely inverse pattern. At the diel level, species richness and diversity showed high values at night, while dominance at dawn. Diversity was strongly associated with dominance inversely and directly correlated with species richness. Canonical correspondence ordination explained a high percentage of the constrained variance of the parameters-environment relationship (99.2 %), revealing salinity and diel effect as the most critical variables driving community structure. The influence of salinity was observed at a monthly and daily level. A negligible effect of biotic variables (chlorophyll *a* and densities of diatoms, dinoflagellates, and cyanobacteria) was also observed. Due to the high environmental variability in estuaries, abiotic factors may play a more important role in community structuring.

Keywords

Abiotic factors, environmental variability, dominant species, predator-evasion, constrained ordination.

Introduction

Zooplankton communities are of great importance in freshwater, brackish, and marine systems, playing an essential role in energy transfer in the aquatic food web between primary producers and higher consumers and contributing to nutrient recycling (Dvoretsky & Dvoretsky, 2021; Muñoz-Colmenares et al., 2021; Rosa et al., 2021). Furthermore, zooplanktonic organisms are susceptible to environmental changes. They are therefore considered good indicators of ecosystems, because a change in abiotic and biotic factors in aquatic systems results in a change in the relative composition and abundance of these organisms (Azevêdo et al., 2015; Arias et al., 2022; Guermazi et al., 2023).

An objective of aquatic ecological research is to know the response of planktonic communities to environmental conditions (Marques et al., 2009). Thus, many studies have demonstrated seasonal and diel changes in the species composition of zooplanktonic communities. Seasonally, these changes have been explained in terms of the influence of abiotic factors, such as salinity, temperature, dissolved oxygen, and light (Shi et al., 2015; Ge et al., 2021; Ursella et al., 2021; Arias et al., 2022), and/or by biotic factors, such as phytoplankton abundance, chlorophyll *a*, predation, and competition (Węgleńska et al., 1997; García-Herrera et al., 2022), which can act separately or in synergy (Liang et al., 2020; Hobbs et al., 2021; Muñoz-Colmenares et al., 2021; Guermazi et al., 2023).

Diel changes are associated with vertical migration, which is a ubiquitous characteristic in marine and freshwater planktonic communities (van Haren & Compton, 2013; Ursella et al., 2021), and these have been mainly related to food availability, predation avoidance and competition, and are generally modulated by diel and tidal cycles (Hobbs et al., 2021; García-Herrera et al., 2022). Indeed, several studies have observed a considerable increase in the number of species during the night (Marques et al., 2009; Primo et al., 2012) and for this reason, samplings throughout 24 h cycles can provide a better understanding of zooplankton richness.

Although the study of zooplankton communities is a multivariate process, because many species are captured in several samples, there are good univariate descriptors that allow condensing and summarizing information about the number, identity, and relative abundance of the species and, consequently, analyze changes in the community structure. These descriptors are community properties or community parameters, which are essentially species richness, diversity, evenness, and dominance (Morin, 2011), which have been used in ecological studies of zooplankton communities (Liang et al., 2020; Arias et al., 2022; Romero et al., 2022; Taniguchi et al., 2023).

There are many studies on the structure of zooplankton communities in freshwater, estuarine, and marine systems. Still, in the particular case of Mexico, there are few studies that simultaneously address seasonal and diel changes in the structure of these communities. In this sense, the main objective of this study was to analyze the seasonal and diel variation of richness, diversity, evenness, and dominance of a zooplanktonic community in La Mancha Lagoon, and the influence exerted by different environmental factors, considering the hypothesis that community structure will be affected mainly by seasonal variability of abiotic factors and diel variation mainly by biotic factors.

Materials and Methods

Study Area

La Mancha Lagoon is a Ramsar site, a category defined as a site that provides for national action and international cooperation in the conservation of wetlands and the rational and sustainable use of their resources. This system is located in the state of Veracruz, Mexico (19°33′55″–19°35′44″ N and 96°22′41″–96°23′39″ W). It is a small intermittent microtidal system with an approximate extension of 1,742 km^2 (Morgado-Dueñas & Castillo-Rivera, 2022). The region has a warm, sub-humid climate (Köppen climate classification: Aw2), with two climatic seasons: a dry season (mean monthly rainfall <60 mm) from November to May and a rainy season (mean monthly rainfall >100 mm) from June to October.

