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.

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Potential Use of Rotifer and Cladoceran Diapausing Eggs as a Tool for Taxonomical, Ecological, and Evolutionary Studies

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Abstract

Rotifers and cladocerans usually reproduce by parthenogenesis. However, under adverse conditions, females turn to sexual reproduction. The final output when females are fertilized is the production of diapausing eggs. They are a remarkable strategy of organisms to recolonize aquatic ecosystems when periods of dryness occur or when adverse conditions in the water prevail. Despite their prominent functionality, the knowledge of diapausing eggs in taxonomy, ecology, and evolution is still poor. Therefore, in this review, we discuss the gaps in the understanding of diapausing eggs and, moreover, their potential to develop further studies.

Keywords

Dormancy, ephippia, resting egg, sexual reproduction, zooplankton.

General Information about Diapausing Eggs

What is a Diapausing Egg, and Where Does it Come from?

Rotifers and cladocerans are two of the most studied groups in zooplankton. These organisms usually reproduce by parthenogenesis. However, females change into sexual reproduction to generate diapausing eggs (see Figure 1) in response to several environmental stimuli that precede unfavorable conditions (Gilbert & Schröder, 2004; Schröder, 2005), environmental uncertainty (García-Roger et al., 2019), but also endogenous signals (Gilbert, 2007).

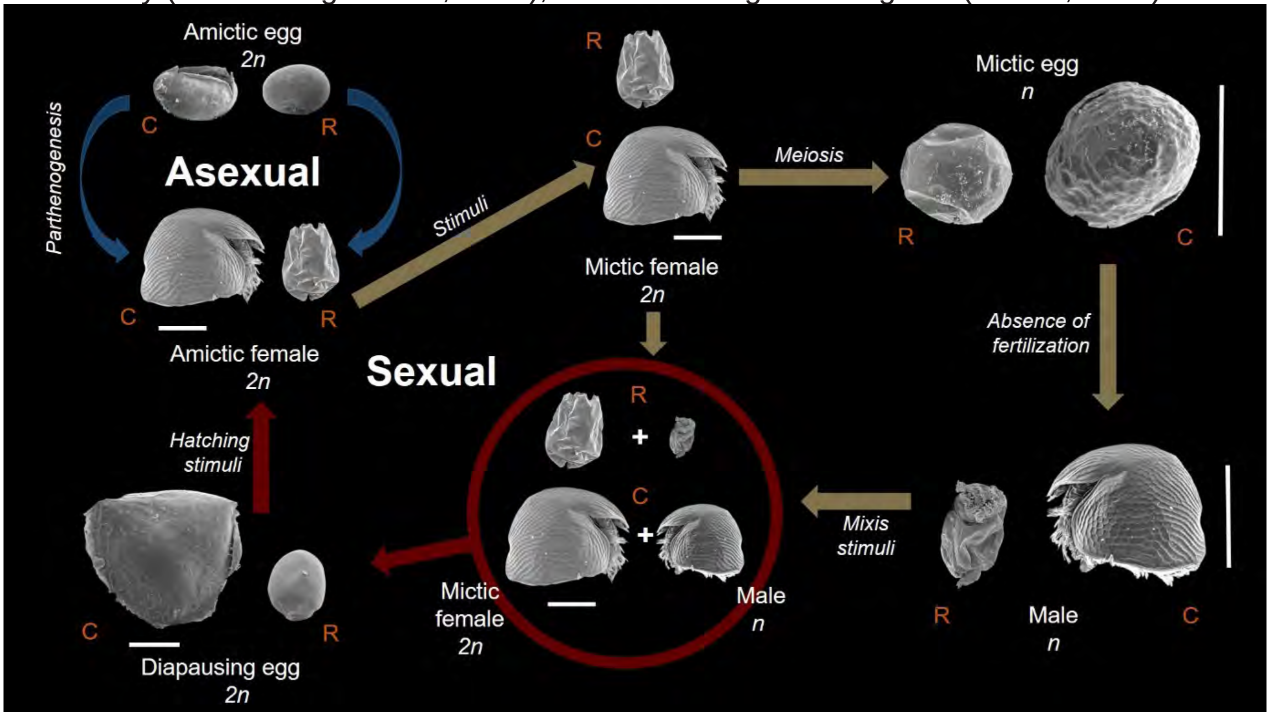

Figure 1. The Life Cycle of Monogonont Rotifers and Cladocerans. In the Life Cycle of Both Rotifers (R) and Cladocerans (C), the Asexual Phase Involves Amictic Females Producing Copies of Themselves in Amictic Eggs by Parthenogenesis. However, Particular Environmental Factors Will Eventually Trigger the Transition to Sexual Reproduction, Meaning that Meiosis Will Take Place in the Production of New Offspring. Females that Undergo this Shift Are Called Mictic Females, and They Produce Haploid Mictic Eggs. If a Mictic Egg Is Not Fertilized, a Haploid Male Will Hatch. If Fertilized, it Will Develop into a Diapausing Egg, and a New Diploid Female Will Hatch Under Stimuli. Scale bar = 100 µm. Figure Edited by Guerrero-Jiménez Gerardo.

Changes in photoperiod, crowding, or diet are some environmental factors that could induce the change to sexual reproduction (Gilbert & Williamson, 1983). Some studies also suggest the role of endogenous signals that delay mixis to reproduce sexually despite environmental stimuli (Gilbert, 2003; 2007). Diapausing eggs (also called resting eggs in rotifers and ephippia - *in Greek "saddle"*- in cladocerans) are embryos that have arrested development after most nuclear divisions and are surrounded by thick-walled, resistant self-made envelopes or shells, which have the ability to persist for extended periods of dormancy (Gilbert & Wurdak, 1978). They are generally ovoid or spherical (Wurdak et al., 1978; Pourriot & Snell, 1983), but there can be some found with irregularities or even kidney-shaped (Guerrero-Jiménez et al., 2020). Diapausing eggs are characterized by a thick, dark, opaque shell that presents surfaces with a wide range of ornamentations (Wurdak et al., 1978) and accessory structures such as knobs, spines, grooves, lobes, wrinkles, and small holes; in cladocerans, peduncles can be found in some species attached to the posterior portion of the ephippia (Guerrero-Jiménez et al., 2020). The diapausing eggs of several rotifers have an operculum delimited by a suture, allowing the female to exit the egg during hatching (Pourriot & Snell, 1983), see Figure 2.

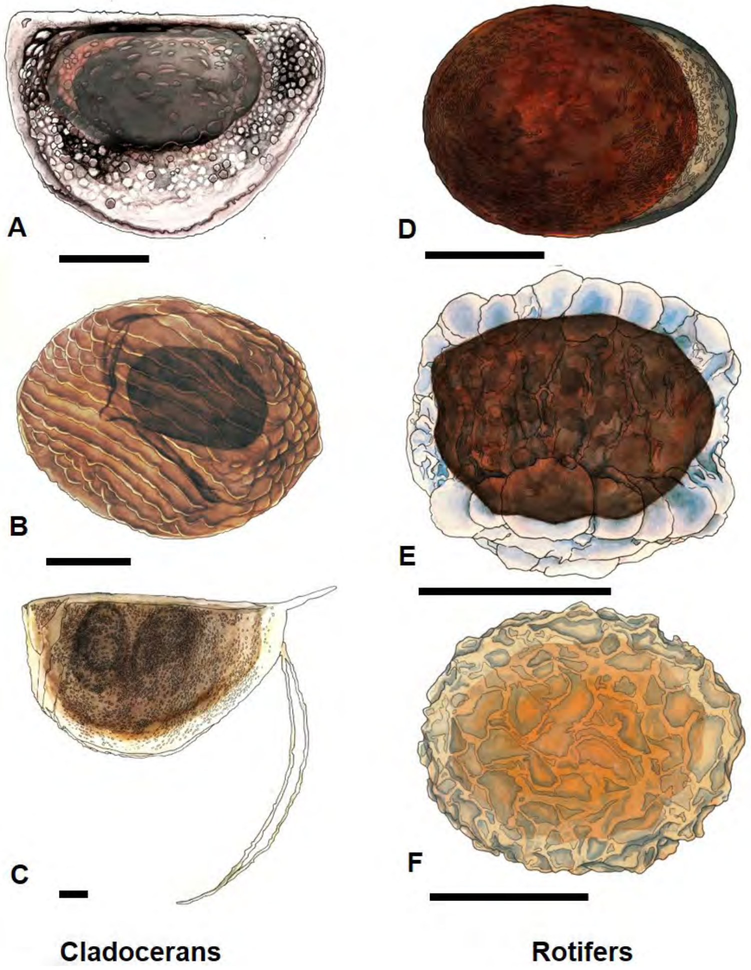

Figure 2. Different Ornamentation in Cladoceran and Rotifer Diapausing Eggs by Merging Optical and Scanning Electron Microscope Pictures. A) *Ceriodaphnia*, B) *Alona*, C) *Daphnia*, D) *Brachionus*, E) *Filinia*, F) *Lecane*. Scale Bar 50µm for Rotifers and 100µm for Cladocerans. Drawings Made by Armas-Chávez R. Natalia.

The mature diapausing egg appears to be composed of three layers in cladocerans: the first one being the ephippium with the ornamentation, the middle one containing the egg or eggs, and the internal layer compounded by a thin membrane (Guerrero-Jiménez et al., 2020). However, in rotifers two layers are generally observed: the external one showing the ornamentations and the internal layer enclosing the embryo, both usually separated by an extraembryonic space (Wurdak et al., 1978), see figure 3.

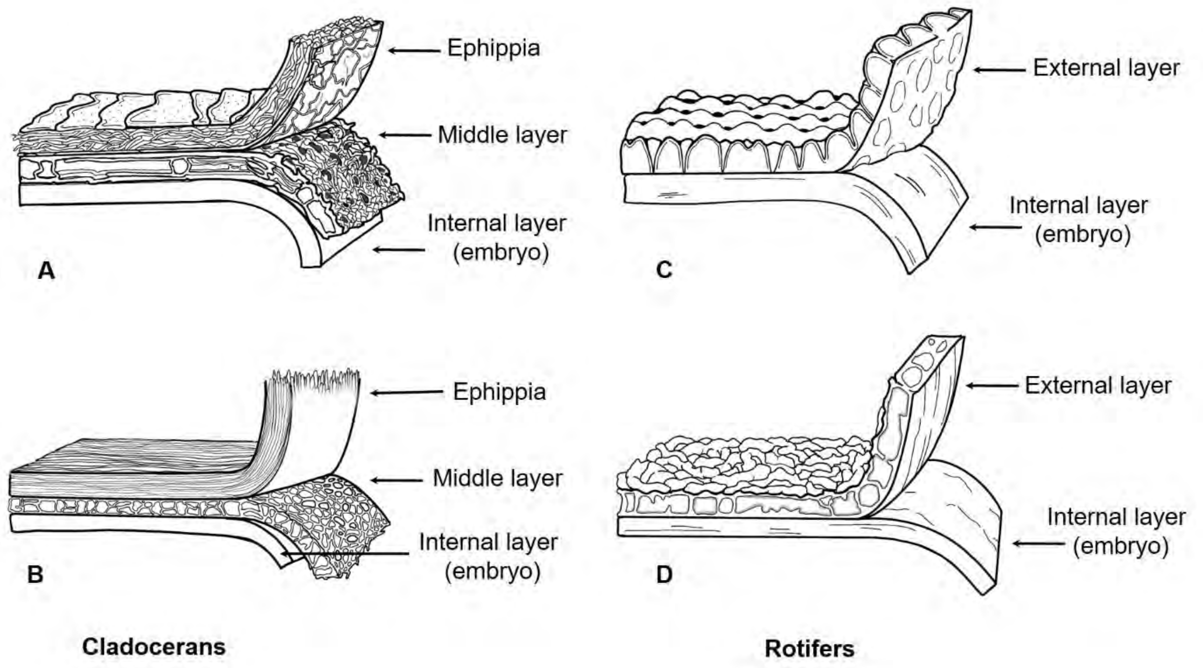

Figure 3. Transversal Cut of Diapausing Eggs of Cladoceran and Rotifer Species. The Figures Represent Layers Attached to Each Other in Some Portions. However, They May also Present a Space between Layers in Other Regions According to their Morphology. Drawings Made by Armas-Chávez R. Natalia.

Piavaux and Magis (1970) confirmed the presence of chitin in the shell of mictic, amictic, and diapausing eggs of several species of rotifers and noted that chitin is regularly and specifically present in the internal layer. These dormancy structures hold one embryo in rotifers but can hold several in cladocerans.

What is the Purpose of a Resting Egg?

Diapausing eggs of cladoceran and monogonont rotifers allow a form of dormancy called diapause, a trait commonly found in organisms that inhabit harsh or unstable conditions and is controlled by an internal mechanism that initiates in response to environmental cues (Radzikowski, 2013; García-Roger et al., 2019). Diapausing eggs provide safety under both biotic and abiotic unfavorable conditions over long periods of time by maintaining basal metabolism to ensure survival (Gremer & Sala, 2013), but diapause also serves the purposes of dispersal, habitat colonization (Schröder, 2005) and genetic variation (Pourriot & Snell, 1983). Despite of its functionality, the biological role of shell ornamentation and accessory structures is still unclear, although it is suggested that it may also have an important role as a defense in egg predation (Dumont et al., 2002). Pourriot and Snell (1983) have suggested that thickness of the shell in diapausing eggs and its reduced porosity allows them to resist the action of digestive enzymes when predated. The eggs accumulate in bottom sediments and create a resting egg bank, and once habitat quality improves or specific environmental cues are set (Radzikowski, 2013), resting eggs hatch, and hatchlings develop in the water column (Vargas et al., 2019). This happens after varying periods of dormancy, some remaining viable in lake sediments for many years (Gilbert & Wurdak, 1978). However, the viability of resting eggs and hatchlings might decrease as resting eggs age and are exposed to extreme conditions (Vargas et al., 2019).

Genetic Recombination

As seen previously, rotifers and cladocerans combine asexual and sexual reproduction in their life cycle. This mechanism is designated as cyclical parthenogenesis (García-Roger et al., 2019), in which the asexual phase predominates, and organisms undergo several rounds of clonal reproduction followed by a sexual event (Rouger et al., 2016). The sexual phase produces genetic variation through recombination (King & Snell, 1977), which implies the exchange of DNA between male and female chromosomes during meiosis (Stapley et al., 2017). This starts the formation of the diapausing egg. Nevertheless, the production of diapausing eggs without fertilization has been reported for some species in both rotifers and cladocerans. Ruttner-Kolisko (1946) reported asexually produced diapausing eggs in *Keratella hiemalis,* and Schröder (1999) reported the same in the rotifer *Notholca squamula.* Gilbert (1995) reported the production of amictic diapausing eggs in the rotifer *Synchaeta pectinata.* In cladocerans, these early diapausing embryos from asexually produced diploid eggs are referred to as pseudosexual resting eggs. They are the result of a gene that suppresses meiosis, acting like the sexually derived resting eggs, but being genetically identical to their mother (Dodson & Frey, 2015). Some cladocerans have made the transition from cyclical parthenogenesis to obligate asexuality (Hebert, 1987), nevertheless, they produce pseudosexual resting eggs or pseudoephippia (Cerny & Hebert, 1993). Gilbert (1995) suggests that the production of diapausing amictic eggs in rotifers may be a strategy to increase the ability of clones to survive food limitations. On the other hand, pseudosexual eggs of *Daphnia* are probably a solution for the need to produce resting eggs in ponds that are too cold (Dodson & Frey, 2015).

Dispersion and Recolonization

The resulting dormant stages settle at the bottom of the water body, creating an egg bank in the habitat that ensures the availability of eggs for future generations, although there are some reports where they were observed floating on the surface of lakes Guerrero-Jiménez et al. (2020). In addition, they may be dispersed in space passively by anemochory (Rivas Jr. et al., 2019), anthropochory (Perrigo et al., 2012), hydrochory (Ricci & Balsamo, 2000), and zoochory (Moreno et al., 2019). Therefore, when the diapausing eggs hatch, they can either replenish an existing population or establish a new one elsewhere (Vargas et al., 2019).