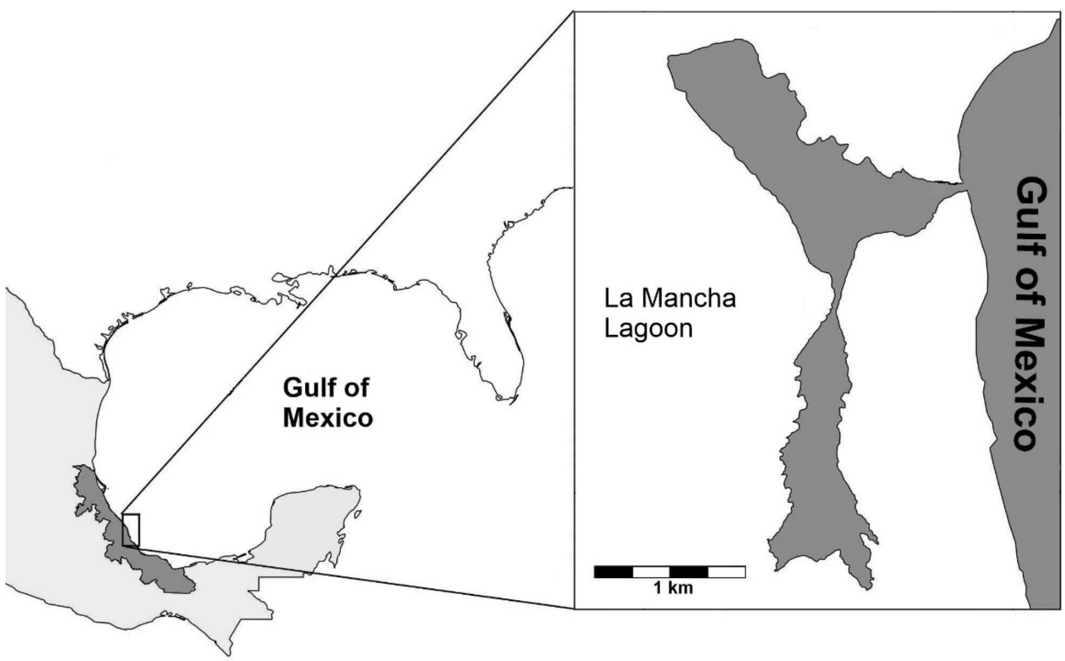


Figure 1. Geographical Location of the the La Mancha Lagoon.

Sampling Collections

For a year, the zooplanktonic community at the mouth of La Mancha Lagoon was sampled through monthly diel cycles. Thus, 24-h cycle was completed each month, taking samples every four hours (6 samples per cycle) during the new moon period to maximize the light/dark effect (Castillo-Rivera et al., 2010). Zooplankton samples were obtained by circular surface hauls using a standard net (100 cm length, 30 cm diameter, and 150 μm mesh size). Organisms were immediately preserved in 4 % borax-buffered formalin. Simultaneously, the biotic factors chlorophyll *a* (spectrophotometric method, SCOR, 1966), and abundance of diatoms, dinoflagellates, and cyanobacteria (Utermöhl method, using an inverted microscope Motic AE31), and the abiotic variables salinity (ATAGO S-10E Refractometer), temperature, dissolved oxygen (YSI 550A DO Instrument), water level (tidal phase), and time of day were recorded, according to Mecalco-Hernández et al. (2018). For quantitative analysis, the time of day was classified into diel periods, considering a light-dark gradient on an ordinal scale with values of 2 (day=10:00 and 14:00 h), 1 (twilight=06:00 and 18:00 h) and 0 (night=22:00 and 2:00 h).

Data Analysis

Fifty-seven zooplankton components were recorded, corresponding to 55 species, in addition to two undetermined stages (zoea larvae of brachyura and fish eggs). Their abundances were expressed as individual numbers per cubic meter (ind/m^3) (Mecalco-Hernández et al., 2018; Mecalco-Hernández & Castillo-Rivera, 2020). From these data, community parameters were estimated for each sample: species richness (number of species), diversity (Shannon-Winer index), evenness (Pielou index), and dominance (Simpson index).

Two-way univariate permutational analysis of variance (PERMANOVA) was applied to evaluate significant differences in the analyzed parameters among months and diel periods, as well as their interactions. PERMANOVA is a routine for testing the response of one or more variables to one or more factors based on a resemblance measure. This method is also appropriate because it uses multiple random permutations to obtain *p*-values; thus, the permutation procedure directly implies normality and homogeneity of variances (Anderson, 2001; Anderson et al., 2008). PERMANOVA was performed using Euclidean distance and permutated residuals under a reduced model, Type III (maximum permutations=999), according to the routine for univariate analysis (Anderson et al., 2008). This analysis was performed using the software PRIMER v7.

To evaluate the influence of environmental factors on community structure, canonical correspondence analysis (CCA) was applied to the parameter data matrix (dependent set: community parameters) and the factor data matrix (explanatory set: abiotic and biotic variables). Inter-set correlations from this analysis were used to determine the environmental variables that were most important in determining the variability of community parameters (McGarigal et al., 2000). The significance of each of these factors was determined using 499 unrestricted Monte Carlo permutations. A biplot of parameters and explanatory factors was constructed to observe any pattern associated with these factors. All of these analyses were performed using the package CANOCO ver. 4.5 (ter Braak & Šmilauer, 2002). In addition, the degree of simple association between two variables was evaluated using non-parametric Spearman correlation analysis (r_S).