This bank is essential as it accumulates resting eggs produced at different periods, facilitating the preservation of genetic variants for active populations (De Stasio, 2007). The viable zooplankton egg bank is found in the top three centimeters of sediment, also known as active sediment (Pérez-Martínez et al., 2013). This stratum not only acts as a vital reservoir for the survival of these organisms but also plays a significant role in recruiting new genetic variants for active populations.

Current Progress Using Diapausing Eggs

Taxonomy: Morphological Traits and their Purpose

Records of diapausing egg taxonomy are historically scarce (Duggan et al., 2002). Furthermore, it has been suggested in latter years that further studies are required to understand diapausing eggs morphotype ultrastructure. In addition, Walsh et al. (2017) also mentioned that taxonomical descriptions were intricate due to a lack of feature standardization. On the other hand, similar conditions are met for cladocerans. Although some isolated studies have reported ultrastructure features of rotifers (Gilbert & Wurdak, 1978) and cladocerans (Kotov, 2013), Guerrero-Jiménez et al. (2020) first developed a useful key to identify rotifer diapausing eggs using six different taxonomical features easy to identify (see Table 1).

Table 1. Taxonomic Standardization with Six Categories to Identify Rotifer Diapausing Eggs of *Brachionus* Genus, According to Guerrero-Jiménez et al. (2020).

Categories by Observation Order			
1. Egg Size	Small (<80µm)	Medium (80-120µm)	Large (>120µm)
2. Egg Shape	Regular	Regular	Regular
3. Color	Brown	Brown	Brown
4. Extraembrionary Space Size	Small (1/8 of the Whole Embryo)	Medium (1/4 of the Whole Embryo)	Large (1/2 of the Whole Embryo)
5. Ornamentation or Accessory	Ornamentation	Ornamentation	Ornamentation
6. Type of Ornamentation or Accessory	Holes	Wrinkles	Grooves
Species	*budapestinensis*	*bidentatus*	*calyciflorus*

Keys to identifying diapausing eggs using their taxonomy are still being developed in cladocerans. Thus, only 40 to 50 species on each taxon have been described in depth.

Ecology: Interaction with Environmental Factors

Studies focused on the effects of different biotic and abiotic factors in diapausing eggs are surprisingly scarce, given the importance of these structures in rotifer and cladoceran life cycles. Among the available literature, effects of light, salinity, temperature, and pollutants have been studied on certain specific species. In fact, Stross (1966) and Vandekerkhove et al. (2005a) have suggested that two of the main factors implicated in activation and interruption patterns of dormancy are light and temperature. Several adverse environmental alterations lead to the production of resting eggs and different factors may be involved in their hatching, which makes it even more difficult to evaluate and establish a pattern for diapausing mechanisms. Among the factors that control diapause in Cladocera are photoperiod, temperature, population density, desiccation, and predation signals (Alekseev, 1990). Additionally, little is known about the endogenous mechanisms that restrict the activation of sexual reproduction regardless of the environmental stimuli that might trigger the sexual phase, as seen in the rotifer *Brachionus calyciflorus* (Gilbert, 2003) and *Hexarthra* populations (Gilbert, 2007).

Light

Studies that consider the effects of light in diapausing eggs of rotifers and cladocerans mainly use white light, which encompasses all the wavelengths of visible light. However, experiments such as the work of Hagiwara et al. (1995) further study the effects of light by testing six different intensities. In this study, it is concluded that hatching of *Brachionus plicatilis* caused by light depends on its intensity and irradiation period, but more hatchings were observed with more irradiation. On the other hand, in cladocerans, Vandekerkhove et al. (2005b) demonstrated different hatching patterns in 45 species from Denmark, Belgium/the Netherlands, and Spain using different photoperiods. They conclude that light is a key factor for the hatching of resting eggs when exposed to a long day photoperiod rather than under continuous illumination. Altogether, light is a determining factor in the hatching of both rotifer and cladoceran diapausing eggs. Indeed, preliminary analysis showed their natural reaction to different wavelengths of light.

Salinity

Overall, studies have demonstrated that increment of salinity in water ponds decrease hatching rate, however, according to Santangelo et al. (2014) and Conde-Porcuna et al. (2018), not all species respond in the same way. In rotifers, a vast majority of studies are focused in marine rotifers belonging to *B. plicatilis* complex group. For example, Minkoff et al. (1983) observed that the hatching of rotifer *Brachionus plicatilis* s.s. diapausing eggs was affected by the increase of salinity. Other studies, such as the work by Gabaldón et al. (2015), also observed differences in the hatching patterns of *B. plicatilis* s.s. and *B. manjavacas* under different salinity conditions. Apparently, the optimal salinity for these species is under 15-18 g/L. However, it is not uncommon to observe hatching with higher salinities. In freshwater rotifers, Conde-Porcuna et al. (2018) demonstrated that species decrease hatchings dramatically when salinity exceeds 8 g/L. Cladocerans studies are more restricted, the most relevant such as the work of Santangelo et al. (2014) studied hatching patterns of 16 different taxa including cladocerans, using a salinity range of 30 g/L. They observed the lowest hatching values at high salinities, 16 and 32 g/L, respectively. On the other hand, Mabidi et al. (2018) in four South African wetlands proved that the hatching rate of cladocerans diminished with salinity levels of 2.5 g/L or higher.

Temperature

This is one of the most direct stimuli for the activation of diapausing eggs, according to Vandekerkhove et al. (2005b). Indeed, experiments in laboratory conditions of May (1987) demonstrated that high temperatures are required for hatching. More specific data using rotifers demonstrated that at 25°C three species belonging to the *B. plicatilis* complex group drastically rushed their hatching rate, and also around 80 % of hatchings occurred in the first five days of exposure, compared to temperatures below 20°C (Walczyńska & Serra, 2014). In cladocerans, Vanderkerhove et al. (2004, 2005a) hatched several European species at 15°C. Komazawa and Endo (2002), using marine cladocerans, observed that at temperatures of 20°C or higher organisms did not hatch. Considering this information, rotifer diapausing eggs seem to be more efficient at higher temperatures (>20°C) compared to those of cladocerans, who increase their hatchings at <20°C.

Contaminants

Heavy metals (Aránguiz-Acuña, 2016) and pesticides (Navis et al*.,* 2013) have been proven to affect rotifer and cladoceran diapausing eggs by diminishing their hatching mechanism. Although the scarcely available studies are more focused towards cladocerans than rotifers. Oskina et al. (2019) showed that exposure time determines the negative effect of toxicants in hatching. Their experiments with the cladoceran *Moina macrocopa* demonstrated that exposure to concentrations of up to 80 g/L of Copper, Cadmium, Zinc, and Nickel for 30 days resulted in hatching rates superior to 80 %. However, when exposed for eight months, the hatching rate with concentrations of 30 g/L or higher was null. Thus, the structure of diapausing eggs is extremely efficient in short time periods. However, during long time periods, several external factors such as heavy metals may play an important role by corroding the external layer and/or permeating into the embryo, modifying the hatchlings and hatching patterns.

Evolution: Species-specific Hypothesis

Specialists have discussed since several years ago whether ornamentation of diapausing eggs in rotifers and cladocerans are specific to their species. Although nowadays most authors (Gilbert & Wurdak, 1978; Kotov et al*.,* 2018; Guerrero-Jiménez et al*.,* 2020) support this species-specific hypothesis, a few have observed in the past that what seemed one species, produced two different types of diapausing eggs. However, these observations did not consider the possibility of encountering cryptic species which are individuals highly morphologically alike but with genetic divergence, and that therefore produce two different morphotypes of eggs. Thus, it is important to merge further taxonomical, ecological, and molecular analyses in order to expand the knowledge of evolutionary mechanisms in diapausing eggs.

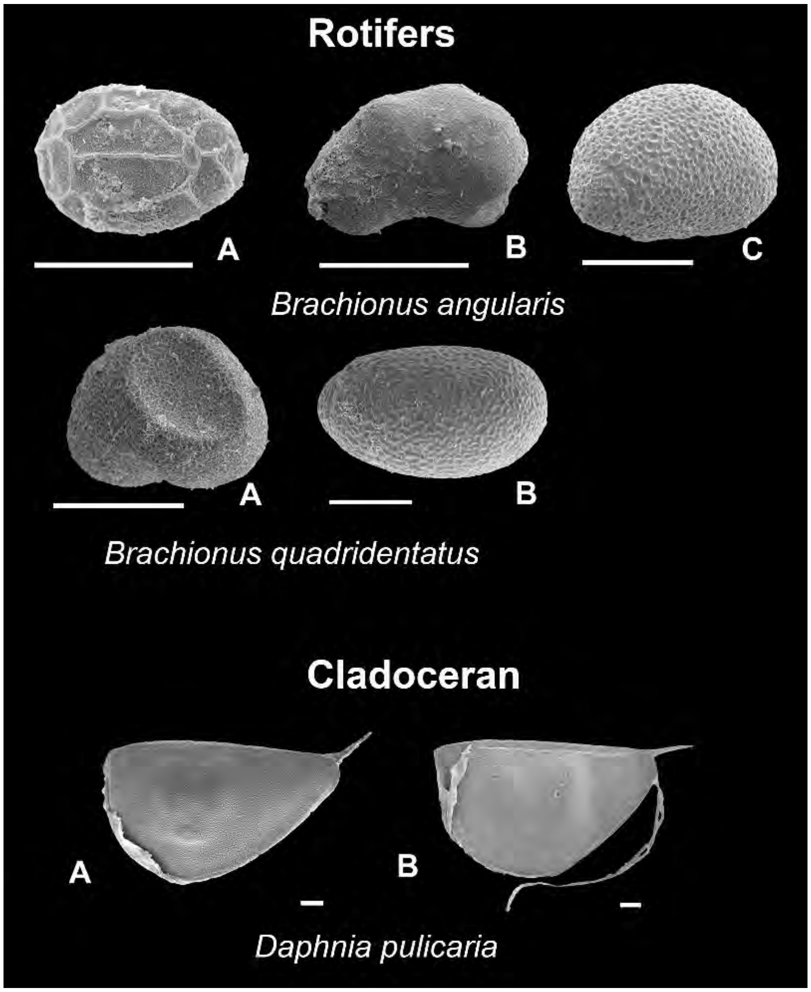

Figure 4. Cryptic Species with Clearly Different Morphotypes of Diapausing Eggs. Differences Are Based on Ornamentation, Size, and Shape. Scale Bar 50 µm for Rotifers and 100 µm for Cladocerans.

Future Perspectives and Opportunities

There is still enough information to be uncovered about biodiversity and descriptions of rotifer and cladoceran diapausing eggs morphotypes. Ecological studies are limited to model species such as *B. plicatilis* complex group for rotifers and *Daphnia* species for cladocerans. In evolutionary studies, data about functionality of structures and the species-specific hypothesis are still speculative.

Biodiversity

Molecular approaches using diapausing eggs are perhaps the most used tools to identify rotifer and cladoceran species nowadays. However, although DNA barcoding of diapausing eggs may yield higher numbers of taxa identified in comparison to taxonomic identification

(Moreno et al., 2017), these molecular studies often require complex methodologies and equipment that might not be accessible to most researchers. Furthermore, DNA barcoding without visual references does not provide solid evidence of biodiversity, especially in cryptic species. Considering this, rotifer and cladoceran diapausing eggs morphology already serves as a more cost-effective tool for identification of species, as their study requires relatively more simple methodologies and more accessible equipment. Furthermore, Vandekerkhove et al. (2005a) have suggested that diapausing egg banks may represent a complementary study approach of zooplankton species based on the wide assessment of community structure and diversity present in a single sample. However, despite its potential as a species identification tool, diapausing eggs are not widely studied, aside from a select set of keys available used with rotifers (Guerrero-Jiménez et al.*,* 2020). In cladoceran species, there are available nomenclature keys in isolated studies (Kotov et al., 2018), although consistent tools to identify diapausing eggs are yet to be developed.

In summary, there are many opportunities to develop studies using taxonomical features in order to uniform the available and new characters that will be observed, which will increase the current list of morphotypes of diapausing eggs described.

Ecology

Three phases within diapausing eggs can be studied: a) the factors that induce the females to produce them; b) the tolerance to adverse factors during dormancy; and c) factors that induce hatching patterns.

a) Most of the data available support that adverse conditions activate the production of diapausing eggs. However, delimiting what an adverse condition is between species is complicated due to the ecology and diversity of species, as well as within individuals. Furthermore, studies usually are focused on model species, such as *B. plicatilis* in rotifers and *Daphnia magna* in cladocerans. *B. plicatilis* is a marine species. Therefore, its studies mainly consider variability in salinity and temperature, which narrows the perspective on diverse factors that could be interacting with the species. In cladocerans, studies are mainly focused on temperature and food concentrations. Thus, there is a lack of information that considers the rest of the species and other factors such as different pollutants, light, and so on.

b) Two topics should be assessed regarding dormancy periods. Firstly, the ecology of the females to place diapausing eggs. Usually, it is assumed that they are placed only in sediments or floating on the surface of the water pond. However, water ponds present different dynamic and therefore species also present miscellaneous strategies to live in aquatic ecosystems which results in diapausing eggs to be found in places different from sediments. Secondly, the capability to tolerate adversity during dormancy is to be addressed. Indeed, studies are mostly focused on this line of investigation, although they are still insufficient, perhaps by the fact that diapausing eggs are too resistant and no effect is assumed. Some studies using salinity and pollutants have demonstrated levels of deterioration within eggshells. For instance, García-Roger et al. (2006) showed how salinity affects the viability of diapausing eggs in *B. plicatilis*. Furthermore, Piscia et al. (2012) in Lake Orta, Italy, observed almost null hatching when they were exposed to copper as well as alterations in the morphology of the eggshells.

c) Finally, hatching patterns are the most studied phase. According to Pourriot and Snell (1996), in rotifers, light, temperature, and salinity are the main factors that determine their hatching patterns, while in cladocerans, data suggests light and temperature to be the key variables (Vandekerkhove et al., 2005). In both taxa, light is mandatory to hatch, however, species have displayed different hatching patterns when exposed to other factors such as temperature or salinity. In the case of contaminants, Oskina et al. (2019) demonstrated that cladoceran ephippia are quite resistant, and hatching rate is not affected in short exposure periods, but after long exposition, ephippia are drastically affected.

Despite the suggestion of Nielsen et al. (2003) that diapausing eggs might be more susceptible to the current environmental changes, studies are still focused in active stages. Thus, a huge opportunity to develop studies and contribute to the understanding of the whole process related with this type of eggs is open to exploration.

Evolution

Studies that try to explain evolutionary processes are complex. Under the vast diversity of mechanisms that work in evolution, one of the most fascinating is how environmental pressure shapes morphological functionality within species. This environmental pressure might work in one or several stages of the life cycle of an organism, for example, in the life cycle of butterflies or beetles. All the stages in their life cycle present high morphological differentiations adapted to the functionality of the stated stage. In the same perspective, dormant stages of rotifers and cladocerans present an extraordinary array of morphological variabilities that integrate crucial mechanisms to recolonize aquatic environments. However, despite the importance of resting eggs as a stage in the life cycle of rotifers and cladocerans, studies focused on their relation with evolution and adaptation mechanisms are scarce. Indeed, diapausing eggs are often credited to be produced by females in unfavorable conditions. However, close observations have revealed that under regular conditions, the production of resting eggs is still present (personal observations, Gilbert & Schröder, 2004; Radzikowski, 2013; García-Roger et al., 2019). It is still unclear if, over time, the production of resting eggs has become a “default” action for rotifers and cladocerans, a doubt that can only be answered by performing more focused studies on this stage.

Another important topic in evolution is related to hatching patterns. Similar to morphology, hatching signals can be highly species-specific, as was observed in studies on egg banks in tropical aquatic systems by Araujo et al. (2013). This extensively studied phenomenon highlights the importance of understanding not only the function of the egg bank as a survival mechanism, but also the complexity of species-specific signals and responses to adverse conditions of hatching patterns. Moreover, a complete analysis of morphology-functionality will provide evidence to solve some species complex groups, as nowadays, cryptic species hypothesis in several taxa of rotifers and cladocerans is strongly accepted (Fontaneto et al., 2009; Garcia-Morales & Elias-Gutiérrez, 2013).

Conclusions and Recommendations

Diapausing eggs comprise a key survival strategy for rotifers and cladocerans. The exploration of these dormant life stages, with their distinctive morphological features and remarkable resilience, opens avenues as we strive to comprehend the complexities and intricate dynamics of aquatic ecosystems.

So far, the significance of diapausing eggs has only been studied superficially. However, studies focused on these structures in taxonomy, ecology, and evolution, as well as other areas of biology, can provide a window into the past, allowing the reconstruction of historical environmental conditions and tracking changes in species composition over time.

This adaptive strategy for survival in adverse conditions also offers insights into the resilience of rotifers and cladocerans and their ability to withstand challenges caused by the impacts of environmental change. By delving into the intricate world of these resilient dormant stages, researchers can contribute not only to scientific knowledge, but also to the development of informed conservation and management strategies of aquatic environments.

Authors' Contributions

GJG conceptualization, writing, supervision, and project administration. ANE, writing, and editing. ACRN writing, drawing, creative design, and editing. ASFS, RRJC funding acquisition and collecting samples for image references. AOA, SBM Scanning Electron Microscopic images.

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Zooplankton Community and Trophic State in Lake Chapala

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Abstract

Lake Chapala is the largest lake in Mexico, it supplies water for the city of Guadalajara and suffers a serious eutrophication problem. In the last 40 years, many indices related to trophic state, based on zooplankton abundance, have been developed for monitoring programs. In this study, we compared different trophic state indices (TSI) based on rotifers, cladocerans, and copepods at the end of the cold season during March 2023 at Lake Chapala, Mexico. We selected four sampling sites where limnological variables such as temperature, dissolved oxygen, pH, conductivity, depth, Secchi transparency, and zooplankton samples were obtained. The temperature was 25.6±1.6°C, dissolved oxygen 7.3±0.4 mg/l, oxygen saturation around 90 %, pH 9.1±0.06, conductivity 1012±5.3 µS/cm with a depth of 4.23±0.13 m and Secchi transparency of 0.46 m. The zooplankton community was composed of 19 species; 10 rotifers, 7 cladocerans, and 2 copepods. The dominant species were both copepods as well as *Ceriodaphnia* spp., *Diaphanosoma* cf. *birgei*, *Chydorus brevilabris*, *Filinia opoliensis*, *F. longiseta*, and *Horaella thomassoni*. Around 75 % of the total zooplankton abundance was represented by copepods, 13 % by rotifers, and 12 % by cladocerans. Carlson TSI based on Secchi transparency and TSI_{ROT} (BAC) indicate hypertrophic conditions, while TSI_{ROT} based on rotifer abundance results in mesotrophic conditions; for most TSI based on crustacean density, the eutrophic state was determined. The implications of calculations of TSI for zooplankton developed in temperate conditions may not completely match with observed conditions for Lake Chapala where heterotrophic bacteria and cyanobacteria dominance play a key factor in the zooplankton community structuration. Formulation of indices in tropical conditions is important for monitoring water assessment.

Keywords

Bioindicators, Cladocera, Copepoda, Rotifera, TSI_{CR}, $TSI_{ROT.}$

Introduction

Eutrophication is one of the main environmental challenges to solve in order to maintain water supply for human activities (Downing, 2014). The eutrophication process generates an increase in phytoplankton biomass with toxic potential and oxygen diurnal fluctuations, causing water quality and diversity reduction and the loss of ecosystem services (Janssen et al., 2020); moreover, climate change and cultural eutrophication enhance this problem (Moss et al., 2011). Hence, trophic state monitoring is critical to the adequate management and conservation of aquatic ecosystems (Dodds & Whiles, 2010).

For surveilling trophic levels on lakes, several trophic state indices have been developed. The Carlson trophic state index (TSI) based on total phosphorus, chlorophyll *a,* and Secchi transparency stands out as one of the earliest and most extensively employed classification schemes devised for assessing lake trophic conditions (Carlson, 1977). Additionally, the biological composition of a given lake is strongly influenced by its trophic state; for instance, a decrease in the average body size of zooplankton is correlated with an increase in trophic level; moreover, an increase in the overall abundance of rotifers and crustaceans exhibits a strong and positive correlation with the trophic state of lakes and some species have particular preferences for determined trophic state and water conditions (Ejsmont-Karabin, 2012; Ejsmont-Karabin & Karabin, 2013). Consequently, trophic state indices based on zooplankton have been proposed to estimate and classify trophic state conditions in freshwater ecosystems (*i.e.,* Slácedêcek, 1983; Ejsmont-Karabin, 2012; Ejsmont-Karabin & Karabin, 2013; Ochocka, 2021).

Freshwater zooplankton is a key component in the food webs of lentic ecosystems because it consumes phytoplankton, protozoans, and bacteria, and determines the abundance of secondary consumers such as macroinvertebrates and fish (Dodds & Whiles, 2010). Many species of zooplankton are abundant, some with wide geographical distribution, high reproductive rate, short generation time, and high sensitivity to environmental changes; therefore, they easily respond to environmental conditions (Beisner & Thackeray, 2023). Thus, these attributes make zooplankton an excellent tool for trophic state monitoring (Ejsmont-Karabin, 2012). Moreover, zooplankton is essential in enabling the provision of ecosystem services, including supporting fisheries, controlling phytoplankton growth, and regulating carbon levels all of which enhance the quality of drinking water and irrigation. Additionally, they contribute to scientific advancements by providing model systems and ecological bioindicators (Declerck & de Senerpont Domis, 2023).

Slácedêcek (1983) proposed the *Brachionus*/*Trichocerca* quotient (B/T_Q) and the saprobic index (SI) for rotifers to determine trophic conditions; nevertheless, genera *Brachionus* and *Trichocerca* are not always present and indicative weight of the species and individual saprobic index are not available for all rotifers. Additionally, indices for rotifers (Ejsmont-Karabin, 2012) and crustaceans (Ejsmont-Karabin & Karabin, 2013) were proposed in temperate lakes. Stamou et al. (2019) evaluated these indices in zooplankton communities of 16 lakes in Greece compared with the trophic state index based on Secchi transparency proposed by Carlson (TSI_{SD}) (Carlson, 1977); they found that these indices exhibited a rise along the eutrophication gradient, but they inaccurately assess the trophic state. Ochocka (2021) developed a multimetric index ($ZIPLA_S$) for Polish lakes considering the taxonomic composition and abundance, diversity, and stressor-sensitive species with the highest correlation with Secchi disk transparency.

In Mexico, there have been some attempts to calculate trophic state using zooplankton indicators in reservoirs and lakes (Muñoz-Colmenares et al., 2017; González-Gutiérrez et al., 2017, 2023; Moreno-Gutiérrez et al., 2018; Torres-Sánchez, 2020); nonetheless, all these studies only use rotifers whereas crustaceans have not been considered. Therefore, comparing these indices in a polymictic lake located at lower latitudes will provide us with information about how these indices respond in tropical conditions. Lake Chapala exhibits significant water quality decline related to an increase of nutrients (mainly nitrogen and phosphorus compounds) from domestic, livestock, industrial, and agriculture wastewater that enhanced primary production (Membrillo-Abad et al., 2016) with elevated presence of potentially toxic cyanobacteria (De Anda & Shear, 2001). Also, high concentrations of heavy metals such as cadmium, chromium, lead, mercury, copper, zinc, and, nickel have been recorded (Hansen et al., 1995). Earlier reports, discarded eutrophication as the main concern because light limitation, due to high inorganic clay turbidity, regulates phytoplankton productivity with a low annual average of 5.4 mg/m^3 and lack of filamentous cyanobacteria without algal blooms (Limón & Lind, 1990).

Recently, degradation of water hyacinth (*Eichhornia crassipes*), inputs from the Lerma River, and excessive use of fertilizers in the agriculture catchment area were related to eutrophic conditions with cyanobacteria blooms of *Anabaena flos-aquae* (De Anda & Shear, 2001). Membrillo-Abad et al. (2016) summarized that Lake Chapala has been in eutrophic condition at least in the last 25 years with mean chlorophyll *a* concentration of 11.7 mg/m^3 and mean Secchi transparency of 0.38 m. Therefore, monitoring and maintaining of water quality in Lake Chapala is a determinant task due to the increasing water demand, because this lake supplies over 60 % of the freshwater requirements of the city of Guadalajara (Membrillo-Abad et al., 2016). Despite the physical and chemical characteristics of this lake being well known, biological data is not complete (Lind & Dávalos-Lind, 2001).

In Chapala 57 species of rotifers (mostly limnetic) were registered by Rico-Martínez et al. (2003); however, there is no data about abundance. For cladocerans and copepods, what we have in Lake Chapala is not clear with no records from recent zooplankton reviews in Mexico (Alcocer et al., 2023; Cervantes-Martínez et al., 2023). In the case of copepods, recent studies (Velázquez-Ornelas et al., 2021) have allowed us to know the diversity of species in the area. Some studies come from gut fish content analysis or gray literature, where taxonomical determination may not be accurate; in these studies, 14 cladocerans and 5 copepods have been registered (Rodríguez-Ruíz & Granado-Lorencio, 1988; Trotter, 1988). Thus, the objective of this study was to compare different trophic state indices (TSI) based on rotifers, cladocerans, and copepods at the end of the cold season during March 2023 at Lake Chapala, Mexico.

Materials and Methods

Study Area

Lake Chapala (Fig. 1) is a RAMSAR site located at the western edge of the Trans-Mexican Volcanic Belt in the eastern part of the state of Jalisco. It is a tectonic warm polymictic lake (20º06’08” - 20º18’08”N, and 102º42’00” - 103º25’20”W) with a maximum depth (Z_{MAX}) of 10.5 m, and a mean depth (Z_{MEAN}) of 7.2 m. Its maximum length (L_{MAX}) is 77 km, and its maximum width (W_{MAX}) 22.5 km, with a volume (V) of 7.9 Km^3. It is located at 1524 m a. s. l. in the Lerma-Santiago basin and has a catchment area of approximately 1,000 km^2. By area and water volume, Chapala is the largest lake in Mexico, turbidic, with highly suspended clay and nutrient content (SRP=0.4-0.5 mg/l, TN=0.5-0.8 mg/l) where the dominance of the cyanobacteria *Microcystis aeruginosa*, *Aphanizomenon flos-aquae,* and *Anabaena* have been recorded (Dávalos-Lind & Lind, 2001; Alcocer & Bernal-Brooks, 2010).

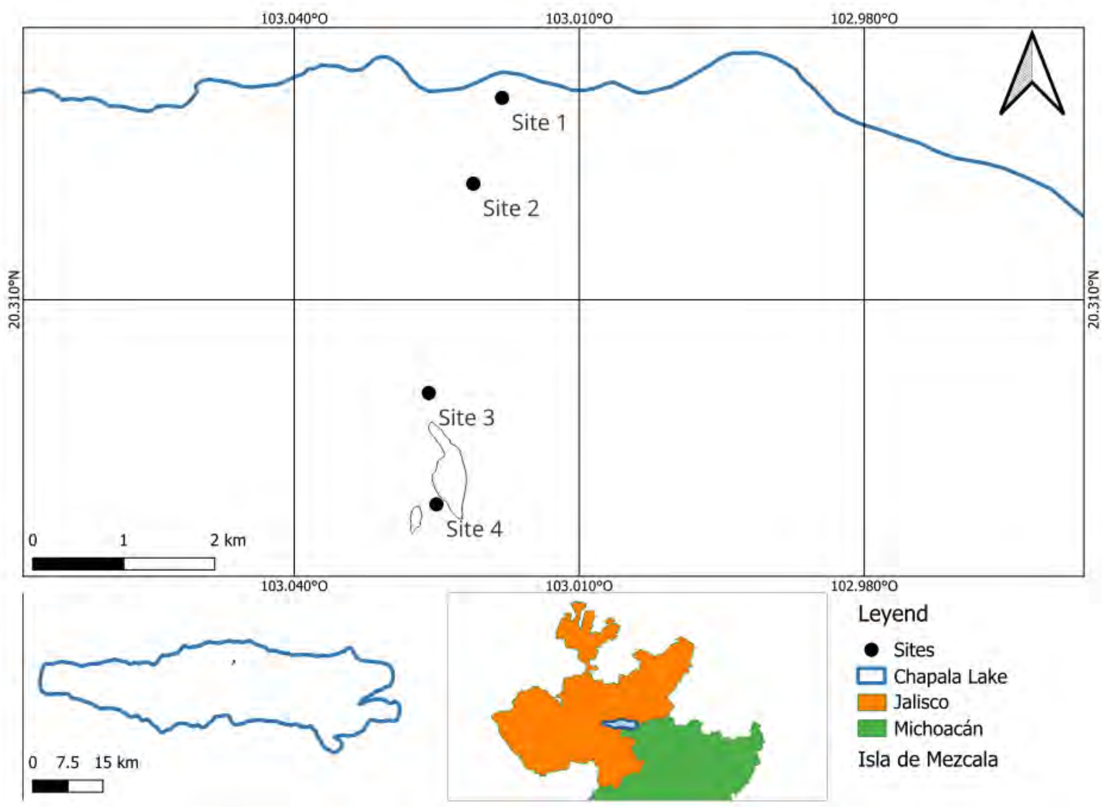

Figure 1. Lake Chapala Showing Sampling Sites.

Sampling

We sampled four sites during March 2023 in a transect from the shore of the town of Mezcala to the island: site 1 inshore in the town of Mezcala (20º19’52.6”N, 103º01’05.3”W); site 2 between site 1 and the island of Mezcala (20º19’20.1”N, 103º01’16.2”W); site 3 close to the island of Mezcala (20º18’0.79”N, 103º01’33.1”W) and site 4 in vegetated area with *Schoenoplectus* sp. (20º17’18.6”N, 103º01’30.2”W). In each sampling point, temperature, dissolved oxygen, and conductivity were measured with a YSI85 probe, pH was registered with a potentiometer conductronic PC-20, depth with an ecosound Hondex digital, and transparency with Secchi disk. Zooplankton was sampled with vertical hauls from 1.5 m in the littoral zone up to 3 m depth in the pelagic zone using a Wisconsin planktonic net of 64 µm mesh size. Later, samples were labeled with sampling data and fixed to a final formaldehyde concentration of 4 %.

Samples Analysis

Each sample was analyzed under a Zeiss Axiostar plus microscope using a Sedgwick-Rafter counting chamber considering a minimum of five subsamples or 400 individuals of the most abundant species (Wetzel & Likens, 2001). Taxonomical determination was done with the taxonomical keys of Koste (1978), Elías-Gutiérrez et al. (2008a), Sarma and Nandini (2017), and Sousa and Elmoor-Loureiro (2021). Zooplankton species photos were taken with an AxioScope A1 with camera Axiocam ICc 5. Names and status of the rotifers were verified in the Rotifer World Catalog database (http://rotifera.hausdernatur.at/); for cladocerans, we used Kotov et al. (2013) and for copepods Elías-Gutiérrez et al. (2008a).

Data Analysis

Trophic State Indices

We calculate the TSI_{SD} of three of four sampling sites according to the following formula (Carlson, 1977):

$$\underline{TSI_{SD}=60-14.41\ \ln(SD)}$$

TSI allows to determine trophic state based on a scale from 0 to 100, and the scale values correspond to different trophic conditions: $0<TSI\leq40$ oligotrophic, $40<TSI\leq50$ mesotrophic, $50<TSI\leq70$ eutrophic, and $70<TSI\leq100$ hypereutrophic.

We also consider trophic state indices based on rotifers (Ejsmont-Karabin, 2012) and crustaceans (Ejsmont-Karabin & Karabin, 2013) for polymictic lakes (POL) and indistinct mixis patterns according to the following formulas:

TSI_{ROT} POL (rotifer numbers)$=4.64\ \ln(N)+25.36$

TSI_{ROT} (rotifer numbers)$=5.38\ \ln(N)+19.28$

TSI_{ROT} POL (BAC, %)$=8.20\ \ln(BAC)+28.63$

TSI_{CR1} POL (crustaceans numbers)$=6.89\ \ln(N)+20.7$

TSI_{CR1} (crustaceans numbers)$=25.5\ N^{0.142}$

TSI_{CR6} POL (ratio Cladocera/Calanoida)$=0.41\ \ln(CL/CA)+59.2$

TSI_{CR7} POL (ratio Cyclopoida/Calanoida)$=1.18\ \ln(CY/CA)+56.6$

These indices calculate trophic state from abundance, bacterivorous percentage (BAC, %), and the ratio between crustacean groups and assumed that those lakes with a TSI_{ROT} and TSI_{CR} lower than 45 are mesotrophic, from 45 to 55 are meso-eutrophic, 55 to 65 eutrophic, and those over 65 are hypertrophic.