Results

The seasonal pattern of zooplankton diversity and species richness showed high values in November-December and April, and low values in May, July, and January (Fig. 2A). In contrast, dominance was high in May (defined by the copepods *Tortanus* (*Acutanus*) *setacaudatus* and *Pseudosiaptomus pelagicus*), October (by zoea larvae of brachyura), and March (by the copepod *Acartia (Acanthacartia) tonsa*), with low values in December and April, while evenness shows a completely inverse pattern to dominance (Fig. 2B).

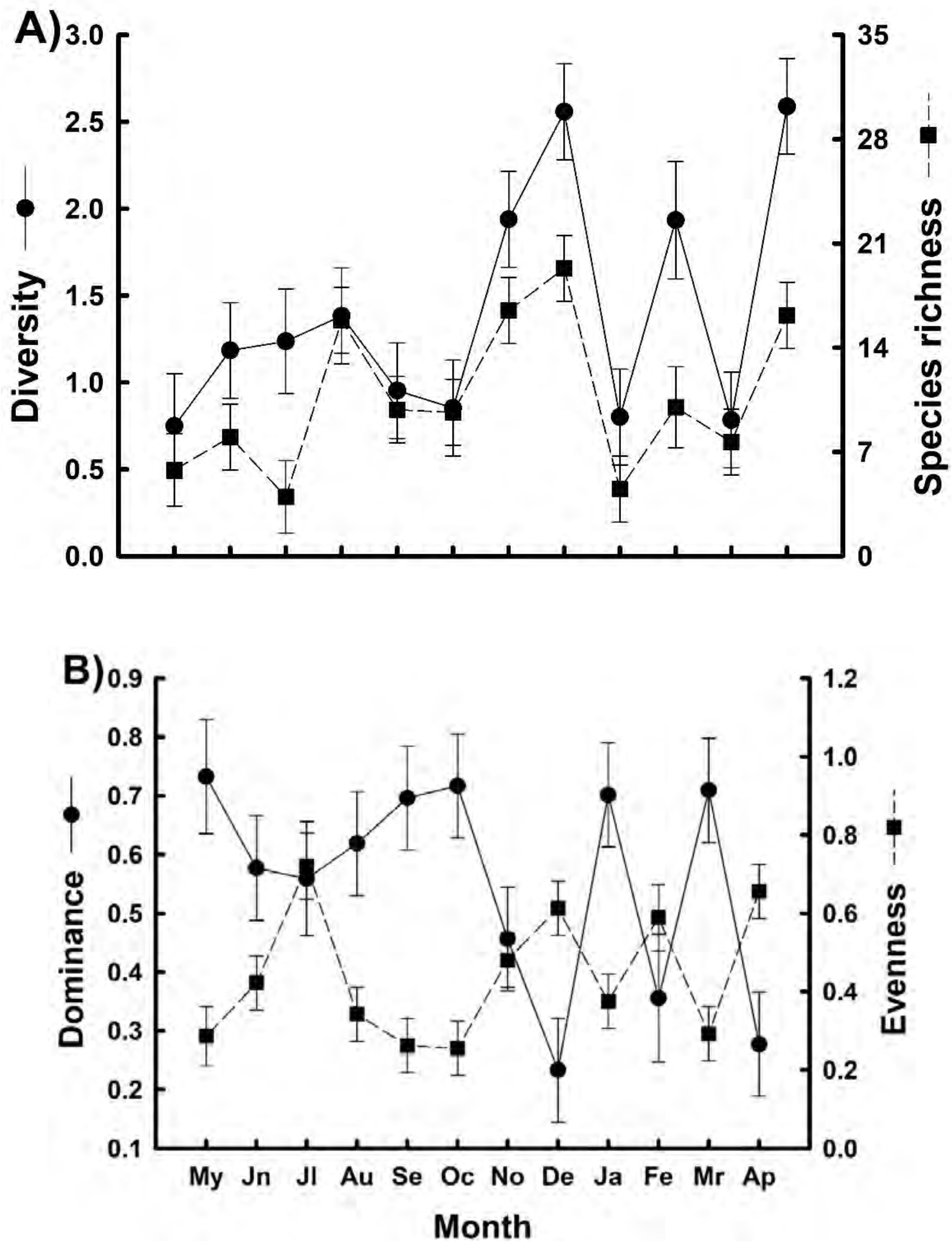


Figure 2. Monthly Variation of: A) Mean and Standard Error Values of diversity and species richness, and B) Mean and Standard Error Values of Dominance and Evenness (for each Monthly Value n=6).

The diel variability of these parameters showed that diversity and richness presented high values at night (22:00 to 02:00 h) and low values at dawn (06:00 h) or dusk (18:00 h) and during the day (10:00 to 14:00 h) (Fig. 3A). On the contrary, the high value of dominance occurred at dawn (06:00 h) dominated by *A. tonsa* and zoea larvae, and low values during the night (22:00 to 02:00 h) while the evenness shows a reverse pattern (Fig. 3B). The community was dominated solely by the abundance of four zooplanktonic components, *A. tonsa*, *P. pelagicus*, *T. setacuadatus,* and zoea larvae, which represented 89 % of the total abundance in number of the entire community.

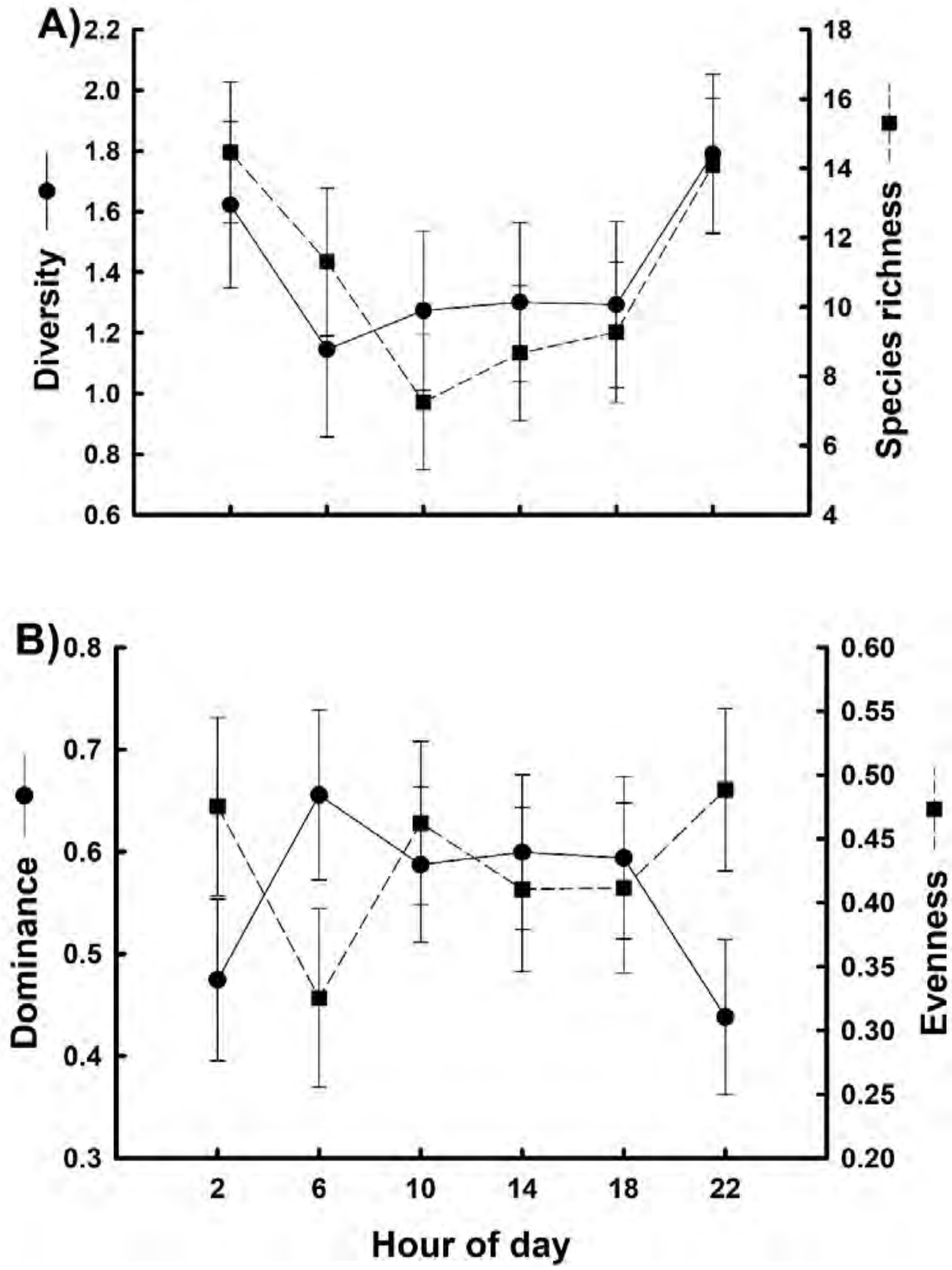


Figure 3. Mean and Standard Error Values by Hour: A) Diversity and Species Richness, and B) Dominance and Evenness (for each Hourly Value n=12).

According to the two-way univariate results (PERMANOVA), all parameters show significant differences among months. Similarly, at the diel level, there were significant differences except for evenness. All interactions between monthly and diel factors were not significant (P’s >0.3, Table 1).

Table 1. Results of Two-way Univariate Analysis of Variance (PERMANOVA) to Test the Effects of the Month and Diel Periods (Day, Twilight, and Night) on the Community Parameters.