Results

The mean values ± standard deviation from the four sampling stations for temperature was 25.6±1.6°C, dissolved oxygen 7.3±0.4 mg/l, oxygen saturation around 90 %, pH 9.1±0.06, conductivity 1012±5.3 µS/cm with a depth of 4.23±0.13 m and Secchi transparency of 0.46±0.005 m (Table 1).

Table 1. Physical and Chemical Variables in Four Sampling Sites of Lake Chapala at the End of the Cold Season in 2023.

Variables	S1	S2	S3	S4
Temperature (°C)	27	24.3	24.1	27
Dissolved Oxygen (mg/l)	7.98	7.27	7.34	6.9
Oxygen Saturation (%)	100.7	88.4	87.6	86.6
pH	9.06	9.19	9.21	9.14
Conductivity (µS/cm)	1016	1009	1006	1017
Depth (m)	3.76	5.1	5.23	2.86
Secchi Depth (m)	0.46	0.47	0.47	-

Table 2 presents 19 zooplankton species found in Lake Chapala; 10 rotifers, 7 cladocerans, and 2 copepods. We found 7 families of rotifers, the majority of species belonging to Trochosphaeridae and Brachionidae where *Filinia longiseta*, *F. opoliensis*, *Horaella thomassoni,* and *Keratella tropica* were the most abundant (Fig. 2A-F). We found five families of cladocerans where *Ceriodaphnia* spp., *Diaphanosoma* cf. *birgei,* and *Chydorus brevilabris* were more abundant (Fig. 3A-H). For copepods, we registered one calanoid and one cyclopoid (*Acanthocyclops* sp.) with a dominance of *Mastigodiaptomus* cf. *albuquerquensis* (Fig. 4A and 4F). We also found abundant *Trichodina* sp. (Fig. 2G) and a microturbellarian (Fig. 2H).

Table 2. Species Richness and Frequency of Metazoa Zooplankton Species Found in Four Sites of Lake Chapala at the End of the Cold Season of 2023.

Species	S1	S2	S3	S4
Crustacea				
Branchiopoda				
Anomopoda				
Bosminidae				
Bosmina cf. *longirostris* (O. F. Müller, 1785)	-	X	-	X
Chydoridae				
Chydorus brevilabris Frey, 1980	X	X	X	-
Ovalona setulosa (Megard, 1967)	X	X	X	X
Daphniidae				
Ceriodaphnia cornuta Sars, 1885	X	X	X	X
Ceriodaphnia cf. *dubia* Richard, 1894	X	X	X	X
Moinidae				
Moina cf. *micrura* Kurz, 1875	X	X	-	-
Ctenopoda				
Sididae				
Diaphanosoma cf. *birgei* Kořínek, 1981	X	X	X	X
Maxillopoda				
Copepoda				
Calanoida				
Diaptomidae				
Mastigodiaptomus cf. *albuquerquensis* (Herrick, 1895)	X	X	X	X
Cyclopoida				
Cyclopidae				
Acanthocyclops sp.	X	X	X	X
Rotifera				
Eurotatoria				
Monogononta				
Flosculariaceae				
Hexarthridae				
Hexarthra mira (Hudson, 1871)	-	X	X	X
Trochosphaeridae				
Filinia longiseta (Ehrenberg, 1834)	X	X	X	X
Filinia opoliensis (Zacharias, 1898)	X	X	X	X
Filinia pejleri Hutchinson, 1964	X	X	-	-
Horaella thomassoni Koste, 1973	X	X	X	X
Ploima				
Brachionidae				
Keratella americana Carlin, 1943	-	-	X	-
Keratella tropica (Apstein, 1907)	X	X	X	X
Euchlanidae				
Euchlanis dilatata Ehrenberg, 1832	-	-	-	X
Lecanidae				
Lecane luna (Müller, 1776)	-	-	-	X
Notommatidae				
Cephalodella sp.	-	X	-	-

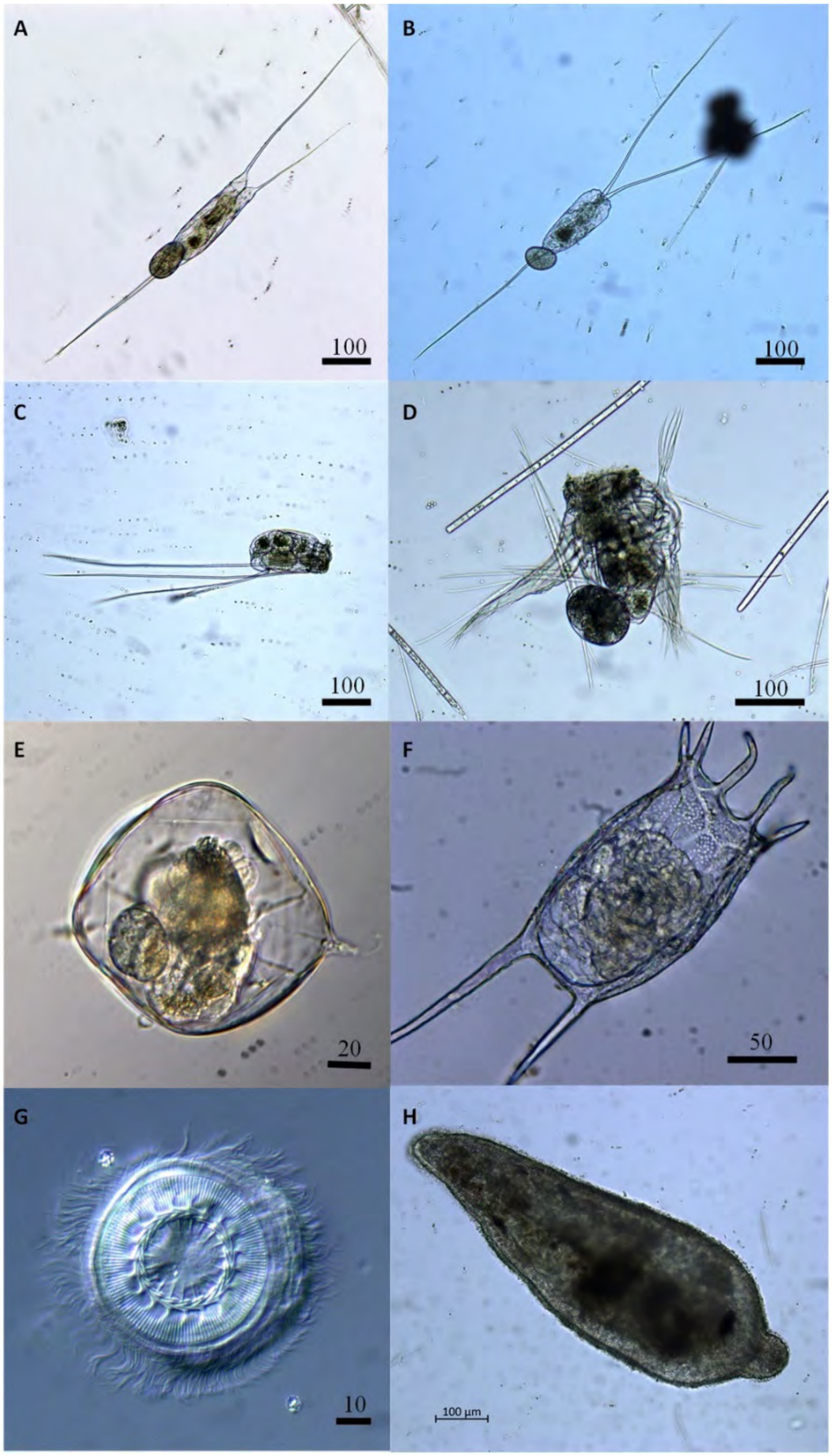

Figure 2. Rotifers, a Protist and Platyhelminth Found in Lake Chapala during the End of the Cold Season of 2023. A) *Filinia opoliensis*, B) *Filinia pejleri*, C) *Filinia longiseta*, D) *Hexarthra mira*, E) *Horaella thomassoni*, F) *Keratella tropica,* G) Protist *Trichodina* sp. and H) Platyhelminth microturbellarian. Scale Measurements are in Micrometers.

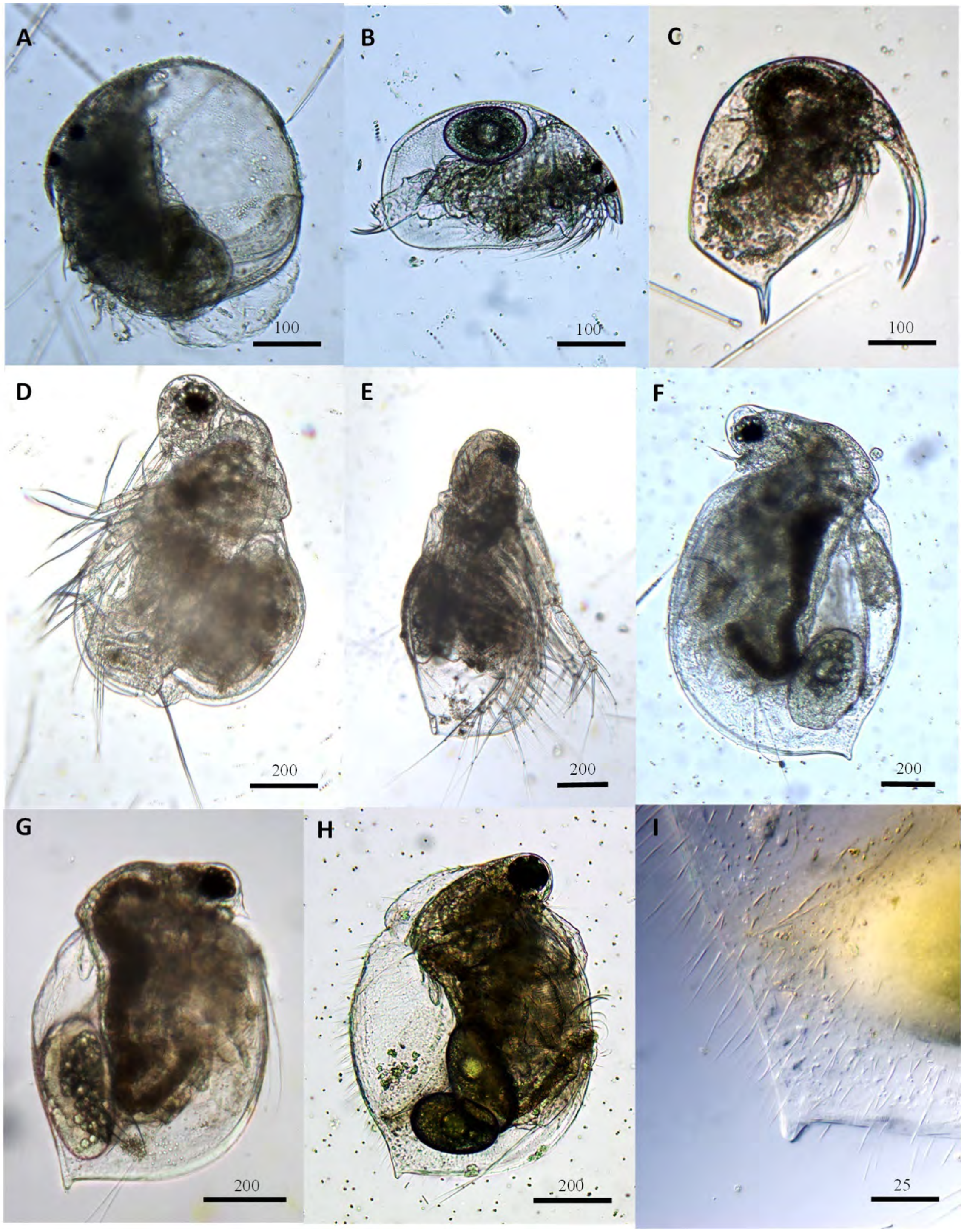

Figure 3. Cladocerans Found in Lake Chapala during the End of the Cold Season of 2023. A) *Chydorus brevilabris*, B) *Ovalona setulosa*, C) *Bosmina* sp., D) *Moina* cf. *micrura*, E) *Diaphanosoma* cf. *birgei*, F) *Ceriodaphnia* cf. *dubia*, G) *Ceriodaphnia cornuta*, H) *Ceriodaphnia* cf. *cornuta* and I) Postero-dorsal Margin of *Ceriodaphnia* cf. *cornuta*. Scale Measurements are in Micrometers.

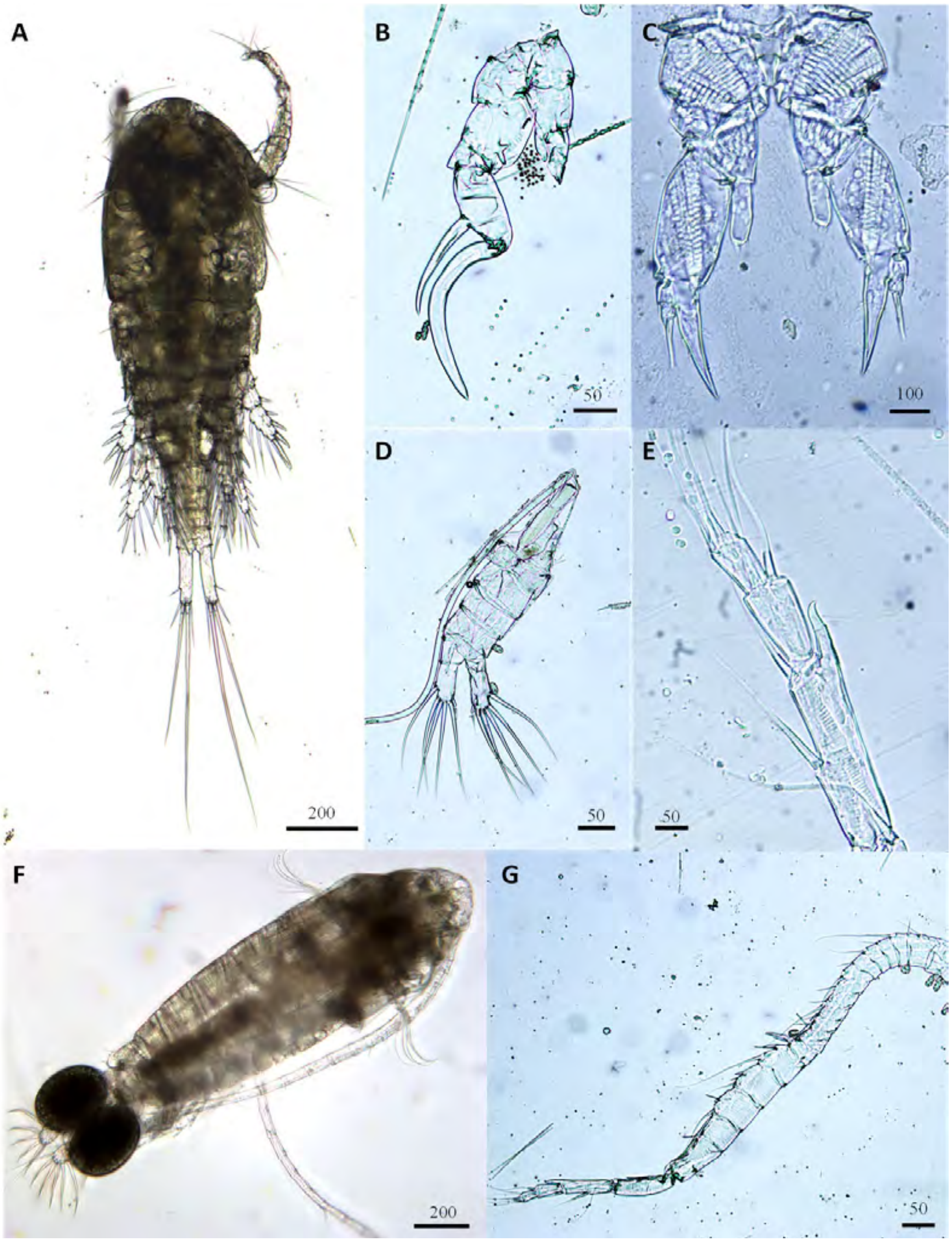

Figure 4. Copepods Found in Lake Chapala during the End of the Cold Season of 2023. A) Male of *Acanthocyclops* sp., B-G) *Mastigodiaptomus* cf. *albuquerquensis* B) Fifth Leg of Male and C) Female D) Urosomite of Male, E) Right Antennule, Segments 20, 21 of Male F) Female Dorsal View, and G) Right Antennule of Male. Scale Measurements are in Micrometers.