Source of Variance	df	MS	Pseudo-F	P (Permuted)
Diversity				
Months	11	2.589	6.053	0.001
Diel	2	1.563	3.655	0.039
Months x Diel	22	0.371	0.866	0.638
Error	32	0.428		
Species Richness				
Months	11	146.19	5.822	0.001
Diel	2	232.96	9.278	0.001
Months x Diel	22	16.320	0.650	0.835
Error	32	25.109		
Dominance				
Months	11	0.178	4.455	0.001
Diel	2	0.179	4.479	0.020
Months x Diel	22	0.044	1.096	0.396
Error	32	0.040		
Evenness				
Months	11	0.127	5.019	0.001
Diel	2	0.041	1.627	0.246
Months x Diel	22	0.030	1.178	0.328
Error	32	0.025		

In this sense, diversity was mainly inversely correlated with dominance (r_S=-0.981, P<0.0001) and directly correlated with species richness (r_S 0.747, P<0.0001), while species richness and dominance were also negatively correlated (r_S=-0.693, P<0.0001).

Concerning environmental factors' influence on community structure, the simultaneous ordination of parameters and environmental matrices in CCA showed that all canonical axes were significant (P=0.010). The first two axes explained 99.2 % (76.9 and 22.3 %, respectively) of the total constrained variance. Intra-set correlations indicated that salinity, the diel effect, and temperature were the most critical variables in structuring the zooplankton community. Likewise, according to Monte Carlo significance tests, only these factors significantly affected the community parameters. Both inter-set correlations and significance tests indicated that biotic factors such as chlorophyll *a* and the abundance of diatoms, dinoflagellates, and cyanobacteria were unimportant in community structuring (Table 2).

Table 2. Inter-set Correlations Between Environmental Factors and Species Scores from the Canonical Correspondence Analysis. The Significance of these Factors (Unrestricted Monte Carlo Permutations) Is also Shown.

Environmental Factors	Inter-set Correlations		
	Axis 1	Axis 2	P(Permuted)
Salinity	-0.510	0.104	0.002
Diel Effect	0.363	0.052	0.020
Temperature	-0.072	-0.284	0.038
Tidal Stage	-0.149	-0.156	0.192
Dissolved Oxygen	0.133	-0.145	0.272
Diatoms	-0.129	-0.066	0.506
Chlorophyll a	0.199	0.068	0.608
Cyanobacteria	0.181	-0.105	0.748
Dinoflagellates	0.059	-0.023	0.934

In the CCA analysis biplot (Fig. 4), the length and direction of the arrows indicate the relative importance and direction of change that each factor has in the ordination. This diagram reveals a main ordination gradient related to salinity that is directly associated with species richness and inversely with dominance. Another major trend, perpendicular to the first, is related to temperature and is in the opposite direction of the diel effect, which shows that diversity is associated with low temperatures and evenness in the daytime.

Thus, salinity was the environmental variable that was most correlated individually with the community parameters, directly with diversity (r_s=0.575, $P<0.0001$), species richness (r_s=0.491, $P<0.0001$), and evenness (r_s=0.486, $P=0.0001$), and inversely with dominance (r_s=-0.536, $P<0.0001$). The direct relationship between salinity, diversity, and species richness can be observed at the seasonal and diel levels (Fig. 5A-B and 5C-D, respectively). Dominance has an inverse clear relationship with salinity only seasonally. Other abiotic and biotic variables did not show significant simple correlations with the parameters.