Zooplankton density was higher in site 4 with 330 ind/l, while site 1 had lower abundance with 194 ind/l. Abundance was mostly represented by copepods with close to 75 % (200±52 ind/l), while rotifers and cladoceran had similar values with 13% (35±17 ind/l) and 12 % (32±12 ind/l), respectively (Fig. 5).

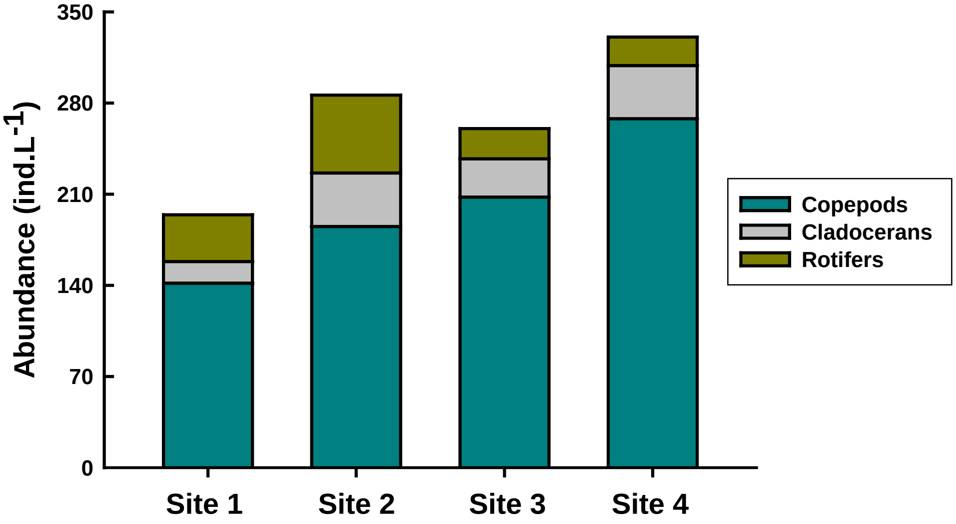

Figure 5. Abundance (ind/l) of Copepods, Cladocerans, and Rotifers in Four Sites of lake Chapala during the Cold Season in 2023.

Carlson TSI based on Secchi transparency determined hypertrophic conditions with values between 70.87 and 71.18. For TSI_{ROT} based on abundances for indistinct mixis pattern and for polymictic lakes, values ranged from 35.89 to 44.33, specifying a mesotrophic state; nevertheless, TSI_{ROT} for bacterivorous species was 66.39 for all sampling sites. TSI_{CR1} based on abundances for indistinct mixis pattern and polymictic lakes, determined in one sampling site meso-eutrophic conditions with a value of 52.33; however, for all the other sites, values ranging from 55.06 to 60.19 indicating the eutrophic state. For $TSI_{CR6,}$ eutrophic conditions were calculated and for $TSI_{CR7,}$ values were close to the eutrophic state (from 53.35 to 54.92) in three sites, while one site was calculated as eutrophic with 55.54 (Table 3).

Table 3. Trophic State Index Based on Rotifers (TSI_{ROT}) and Crustacean (TSI_{CR}) Densities in Four Sites of Lake Chapala during the Cold Season in 2023. H=Hypertrophic, E=Eutrophic, M=Mesotrophic.

Trophic State Index	S1	S2	S3	S4
TSIZSD	71.18 (H)	71.18 (H)	70.87 (H)	-
TSIROT Pol	41.97 (M)	44.33 (M)	39.94 (M)	39.68 (M)
TSIROT	38.54 (M)	41.28 (M)	36.18 (M)	35.89 (M)
TSIROT Pol BAC, %	66.39 (H)	66.39 (H)	66.39 (H)	66.39 (H)
TSICR1 Pol	55.59 (E)	58.05 (E)	58.38 (E)	60.19 (E)
TSI CR1	52.33 (M-E)	55.06 (E)	55.43 (E)	57.55 (E)
TSICR6 Pol (CL/CA)	58.34 (E)	58.72 (E)	58.48 (E)	58.49 (E)
TSICR7 Pol (CY/CA)	53.35 (M-E)	55.54 (E)	54.92 (M-E)	54.58 (M-E)

Discussion

Our results from environmental variables coincide with previous reports by Lind and Dávalos-Lind (2001), who mentioned that the annual Secchi depth is 0.5 m, with a mean annual temperature of 22°C. Reported pH values ranging from 8.54 to 8.9 and oxygen concentrations from 6.84 to 7.13 mg/l with oxygen saturation over 90 % due to wind mixing (Limón & Lind, 1990; de Anda & Shear, 2001).

From the 10 rotifers found, *Hexarthra mira*, *Filinia longiseta*, *F. opoliensis*, *Horaella thomassoni*, *Keratella americana*, *K. tropica*, *Euchlanis dilatata,* and *Lecane luna* were previously reported for Lake Chapala by Rico-Martínez and Silva-Briano (1993) and Rico-Martínez et al. (2003). *Euchlanis dilatata*, *Lecane luna,* and *Cephalodella* sp. were only found once in one sample; therefore, TSI_{ROT} was mainly calculated based on the other 7 species. According to Gilbert (2022), these 7 species are microphagous feeding on small particles where bacteria is an important component in their diet. Some studies have found that the trophic relations in Lake Chapala are not completely sustained by phytoplankton productivity, where bacteria play an important role with an annual production that represents 42 % of total edible small particles for zooplankton (Lind & Davalos-Lind, 2001), which explains the dominance of bacterivorous rotifers.

Zooplankton community structure is strongly shaped by the interaction of different factors, such as vagility, physico-chemical variables, and biological attributes of the habitat, where selective predation is the main driving force (Beisner & Thackeray, 2023). In addition, cyanobacterial blooms also differentially affect zooplankton species and it is well known that the proportion of large-bodied cladocerans significantly decline into small-bodied species when microcystin concentration increased in lake sediments (Moss et al., 2011; Kâ et al., 2012; Pérez-Morales et al., 2015; Jiang et al., 2017).

Although there is currently no data on cyanotoxins in Lake Chapala, the samples revealed a high density of potentially toxic cyanobacteria, including *Aphanizomenon* sp., *Microcystis aeruginosa*, *M. wesenbergii*, and *Dolichospermum* sp. Moreover, large filamentous cyanobacteria such as those found in Lake Chapala mechanically interfere with the feeding process of large-bodied cladocerans (Gliwicz, 2003), while small cladocerans, rotifers, and copepods are more selective than large cladocerans (Thackeray & Beisner, 2023). Hence, selective predation and the dominance of cyanobacteria may shape the zooplankton community in Lake Chapala.

Despite food availability for rotifers not being limited in Lake Chapala, their abundances were low (35±17 ind/L) in comparison with microcrustaceans (232±61 ind/l), where cladocerans had similar abundances to rotifers (32±11.6 ind/l), while copepods reached the highest abundances (200±53 ind/l). Rotifer abundances are mainly affected by exploitative competition when food resources are scarce, interference competition with large-size cladocerans, and selective predation (Thackeray & Beisner, 2023). MacIsaac and Gilbert (1989) demonstrated in laboratory experiments that cladocerans smaller than 1.2 mm can easily coexist with rotifers such as we observed for Lake Chapala. Therefore, selective predation may explain low rotifer abundance; Nandini et al. (2011) showed how turbellarians reduce rotifer abundance through the production of toxins and direct predation and despite not registering turbellarian abundance, we observed many specimens in each counting. On the other hand, cyclopoid copepods also exert high predation pressure on rotifers, Sarma et al. (2019) found in field samples that *Acanthocyclops americanus* consume different rotifer species. Under laboratory conditions, it was observed that female *Acanthocyclops* consumed nearly twice as much as males, depending on food availability, ingesting between 40 to 400 rotifers per hour. Hence, the presence of *Acanthocyclops* in our samples may also lead to a decrease in rotifer abundance.

For cladocerans, *Diaphanosoma* cf. *birgei* is the ctenopod with more records in Mexico. Recently, Velázquez-Ornelas et al. (2021) registered this species for Laguna de Cajititlán and there is evidence of this species in the report of the international training course: “zooplankton a tool in lake management” (Rico-Martínez, 1992). Former studies (Rodríguez-Ruíz and Granado-Lorencio, 1988; Trotter, 1988) identified Chapala *Diaphanosoma brachyurum* (originally described for Europe); nevertheless, this species is not confirmed for México (Elías-Gutiérrez et al., 2008a); Dumont et al. (2021) mentioned that *D. brachyurum* is the ctenopod with many citations without figures or morphological evidence, while Alexiou et al. (2021) observed that insufficient knowledge of *Diaphanosoma* morphology resulted in *D. brachyurum* being the most commonly documented species globally. The specimens we found have the posteroventral margin with group denticles increasing in size and one setule between each group. Moreover, Elías-Gutiérrez et al. (2008b) mentioned that this is a complex species with at least 4 species in Mexico with divergence up to 14.5 % from its type locality.

Ceriodaphnia is a very confusing genera, records from Lake Chapala listed *Ceriodaphnia lacustris*, *C. pulchella* (Trotter, 1988), and *Ceriodaphnia* cf. *reticulata* (Rodríguez-Ruíz & Granado-Lorencio, 1988) and we also found three morphospecies but it does not coincide with previous records (Trotter, 1988). One of the species we found was determined as *Ceriodaphnia* cf. *dubia* (Fig. 3G) which is highly variable and widely distributed in Mexico. We also found two morphotypes of *C. cornuta* species complex (Fig. 3G and 3H), one of them is referred by Elías-Gutiérrez et al. (2008b) such as *Ceriodaphnia cornuta-rigaudi*; nevertheless, *C. rigaudi* is *species inquirenda* according to the Cladocera checklist (Kotov et al., 2013). Elías-Gutiérrez et al. (2008b) discussed that *Ceriodaphnia cornuta* belongs to the species complex *C. cornuta-rigaudi* with high morphological diversity, broad distribution, and three lineages in Mexico. In addition, Berner (1985) worked with three typical forms of this species complex and mentioned that *C. rigaudi* is synonymous with *C. cornuta*. She also reported a *C. cornuta* form that lacks the rostral projection and it has a hairy surface carapace similar to the population found in this study, which was identified as *C*. cf. *cornuta*. *Moina micrura* s str. is a Palaearctic species but is considered a complex where at least three species are registered for Mexico. However, formal descriptions of these species have not been made (Elías-Gutiérrez et al., 2019). Chydorids also represent new records for Lake Chapala (*i.e., Chydorus brevilabris* and *Ovalona setulosa*).

On the other hand, *Acanthocyclops vernalis* and *Mastigodiaptomus albuquerquensis* were previously registered by Rodríguez-Ruíz and Granado-Lorencio (1988) and Trotter (1988), respectively. In addition, Velázquez-Ornelas et al. (2021) indicate the presence of *M. montezumae* in another lake close to Lake Chapala, but it was not recorded in our samples. However, due to the recent description of complexes of cryptic species in both genera, it is necessary to carry out genetic and detailed morphological studies to corroborate the identity of the collected specimens.

The trophic state condition of Lake Chapa is eutrophic. Lind and Dávalos-Lind (2001) mentioned that regarding nutrients, Lake Chapala indicates the eutrophic-hypertrophic condition. According to remote sensing analysis, Membrillo-Abad et al. (2016) showed that Mezcala is an area with high chlorophyll *a* concentration (up to 65 mg/m^3) with low transparency and Carlson TSI from 40 and 70 cm in the inshore of the town of Mezcala. Cyanobacteria abundance is high with dominance of filamentous and colonial species such as *Anabaena limnetica* (Lind & Dávalos-Lind, 2001), *Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *M. flos-aquae* (Mora-Navarro et al., 2004). Despite the trophic state being clear, our idea was to compare some zooplankton trophic state indices to test how these come across Lake Chapala conditions.

Our data reveal mesotrophic conditions using rotifers abundances, hypertrophic state when calculations are based on the percentage of bacterivorous rotifers, and mostly eutrophic conditions using crustacean ratios and abundances. González-Gutiérrez et al. (2023) derived rotifers as indicators through the saprobic index, the *Brachionus*:*Trichocerca* quotient, and TSI_{ROT} in a high-altitude the El Llano Reservoir ,where they determined oligosaprobic, oligotrophic and meso-eutrophic conditions, respectively. Ejsmont-Karabin (2012) mentioned that discrepancies may be expected and the use of different methods and indices of different scales are not always in close agreement where TSI_{ROT} BAC % does not seem to be a strong predictor of trophic state for polymictic lakes. Even though generally rotifers seem to be better indicators of trophic state than microcrustaceans because of their susceptibility to the negative influence of algal blooms and toxic effects of cyanobacteria (Ejsmont-Karabin & Karabin, 2013), in Lake Chapala, microcrustaceans coincide with the eutrophic condition of Lake Chapala in a better way than rotifers.

It is also relevant to the role of copepods where calanoids were much more abundant (164±45 ind/l) than cyclopoids (36±19 ind/l). Ejsmont-Karabin and Karabin (2013) mentioned that usually, an increase in a lake trophy may cause an increase in the ratio Cladocera to Calanoida numbers and an increase in the ratio of Cyclopoida to Calanoida numbers; however, it does not occur in Lake Chapala during cold season. It is important to consider this study is based on a sampling taken during one moment; however, according to its water chemistry, Lake Chapala exhibits less than 20 % spatial and seasonal variation (Limón & Lind, 1990); hence, our observations may open a window to research on zooplankton dynamics and bioindicator in Lake Chapala.

Conclusion

In summary, we registered, for the first time, for Lake Chapala *Filinia pejleri*, *Diaphanosoma* cf. *birgei*, *Ceriodaphnia* cf. *dubia*, *C*. cf. *cornuta*, *Ovalona setulosa*, and *Chydorus brevilabris*, where the zooplankton community may be mainly shaped by selective predation and dominance of bacteria (heterotrophic and cyanobacteria). TSI based on rotifers was not precise about Lake Chapala conditions, instead, TSI based on crustaceans was useful to determine trophic state.

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Authors' Contributions

CAER: Conceptualization; sampling; identification of rotifers and cladocerans; photography; data analysis; original draft preparation; review, and editing manuscript. LCP: Description of the study area; photography; samples and data analysis; original draft preparation; review, and editing manuscript. OABM: Identification of copepods, writing, original draft preparation, review, and editing manuscript. All authors have read and agreed to the published version of the manuscript.

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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.

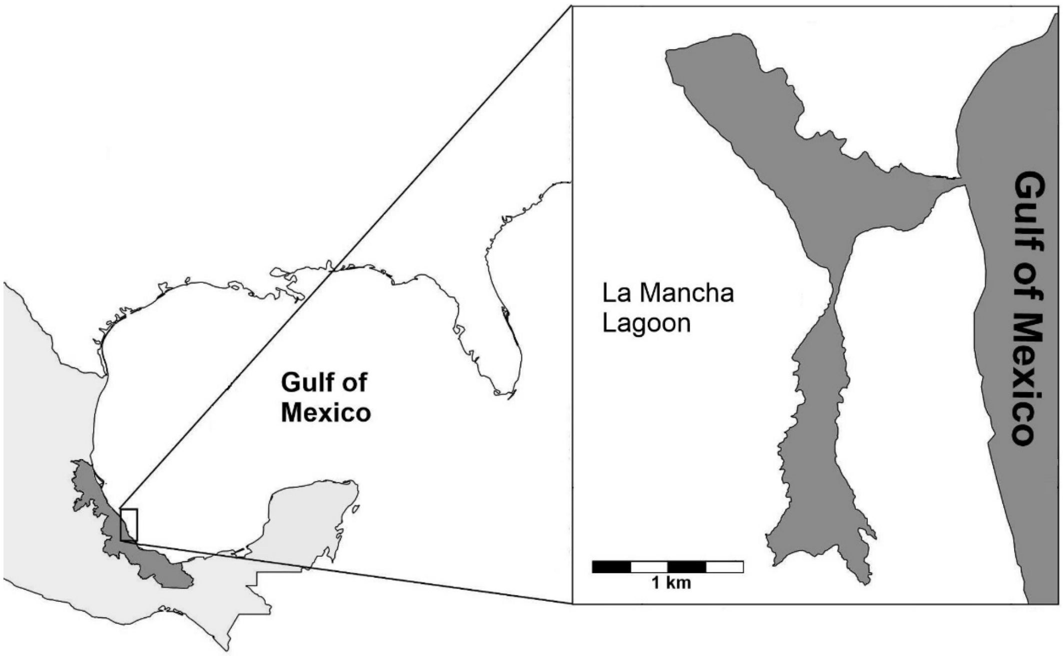


Figure 1. Geographical Location of the the La Mancha Lagoon.

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).

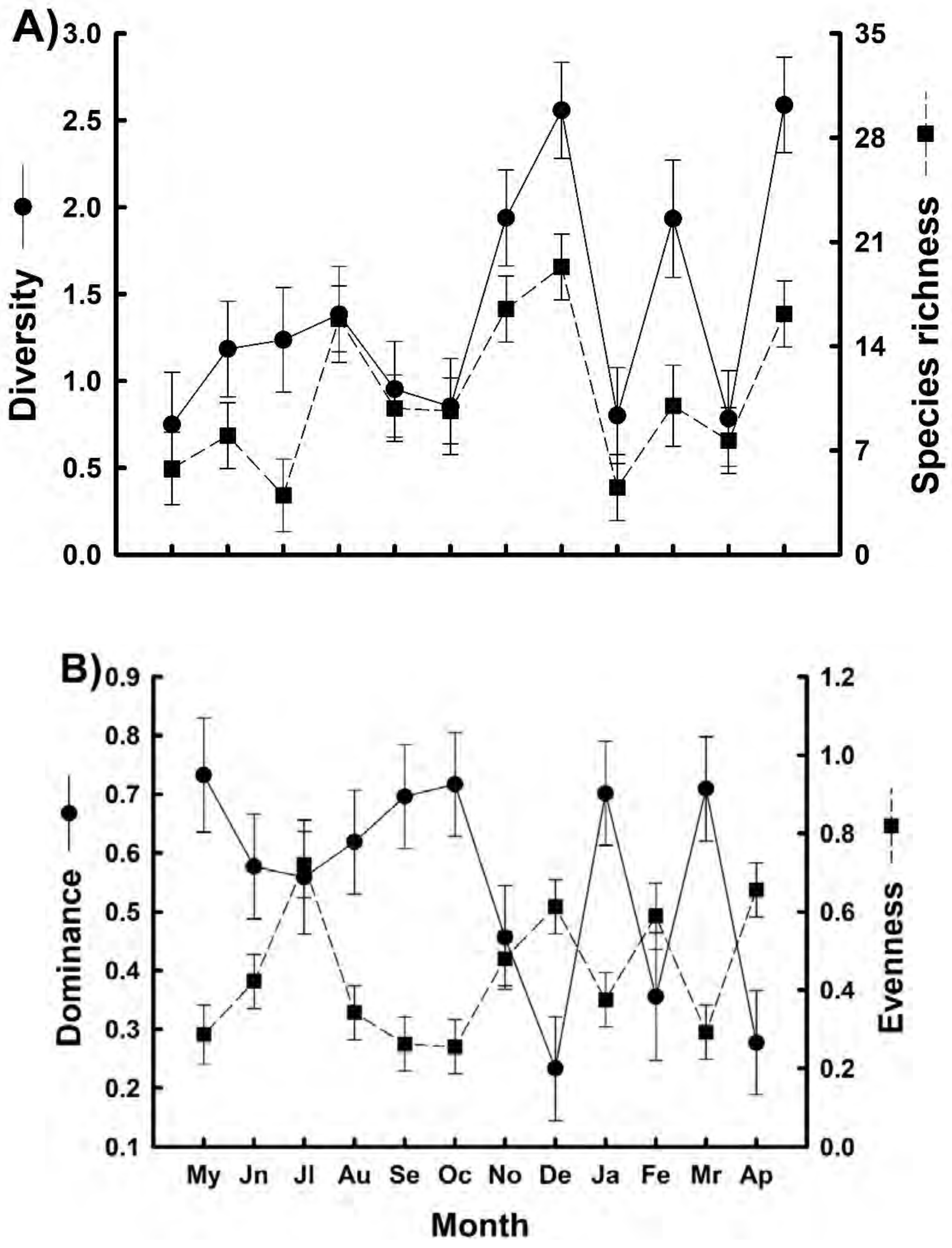


Figure 2. Monthly Variation of: A) Mean and Standard Error Values of diversity and species richness, and B) Mean and Standard Error Values of Dominance and Evenness (for each Monthly Value n=6).

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.

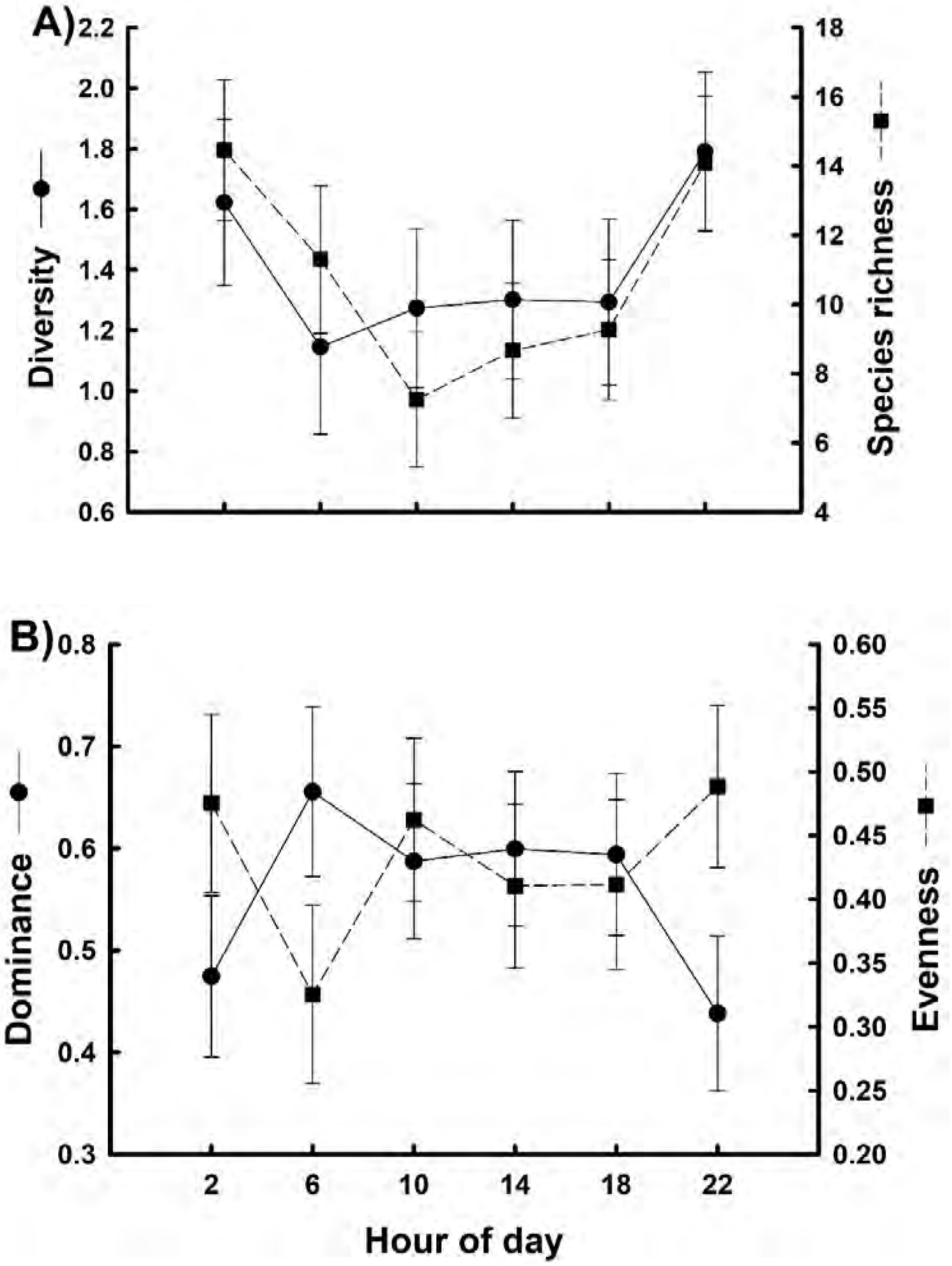


Figure 3. Mean and Standard Error Values by Hour: A) Diversity and Species Richness, and B) Dominance and Evenness (for each Hourly Value n=12).

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 (rs=0.575, P<0.0001), species richness (rs=0.491, P<0.0001), and evenness (rs=0.486, P=0.0001), and inversely with dominance (rs=-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.

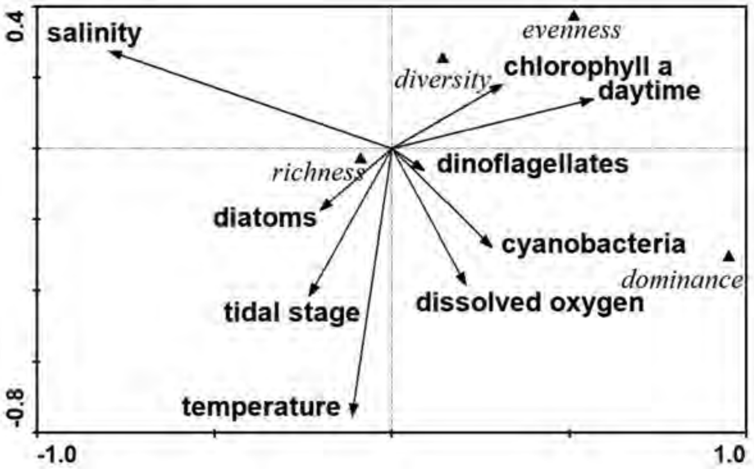
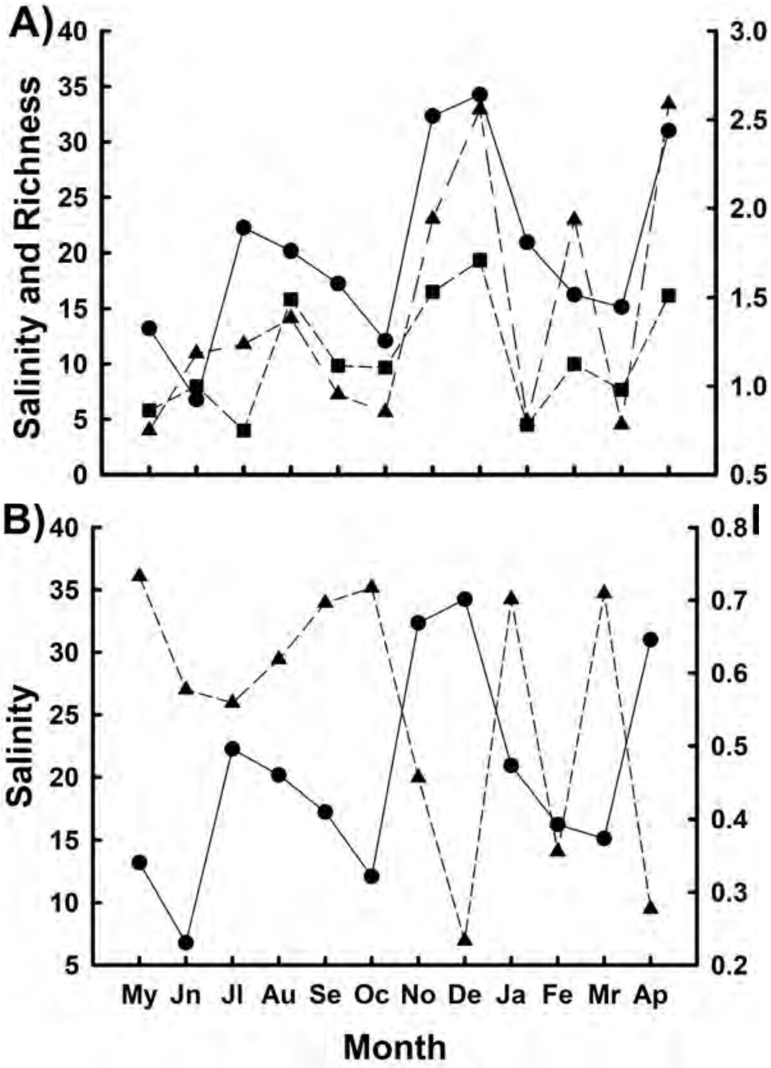


Figure 4. Bi-plot of Canonical Correspondence Analysis of the Overall Community Parameters and Environmental Variable Data Matrices. Data Points Represent Parameters (▲), and Arrows Represent the Direction and Relative Importance of Explanatory Variables.



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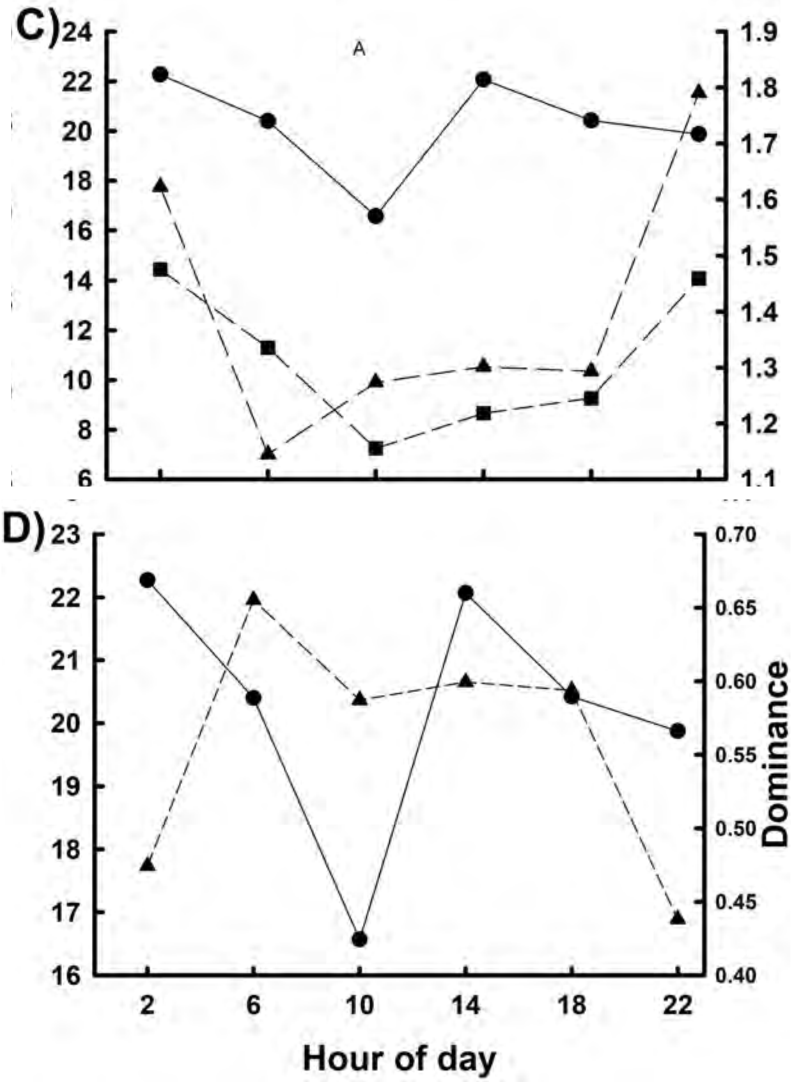

Figure 5. Monthly Mean Values of Salinity and Community Parameters: A) Direct Relationship between Salinity (●), Species Richness (■), and Diversity (▲), and B) Inverse Relationship between Salinity (●) and Dominance (▲) (for Mean Monthly Values n= 6). Mean Values by Hour of Salinity and Community Parameters: 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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Utilization of Zooplankton in Environmental Risk Assessment in Mexico

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Abstract

This brief review focuses on the use of zooplankton as a key indicator to evaluate environmental risk in the aquatic ecosystems of Mexico. It explores some ecotoxicological studies that assess the impacts of toxic agents on individual and population levels. The role of zooplankton in food webs, susceptibility to environmental changes, and significance as an indicator of both direct and indirect pollution effects are emphasized. The study underscores the crucial role of ecotoxicological tests in preventing environmental damage, guiding decision-making, and managing ecosystems. Special attention is given to the ecotoxicology of rotifers, cladocerans, and copepods, providing insights into cultivation protocols, their relevance in ecotoxicology, and key species used in Mexico. It further explores testing methodologies, advantages, and the range of pollutants assessed. The review also examines the geographical distribution of zooplankton research in Mexico, underlining the necessity to broaden investigations to diverse aquatic systems. Challenges, such as the importance of including native species in toxicity studies and the development of specific protocols for freshwater copepods, are addressed.