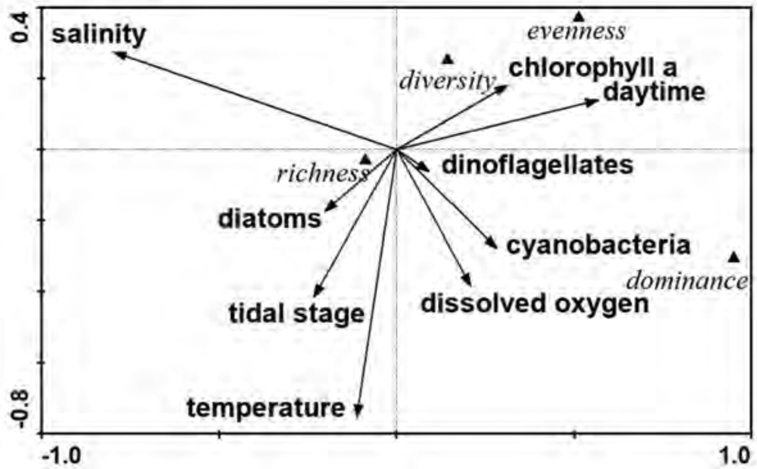
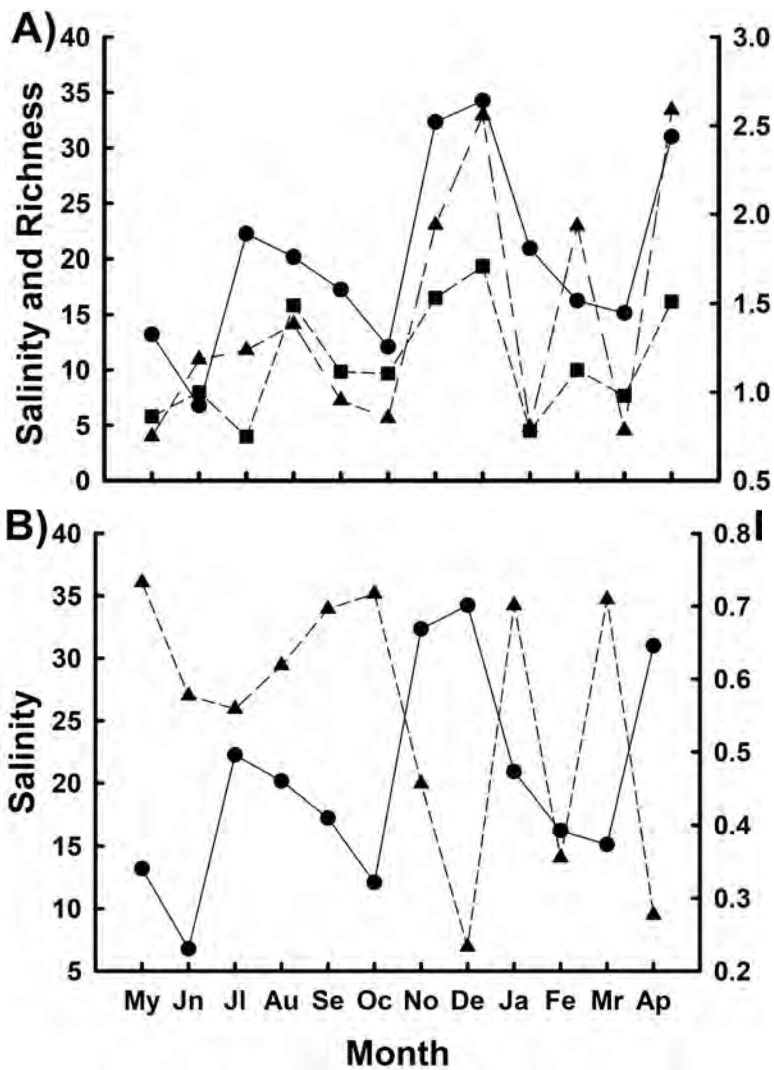


Figure 4. Bi-plot of Canonical Correspondence Analysis of the Overall Community Parameters and Environmental Variable Data Matrices. Data Points Represent Parameters (▲), and Arrows Represent the Direction and Relative Importance of Explanatory Variables.



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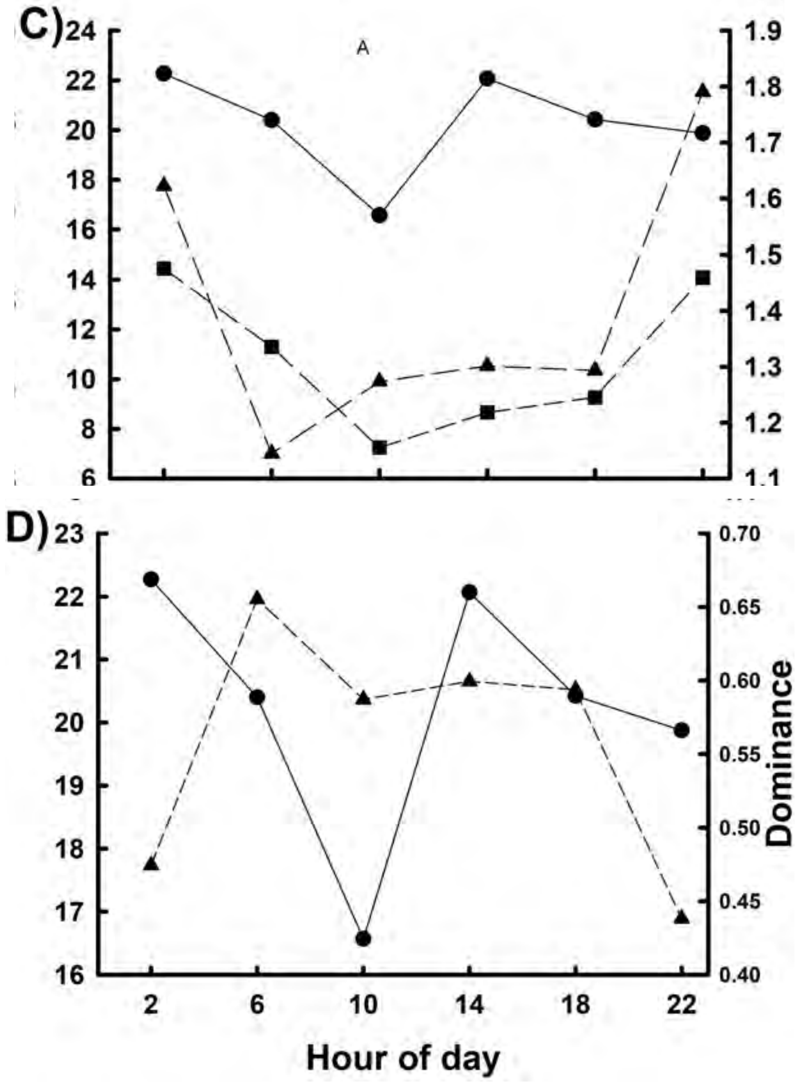