Keywords

Ecotoxicology, Acute toxicity, Chronic toxicity, Rotifers, Cladocerans, Copepods.

Introduction

Environmental Risk Assessment

The environmental risk assessment (ERA) is a method that assesses the probability of adverse ecological effects arising from the exposure of organisms and communities to one or more chemical compounds, either currently happening or likely to occur (Di Lorenzo et al., 2023). In Mexico, researchers have incorporated the use of aquatic invertebrates into ERA for several years. The selection of these organisms in these evaluations is based mainly on ecological relevance (validity), reliability (reproducibility), representative test species, and sensitivity, as noted by Breitholtz et al. (2006). ERA is carried out through ecotoxicological studies conducted in both laboratory and field settings. Ecotoxicology is comprised of three disciplines: ecology, toxicology, and chemistry and examines the effects of toxic compounds at different levels of biological organization, including individuals, population, and community levels (Pastorino et al., 2024). Measurable outcomes encompass physiological homeostasis, reproductive behavior, morphological alterations, and mortality (Zimmermann and Sures, 2023). This approach employs sensitive organisms as reliable indicators, connecting compound exposure to organism response. These data enable ecotoxicologists to identify concentrations indicating adverse conditions (OECD, 2011).

Ecotoxicological studies play a crucial role in both preventing environmental damage and understanding the chemical charactieristics of the environment. They are indispensable in decision-making processes related to resource protection and ecosystem management (Relyea & Hoverman, 2006). These assessments provide valuable insights into the effects of pollutants on aquatic organisms and ecosystems, thereby influencing the formulation guiding the development of environmental protection guidelines. Additionally, these studies help identify sensitive stress indicators, facilitating in the evaluation of mitigation measures (Montalvo & Luque, 2009).

Mexico has a wide variety of aquatic species that can be used in ecotoxicological tests. These tests are essential for conducting a comprehensive Environmental Risk Assessment (ERA), particularly studies focused on evaluating water quality over time and space in waterbodies impacted by pollutants (Santos-Medrano et al., 2007; Guzmán-Colis et al., 2011). In the present review, we emphasize the importance of ecotoxicological studies carried out in Mexico that use native zooplankton species as model organisms. We have compiled various relevant research that addresses the use of rotifers, cladocerans, and copepods in the assessment of environmental risk associated with wastewater treatment plant effluents, heavy metals, pesticides, cyanotoxins, pharmaceuticals, and microplastics, all of which are frequent pollutants in the aquatic environments of Mexico and other regions of the world.

Zooplankton Applications in Ecosystem Health

Zooplankton is vital for aquatic ecosystems, contributing to food webs, nutrient cycling, biogeochemical processes, and algal bloom regulation (Declerck & de Senerpont, 2023). Marine zooplankton, spanning 12 phyla, is diverse, with copepods being the most abundant, constituting 80 % of biomass (Gasca, 2010; Peijnenburg & Goetze, 2013). In freshwater communities, rotifers, cladocerans, and copepods dominate, with rotifers significantly contributing to biomass (Sarma & Nandini, 2017; Elías-Gutiérrez & Ortiz, 2017).

Zooplankton is highly vulnerable to environmental changes, impacting other organisms through trophic interactions (Gutiérrez & Gagneten, 2011). Due to its ease of cultivation and sensitivity, with well-known nutritional requirements and short life cycles, it’s an ideal model for ecotoxicological evaluations (Declerck & de Senerpont, 2023). Ecotoxicological tests use rotifers, cladocerans, and copepods as indicators to assess direct and indirect effects (Elías-Gutiérrez & Gagneten, 2011). For example, effluent quality is often assessed based on physical and chemical parameters alone; however, zooplankton have proven useful in assessing the effectiveness of wastewater treatment plants through acute toxicity tests (Torres-Guzmán et al., 2010).

Zooplankton Species Used Globally

Researchers employ zooplankton models tested in controlled conditions or micro/mesocosms (Moreno et al., 2022). Microcosms maintain consistent but less complex conditions, while mesocosms, offering greater complexity, simulate controlled or natural environments indoors or outdoors (Lozano, 2020). Outdoor systems, while authentic, face weather unpredictability, complicating replication and causing data variation. Researchers must align conditions with their study focus and logistical factors, especially in ecotoxicology (Hjorth et al., 2006).

According to De Meester et al. (2023), the majority of zooplankton tests have centered around the *Daphnia* genus due to its well-researched ecology over the past 120 years. Copepod research has focused on risk assessment in both marine and freshwater environments, particularly emphasizing the naupliar stage (López, 2018). *Acartia tonsa* is common in bioassays for evaluating environmental hazards due to its ecological significance and adaptability (Rotolo et al., 2021). Studies indicate that *Tisbe battagliai*, *Tigriopus japonicus*, *Nitocra spinipes*, and *Mesocyclops leuckarti* are more sensitive to various contaminants than *Daphnia magna* (OECD, 2011).

Rotifers are cost-effective tools for environmental protection. The *Brachionus* genus (*B. plicatilis*, *B. calyciflorus*, and *B. havanaensis*) is recognized by the American Public Health Association for assessing xenobiotics, endocrine disruptors, and disinfectants in both freshwater and marine environments (Alayo & Iannacone, 2002; Sarma et al., 2014).

Zooplankton Groups in Mexico for Environmental Risk Assessment

As of January 2024, in the Scopus database, there are roughly 450 research studies on zooplankton in Mexico, with 80 of them specifically focusing on environmental risk assessment. These studies have highlighted 50 different species of zooplankton with the primary attention given to three main groups: rotifers, cladocerans, and copepods. Other groups, including Anostraca (*Artemia franciscana*), Amphipoda (*Hyalella azteca*), and Ostracoda (*Diaphanocypris meridana*), have also been studied (Fig.1). The majority of research has been conducted in entities such as the State of Mexico, Mexico City, Aguascalientes, Veracruz, Baja California Sur, and Quintana Roo. However, there are still areas, like Oaxaca, Durango, Zacatecas, Colima, and Coahuila, where research is scarce. This emphasizes the need to promote research in these areas to gain a better understanding of the environmental risk in Mexico.

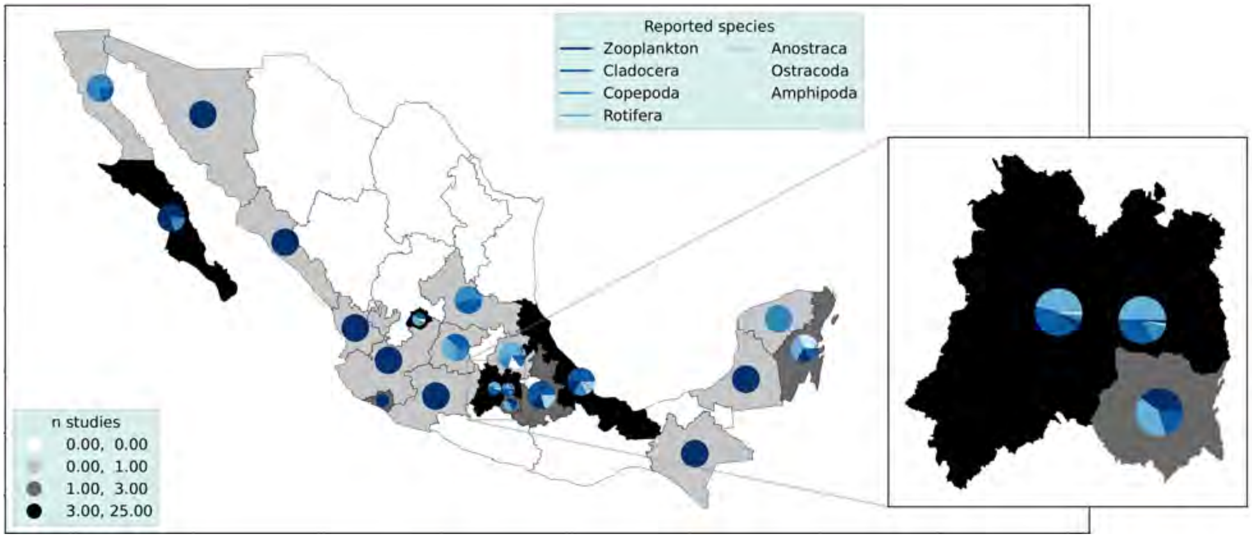

Figure 1. Distribution of Research on Zooplankton in Mexico with a Focus on Environmental Risk and the Main Groups Studied.

Rotifers

Diversity, Behavior, and Reproductive Strategies

Rotifers are microorganisms (approximately 50–2,000 µm in length) ubiquitously found in diverse ecosystems, ranging from fresh and brackish waters to marine environments worldwide. Phylum Rotifera has two classes: Pararotatoria with subclass Seisonidea and Eurotatoria with subclasses Bdelloidea and Monogononta (Fontaneto & Plewka, 2021). Globally, approximately 2,300 species have been described, while in Mexico, around 400 species have been recorded (Sarma et al., 2021). In general terms, the life cycle of monogonont rotifers begins with the hatching of amictic females from diapause eggs. When environmental conditions are conducive, such as optimal temperature, salinity levels and food availability, reproduction occurs asexually through parthenogenesis.

Conversely, in unfavorable situations, the reproductive process takes a sexual phase. In the sexual phase, mictic females produce diapause eggs stored in the sediments of aquatic systems and can remain viable for many years (Fontaneto & Plewka, 2021). The distinctive ability of rotifers to produce diapause eggs makes them valuable resources for laboratory experiments, including ecotoxicological studies (Won et al., 2017).

Use of Rotifers in Ecotoxicology

Early ecotoxicological studies involving rotifers commenced in the 1980s, as reported by Halbach et al. (1983). Since then, rotifers have been pivotal in evaluating environmental risks linked to a spectrum of emerging contaminants, including pharmaceuticals, pesticides, and microplastics. Additionally, they have contributed significantly to assessing heavy metals, emerging pollutants, and the impact of harmful algal blooms. Various reasons support the position of rotifers as model organisms in this ecotoxicology: a) their ease of culture and manipulation in the laboratory; b) a short life cycle (7-20 days), which facilitates short-term analysis of demographic parameters such as average lifespan, life expectancy, reproductive rates, generation time and increase rates; c) parthenogenetic reproduction, which ensures genetic homogeneity and rapid population growth; d) its high sensitivity to changes in water quality; and e) ecological relevance and reliability in reproducibility (Dahms et al., 2011; Rico-Martínez et al., 2017; Won et al., 2017). These characteristics meet the requirements to consider rotifers as representative test species in environmental risk assessments.

Main Rotifer Species in the Ecotoxicology of Mexico

Recently, Sarma et al. (2021) carried out an exhaustive compilation of rotifer species present in freshwater bodies in Mexico. Among the rotifer families analyzed it was observed that the most diverse were Flosculariidae (50 species), Brachionidae (51 species), Lecanidae (68 species), Notommatidae (48 species), and Trichocercidae (31 species). It is relevant to highlight that the most significant diversity of species was found in the state of Mexico, where 323 species were recorded, followed by Michoacán with 164, Veracruz with 155, Aguascalientes with 150, and Yucatan with 129 species reported. In Mexico, various species of rotifers serve as model organisms in ecotoxicological tests. According to the data included in the Scopus database (November 2024), rotifer species used in ecotoxicological studies in Mexico include *Anuraeopsis fissa*, *Asplanchna sieboldii*, *Brachionus calyciflorus*, *B. angularis*, *B. rubens*, *B. havanaensis*, *Lecane hamata*, *L. luna*, *L. quadridentata*, *L. papuana*, *Euchlanis dilatata*, and *Plationus patulus*.

The basic rotifer bioassays include acute toxicity tests, like the 24 h LC_{50} (lethal concentration for 50 % of the population) and the EC_{50}, indicating the effective concentration inhibiting 50 % of biological responses to contaminants. Chronic toxicity tests assess life table parameters and population growth in organisms exposed to toxicants (Dahms et al., 2011).

In Mexican aquatic ecosystems, *B. calyciflorus* is commonly used in studies on environmental risks. For example, Zamora-Barrios et al. (2017) evaluated the effects of crude extracts of cyanobacteria detected in Lake Nabor Carrillo, which is part of what was once Lake Texcoco (Mexico City), on *B. calyciflorus* isolated from the same waterbody. Thus, demonstrating the impact that cyanobacteria blooms in tropical waters have on key species. The rotifer *B. angularis*, isolated from a pond in the Park of Tezozomoc (Mexico City), has been helpful in evaluating the effects of methyl parathion, a commonly used insecticide in Mexico, to eradicate insect pests (Gama-Flores et al., 2004). This study illustrates the potential risk associated with the presence of pesticides in aquatic systems and their impact on the population dynamics of invertebrates, which contend with constant changes in water quality and food availability. It also underscores the organisms' usefulness in short-term assessments of environmentally relevant pesticides in Mexico, particularly in agricultural areas. In Aguascalientes, Tovar-Aguilar et al. (2019) used the rotifer *L. papuana* to evaluate the effects of the pharmaceutical diclofenac, detected in surface and groundwater due to its extensive use in human and veterinary health. This study exhibits the vulnerability of zooplankton to relevant emerging pollutants and stresses the potential for bioaccumulation of xenobiotics, which can induce disturbances in the ecological structure of aquatic environments. Heavy metal pollution in aquatic environments is a growing concern due to high concentrations, persistence, and biomagnification. The first reports of lead biomagnification in predatory rotifers were published by Rubio-Franchini and Rico-Martínez (2008, 2011) at Niagara Dam in Aguascalientes. Their research focused on the species *A. brightwellii* and emphasized the importance of conducting *in situ* studies while confirming the findings through laboratory tests. Similarly, another study highlights the relevance of assessing the toxicity of metals (Al, Fe, and Zn) in the San Pedro River using acute toxicity tests on *L. quadridentata* (Torres-Guzmán et al., 2010). This approach allowed the estimation of each metal's contribution to overall toxicity, identifying zinc as the most toxic metal, underscoring the value of combining field and laboratory analyses for a comprehensive evaluation of metal pollution.

A recent study in Manatí Lagoon, a protected area in Cancún (Quintana Roo), evaluated the risk through zooplankton, including rotifers (Demidof et al., 2022). These key indicators of aquatic health underscore the urgency of addressing pollution in protected environments. This comprehensive approach, involving the evaluation of key organisms such as rotifers, highlights the urgent need for effective strategies to counteract the detrimental effects of heavy metal pollution in aquatic environments, especially in protected areas such as Laguna Manatí. The rotifers *P. patulus* and *A. sieboldii*, isolated from Lake Xochimilco (Mexico City), were used to analyze the effects of microplastics and their interaction with heavy metals on the predator-prey dynamics and demographic variables of the rotifers (Hernández-Lucero et al., 2023). This study revealed that mixtures of heavy metals and microplastics can accentuate the vulnerability of key species to pollution. Thus, it highlights the importance of rotifers in the ecological risk assessment of microplastics in Mexico, emphasizing the need to understand the interaction between these contaminants and aquatic fauna to preserve the health of ecosystems.

Challenges

Most ecotoxicological studies with freshwater rotifers focus on the cities of Mexico and Aguascalientes. This is presumed due to the presence of groups of experts on the subject in these states. While there is evidence of ongoing efforts in the states of Veracruz and Yucatan. It's crucial to intensify these efforts and expand research to diverse aquatic systems in Mexico, leveraging the potential of rotifers. These organisms can be tools in developing mitigation strategies and deepening our understanding of the effects of pollution in different aquatic environments in the country. The study of the effects of heavy metals on rotifers is more common than research on other contaminants. It's essential to explore the environmental risks of emerging contaminants of global relevance, such as pharmaceutical waste and microplastics which still require more detailed investigations. Furthermore, it is crucial to consider more realistic scenarios in studies that reflect aquatic systems contaminated by a mixture of substances, an evaluation made possible thanks to the advantages that rotifers offer as model organisms. Surprisingly, in rotifer studies in Mexico, environmental genomics still needs to be fully integrated despite being a tool that could provide a deeper understanding of the toxicity mechanisms of various toxic substances.