Figure 5. Monthly Mean Values of Salinity and Community Parameters: A) Direct Relationship between Salinity (●), Species Richness (■), and Diversity (▲), and B) Inverse Relationship between Salinity (●) and Dominance (▲) (for Mean Monthly Values n= 6). Mean Values by Hour of Salinity and Community Parameters: C) Direct Relationship between Salinity (●), Species Richness (■), and Diversity (▲), and D) Relationship between Salinity (●) and Dominance (▲) (for Mean Hourly Values n = 12).

Discussion

Although the formal study of zooplankton in Mexican waters began more than a century ago, most of the studies carried out correspond mainly to research in freshwater and marine systems with central reference only to some groups of zooplankton (Mecalco-Hernández & Castillo-Rivera, 2020; Alcocer et al., 2022; Cervantes-Martínez et al., 2023), there are few studies in estuarine systems, especially in the state of Veracruz. Likewise, few studies have inferred diel changes in zooplankton communities from low-frequency temporal sampling which allows a more precise assessment of the timing of diel changes throughout the 24 h cycle and the influence of environmental factors on these changes over short periods.

In the research of zooplankton communities, many studies have used community parameters to describe changes in community structure adequately (Liang et al., 2020; Arias et al., 2022; Romero et al., 2022; Taniguchi et al., 2023). In the present study, all community parameters showed a significant monthly variation, which is related to the strong environmental variability that characterizes estuarine ecosystems and to the fact that zooplankton usually presents a relatively rapid response to environmental changes (Benfield, 2013; Guermazi et al., 2023).

In this way, diversity and species richness showed pulses in December and April and low values in May, while dominance showed a completely inverse pattern. Indeed, simple correlations showed that diversity and species richness had a strong inverse correlation with dominance. Concerning environmental stability, diversity can be determined primarily by evenness in habitats with low variability. However, in environments with strong variability, such as estuaries, few eurytopic species (tolerant to a wide range of ecological conditions) would be expected to be dominant, so diversity would mainly be inversely affected by dominance. Indeed, in La Mancha Lagoon, almost 90 % of the numerical abundance of the entire community was dominated by only four zooplankton components (*A. tonsa*, *P. pelagicus*, *T. setacuadatus* and zoea larvae).

At the diel level, all parameters showed significant differences among hours, except evenness. Species richness and diversity showed high values during the night and low values during the day. According to the PERMANOVA results, there was no significant interaction between the month and diel period factors, for all four parameters, indicating that the diel pattern was consistent across all sampled months. In this way, many studies have indicated that during the night there is a significant increase in the number of species (Marques et al., 2009; Primo et al., 2012). This behavioral pattern has been considered the most common characteristic in marine and freshwater planktonic communities, which is characterized by an evening ascent and a morning descent (van Haren & Compton, 2013; Ursella et al., 2021).

Considering the predator avoidance hypothesis, the vertical migration of zooplankton to deeper waters during daylight hours, where the probability of being detected by visually searching predators is lower than if they remained in shallow waters with more illuminated conditions, and during the night, under dark conditions, zooplankton migrate upward to feed and shelter (Węgleńska et al., 1997; Ursella et al., 2021; Garcia-Herrera et al., 2022). These vertical patterns may also appear to be influenced by abiotic factors such as hydrological regime (inputs of freshwater flow), water currents, light variation, tidal phase, and salinity (Primo et al., 2012; Benfield, 2013; Hobbs et al., 2021; Ge et al., 2021).

The dominant zooplanktonic components, *A. tonsa* and zoea larvae, showed a typical crepuscular occurrence with pulses at dawn. In this sense, the increase in activity during twilight hours may be related to compensation strategies that attempt to resolve the trade-off between feeding and avoiding predators. Twilight conditions may mitigate visual detection by visual predators, but provide sufficient light to detect prey. Indeed, considering a predator-prey encounter model (Giske et al., 1994), for smaller zooplankters the risk of mortality will generally be reduced in accordance with a general decrease in ambient light.

Regarding the knowledge of biodiversity in zooplankton communities, studies over short periods throughout sampling in 24 h cycles can provide a better understanding of zooplankton richness. Indeed, in the present study, of the total 57 zooplanktonic components recorded, 13 (~23 %) were collected only at twilight and during the night.

About the multivariate influence of environmental factors on community parameters, the CCA ordination explained a high percentage of the constrained variance of the parameters-environment relationship (99.2 %), which implies that the environmental variables considered give an adequate description of the community structure. According to inter-set correlations and Monte Carlo significance tests, abiotic factors salinity and diel effect (related to light gradient) were the most critical variables driving community structure.

Indeed, salinity is one of the main factors driving the structuring of zooplankton communities in estuarine and marine systems (Benfield, 2013; Shi et al., 2015; Dvoretsky & Dvoretsky, 2017; Chen et al., 2023), affecting the richness and diversity species inversely (negative correlations) or directly (positive correlations), depending on whether the communities are dominated by freshwater or marine species (Paturej & Gutkowska, 2015; Helenius et al., 2017; Yuan et al., 2020).

In the present study, according to CCA results salinity has a positive effect on species richness, while it has a negative effect on dominance. These results were also confirmed by simple correlations, which indicated significant direct correlations of salinity with species richness and diversity and a significant inverse correlation between salinity and dominance. Higher salinities allowed the entry of a greater number of neritic species to the lagoon, thus increasing richness and diversity. In contrast, in low-salinity conditions only tolerant species remain dominant in the community. Thus, the effect of salinity was observed at monthly and diel levels. The light gradient showed that species richness was more significant during the night, while other abiotic factors such as dissolved oxygen and tidal stage showed little incidence on the community structure (low inter-set correlations and no significant effect). This is because the dissolved oxygen values in the system are probably greater than the limits of lethal and sublethal hypoxic conditions. Likewise, although some studies have observed the importance of the tide in the structuring of the community (Marques et al., 2009; Primo et al., 2012), for the zooplanktonic community of La Macha, the tide stage had little influence mainly because the southwest coast of the Gulf of Mexico is predominantly microtidal (Ellis & Dean, 2012), with <20 cm within the lagoon.

CCA results also showed the negligible effect of biotic factors on community structuring. Many studies have observed that zooplankton communities can be affected by biotic factors such as phytoplankton density (García-Herrera et al., 2022; Guermazi et al., 2023) and chlorophyll *a* (Liang et al., 2020; Muñoz-Colmenares et al., 2021; Chen et al., 2023), but in the present study, chlorophyll *a* and the densities of diatoms, dinoflagellates, and cyanobacteria were not significant. Thus, both abiotic and biotic conditions can have an important incidence in a structuring community, but their relative importance may vary among different environmental conditions and across temporal and spatial scales. While abiotic factors can affect community structure by setting the limits of abiotic tolerance of species, biotic factors may also affect diversity patterns by influencing species abundance and composition (Måsviken et al., 2023).

In this way, many studies have compared the relative effect of these factors on zooplankton communities, observing that both can act synergistically (Gray et al., 2012; Mecalco-Hernández et al., 2018; Yang et al., 2019; Chará-Serna and Casper, 2021) or at a different temporal scale (Gabaldón et al., 2019; Rollwagen-Bollens et al., 2020). In this way, the variability of abiotic factors can also modify the biological response of species (Begon & Townsend, 2021), as observed in La Mancha Lagoon, where the light/dark cycle affects predator-evasion patterns.

Notwithstanding the above, it would be expected that in environments with low environmental variability (stable), biotic factors such as food availability, predation, and competition would be the main regulators of the community. In contrast, in environments with high environmental variability, abiotic factors would play a more important role, as is also observed in the zooplanktonic community of La Mancha Lagoon and other similar systems (Sahuquillo & Miracle, 2019; Sgarzi et al., 2019).

Conclusion

A better understanding of the zooplanktonic community dynamics of aquatic ecosystems can be achieved by sampling over 24 h. Thus, species richness was consistently greater during the night, which was related to predator-evasion strategies modulated by the light/dark cycle. The environmental variables considered in the present study explained a very high percentage of the community structure's temporal variability, allowing a more reliable interpretation of the results. The high environmental variability characteristic of estuaries caused the community structure to vary significantly among months and hours. As a consequence of this variability, diversity was mainly associated with dominance, and the abiotic factors salinity and diel effect played a more important role in determining the community structure, while the biotic variables chlorophyll *a*, and densities of diatoms, dinoflagellates, and cyanobacteria had negligible importance.

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This book takes a significant step in showcasing the relevance of limnology to our survival. Freshwater habitats, though they cover less than 1 % of the Earth's surface, are home to a substantial portion of the world's biodiversity—at least 10 % of all known species. Freshwater habitats and the biodiversity they support are under threat. Moreover, our survival depends on access to high-quality freshwater. This book not only highlights the beauty of limnology and the scientific methods used to study it, but it also draws attention to the major causes of biodiversity loss in freshwater ecosystems. It shows all readers what it means to deal with inland waters as a scientist interested in understanding ecosystems and protecting them.

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