Cladocerans

Diversity, Behavior, and Reproductive Strategies

Cladocerans, commonly referred to as “water fleas,” belong to the Phylum Arthropoda and the class Branchiopoda, encompassing four recognized Orders: Anomopoda, Ctenopoda, Haplopoda, and Onychopoda. With a size range of 0.25 to 18 mm, there are nearly 850 described species, including 150 recorded in Mexico (Cervantes-Martínez et al., 2023). They are the connection between the microbial loop, primary producers, and higher-level consumers (Kalinowska, 2015).

Cladocerans employ their thoracic appendages to filter particles, optimizing nutrient consumption for efficient growth and reproduction (Riisgård, 2015; Smirnov, 2017). Most species exhibit facultative parthenogenesis, where males are associated with seasonality or environmental unpredictability. They produce resting eggs (ephippia), serving as a genetic reservoir and facilitating passive dispersal (Bernatowicz et al., 2018). However, certain species within the *Daphnia pulex* complex may display obligatory parthenogenesis (Huynh et al., 2023).

Use of Cladocerans in Ecotoxicology

The utilization of cladocerans in bioassays is supported by their easy maintenance in laboratory settings and sensitivity (Terekhova et al., 2018). Since the 1970s, environmental agencies have standardized protocols for evaluating diverse toxicants using cladocerans (Versteeg et al., 1997). Toxicological studies on cladocerans involve acute tests (LC_{50} determination within 24-48 h) (OECD, 2004; U.S. EPA, 2002) and chronic tests, assessing life history, physiology, and molecular responses over extended periods (>30 % of the life cycle) (Connors et al., 2022). Population growth and life table experiments offer vital insights into their fitness, stress responses, and reactions to chemical compounds (Sibly & Hone, 2002; Wilson et al., 2006; Sarma & Nandini, 2006).

Main Cladocerans Species in the Ecotoxicology of Mexico

In Mexico, 17.6 % of the globally recognized cladoceran species have been identified, with ongoing efforts to expand this number. However, by 2008, only 1 % of watersheds had been thoroughly explored, indicating vast potential for further study (Elías-Gutiérrez et al., 2008a). Additionally, the use of molecular markers has brought to light a large number of cryptic species (Elías-Gutiérrez et al., 2008b).

The first study to use cladocerans as a model assay in Mexico was focused on evaluating the chronic toxicity of wastewater from the paper industry (Martínez-Jerónimo et al.,1993). Since then, there has been an exponential increase in publications exploring the effects of various chemical, physical, and biological compounds, such as heavy metals, pesticides, surfactants, personal care products, pharmaceuticals, hormones, phytotoxins, microplastics, and wastewater. These studies have been conducted across a limited range of species, including *Daphnia magna*, *D. pulex, D. laevis, D. exilis, D. schoedleri, D. ambigua, Ceriodaphnia dubia*, *Moina macrocopa*, *M. micrura*, *Alona glabra*, *Diaphanosoma birgei*, *Bosmina longirostris*, and *Macrothrix triserialis*. This surge in research highlights the growing recognition of the important role of cladocerans in aquatic ecotoxicology within the Mexican scientific community.

Cladocerans have proven to be a reliable model organism in Mexico's field of environmental assessment. A pioneering study conducted by López-López and Serna-Hernández (1991), linked seasonal zooplankton variation in reservoirs and identified species like *Bosmina longirostris*, *Diaphanosoma birgei*, and *Daphnia parvula* as excellent indicators of water quality changes associated with eutrophication (Mendoza-Chávez et al., 2022). Recent research in San Luis Potosí revealed a correlation between arsenic levels and microcrustacean diversity in reservoirs, suggesting *Simocephalus punctatus* as a potential reliable bioindicator. Furthermore, saprobity indices have been devised for assessing water quality in the Xochimilco canals (Nandini et al., 2016).

Studies on urban lakes in Mexico City have focused on the impact of different feeding conditions, particularly in the presence of toxin-producing cyanobacteria. Cladocerans, including *Simocephalus mixtus*, *Daphnia mendotae*, *D. pulex*, *Moina micrura*, *M. macrocopa*, and *Ceriodaphnia dubia*, actively consume cyanobacterial cells, leading to alterations in filtration rates and fitness (Pineda-Mendoza et al., 2012; Pérez-Morales et al., 2014, 2020; Nandini et al., 2020) or inducing cyanotoxin production (Pérez-Morales et al., 2015). Additionally, cladocerans have been observed to accumulate heavy metals, cyanotoxins, and microplastics, subsequently transferring them within the food chain (Rubio-Franchini et al., 2016; Zamora-Barrios et al., 2019; Manríquez-Guzmán et al., 2023).

Research with Cladocera strains isolated from Mexican waterbodies examined the impact of Hexavalent Chromium on *Ceriodaphnia dubia*, emphasizing precise short-term assays, including volume, exposure duration, and temperature measurements (Martínez-Jerónimo & Martínez-Jerónimo, 2023). In Aguascalientes, a study revealed high susceptibility of the indigenous species *Alona guttata* to pesticides, even at concentrations similar to guava field applications, causing chronic exposure-related somatic growth alterations. Furthermore, the Holarctic species *Daphnia magna* has been utilized to evaluate the impact of toxic substances such as nonsteroidal anti-inflammatory drugs (NSAIDs) on oxidative stress and genetic material damage (González-González et al., 2014). Additionally, Mexican laboratories participated validating a two-generational reproduction test (Barata et al., 2017). Recent researches are focused on the effects of multiple stressors to assess the synergistic or antagonistic impacts of a wide range of emerging contaminants found in domestic, textile, and hospital wastewater, as well as pesticides. These contaminants include a mixture of detergents, metals such as Zinc, Cadmium, and Arsenic, anti-corrosion agents, cardioactive drugs, antibiotics, NSAIDs, antidepressants, etc. (Hernández-Zamora & Martínez-Jerónimo, 2019; Aguilar-Aguilar et al., 2023; Hernández-Zamora et al., 2023). All the works above highlight the relevance of cladocerans as valuable tools for understanding the response of aquatic ecosystems to factors such as pollutants, changes in feeding, and environmental conditions, providing crucial information for the management and conservation of aquatic resources in Mexico.

Challenges

Mexican legislation designates *Daphnia magna* as a sentinel for toxicity tests (NMX-AA-087-SCFI-2010). However, smaller herbivores such as, *Diaphanosoma*, *Moina*, *Ceriodaphnia*, *Chydorus*, *Alona*, and *Macrothrix* genus, dominate Mexican freshwater ecosystems. These species have shorter lifespans, faster reproduction, lower fecundity, and potentially greater sensitivity than *D. magna*. Martínez-Jerónimo et al. (2008) have proposed to replace *D. magna* with the American cladoceran *Daphnia exilis* in ecotoxicological bioassays due to its taxonomic similarities. Following the same approach, Santos-Medrano and Rico-Martínez (2019) suggest determining the relative sensitivity of native species to *D. magna* using the formula proposed by Von der Ohe and Liess in 2004:

$$S=\log\left(\mathrm{LC}_{50\,Daphnia\ magna}/\mathrm{LC}_{50i}\right)$$

Where: S=relative sensitivity; $\mathrm{LC}_{50\,Daphnia\ magna}$ =LC_{50} value for *D. magna*, and LC_{50i} =experimental LC_{50} for a species *i*. A zero value indicates a sensitivity equal to that of *D. magna*, a positive value suggests that *D. magna* is less sensitive, and a negative value indicates that *D. magna* is more sensitive.

In a preliminary experiment designed to assess the impact of Potassium dichromate, *Daphnia magna* exhibited LC_{50} values of 0.93 at 24 h and 0.66 mg L^{-1} at 48 h. The native species *C. dubia*, *D. laevis*, and *S. vetulus* showed greater sensitivity. *D. laevis* presented an LC_{50} of 0.34 mg L^{-1} at 48 h, resulting in an S value of 0.28. *S. vetulus* was the most sensitive species, with a S=0.81 (Fig.2).

Despite the absence of *D. magna* records in Mexican water bodies, recent studies identify it in Ciénegas del Lerma (Espinoza-Rodríguez, 2023). This underscores the importance of considering native species in ecotoxicological studies for a more realistic scenario and reducing the likelihood of introducing exotic species.

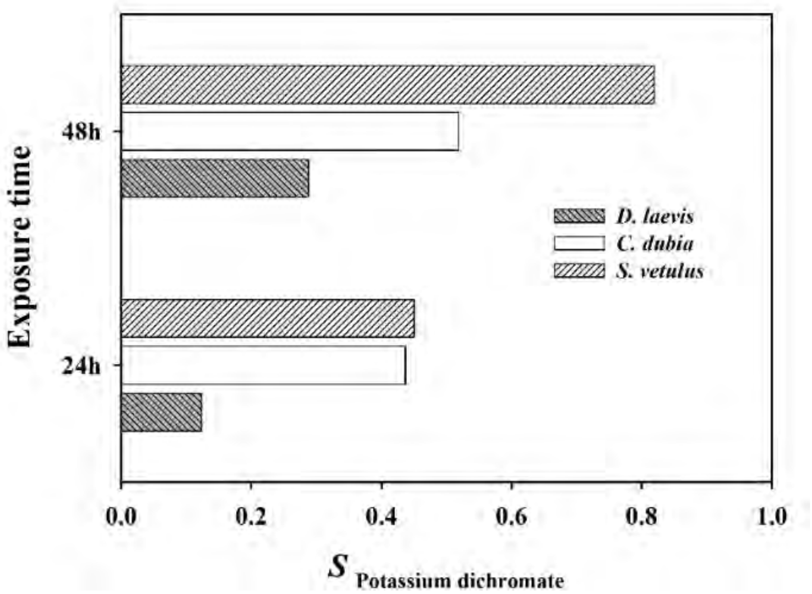

Figure 2. Relative Sensitivity Values of Native Species (*Ceriodaphnia dubia*, *Daphnia laevis*, and *Simocephalus vetulus*) Exposed to the Reference Toxicant (Potassium dichromate) during 24 and 48 h Experiments.

Copepods

Diversity, Behavior, and Reproductive Strategies

In general, most copepods are found in marine or brackish waters (~14,000 registered), with around 3,000 species in freshwater (Uc-Castillo et al., 2022). Copepods in continental waters are classified into three orders: Calanoida, Cyclopoida, and Harpacticoida (Dole-Olivier et al., 2000). Approximately 110 species have been documented in Mexican aquatic ecosystems (Gómez & Morales-Serna, 2014). Copepods typically measure between 1 and 5 mm in length, exhibiting a cylindrical body, segmented exoskeleton, and articulated appendages for swimming and feeding. Copepods display sexual dimorphism, and sexual reproduction is the most common form of reproduction; however, parthenogenesis has been observed in certain harpacticoid species (Poulin, 1996). Most copepods hatch from fertilized eggs, involving the union of a spermatophore, delivered by the male, to the copulatory pore of the female (Reid & Strayer, 1994). Copepod development involves eleven stages, including six naupliar and five copepodite stages with molting occurring between each stage and metamorphosis from the last naupliar to the first copepodite stage (Kwok et al., 2015).

Use of Copepods in Ecotoxicology

Copepods are acknowledged as highly effective bioindicators of ecosystem pollution, with various toxicity testing protocols developed, including acute tests, multi-generation life cycle tests, and short-term toxicity tests, assessing responses in individual actions, immune and endocrine processes, development, growth, and reproduction (Hussain et al., 2020). Since the 1940's, copepods have remained a popular model organism with most toxicity studies utilizing either static or static-renewal systems. Among copepod species, *Amphiascus tenuiremis*, *Nitocra spinipes*, and *Acartia tonsa* have seen the establishment of standardized full life-cycle testing protocols (Raisuddin et al., 2007). Unfortunately, freshwater copepods have not received sufficient attention, lacking protocols for toxicity tests. Nevertheless, *Mesocyclops* genera have been identified as a suitable option (Kulkarni et al., 2013).

Main Copepods Species in the Ecotoxicology of Mexico

Research on copepods in Mexico has traditionally focused on their geographic distribution and taxonomic description. However, there is a growing interest and recognition of the important role copepods play in ecotoxicological studies. Several copepod species have become essential models for evaluating environmental impacts and conducting ecotoxicological tests. A simple search in the Scopus and Web of Science databases using the words "toxicology," "copepods," and "environmental assessment" shows that some of the marine species examined include *Acartia tonsa*, *A. clausi*, *A. spinata*, *A. lilljeborgii*, *Corycaeus amazonicus*, *Temora discaudata*, *Subeucalanus subcrassus*, *Acrocalanus longicornis*, *Calanus pacificus, Euterpina acutifrons,* and *Pseudodiaptomus euryhalinus*. Additionally, freshwater species such as *Acanthocyclops robustus*, *A. vernalis*, *A. americanus*, *Mastigodiaptomus montezumae*, *Paracyclops novenarius*, and *Eucyclops chihuahuensis* have also been used.

The research on copepods in Mexico is limited but existing studies emphasize their importance. A specific study examined the reproductive response of the copepod *A. clausi* to the toxic dinoflagellate *Gymnodinium catenatum* suggesting that this species plays a crucial role in controlling red tides in Concepción Bay (Palomares-García et al., 2006). Another work identified the high tolerance of *P. novenarius* in a water body with high Arsenic concentrations (>50 mg L^{-1}), revealing that despite the high concentrations, there was no impact on its morphology or development (Uc-Castillo et al., 2022). Additionally, sensitivity and response were evaluated using oxidative stress biomarkers on *A. americanus* exposed to Cadmium, Chromium, Copper, Mercury, Manganese, Nickel, and Lead, emphasizing the need to understand how copepods, both marine and freshwater, respond to various environmental factors and contaminants (Sobrino-Figueroa et al., 2020). A recent investigation examines the impact of invasive species, such as *M. pehpeiensis*, not only from an ecotoxicological perspective but also considering their effects on biodiversity reduction and the potential impact on Mexican planktonic communities (Valencia-Vargas et al., 2023).

Challenges

Ecotoxicological risk assessment commonly involves selecting species based on their sensitivity to various toxins and their suitability for laboratory cultivation. However, this approach often overlooks the diverse life history strategies copepods adopt in their natural environments. This oversight could have substantial implications for these species' vulnerability to contaminant exposure. Consequently, there is an urgent call for detailed and carefully orchestrated research within the realm of copepod ecotoxicology. Such research is pivotal in addressing the current disparity between ecological and ecotoxicological studies on copepods, with the goal of accurately identifying and incorporating representative species into assessments.

Conclusions and Recommendations

The focus of this comprehensive brief review is on the significance of ecotoxicology in Mexican aquatic ecosystems, specifically directing attention towards zooplankton. The urgency to advance research in this field highlights the need to explore diverse ecosystems, particularly those in understudied regions. The inclusion of native species in toxicity studies emerges as a crucial aspect to ensure realistic outcomes and prevent the introduction of invasive species. Key approaches proposed for enhancing understanding include conducting detailed research on emerging contaminants (pesticides, animal pharmaceuticals, pharmaceuticals and personal care products, industrial compounds), heavy metals, detergents, as well as integrating environmental genomics into zooplankton studies. Furthermore, the establishment of standardized protocols, specifically with freshwater copepod species, is emphasized as an imperative need. Overall, these future perspectives collectively aim to strengthen the knowledge base in aquatic ecotoxicology in Mexico, providing valuable insights for the enduring preservation of the country's aquatic ecosystems.

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Authors' Contributions

CAZB, UAR, MGRM, JMEH, and FJTM designed, analyzed, and wrote the study; JMEH and CAZB developed the graphic representation. FJTM acquired financial funds.

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Exploring Zooplankton-Macrophytes Interaction Research in Mexico: Bibliometric Analysis

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Abstract

This study conducted a bibliometric review of the Mexican scientific literature on the interactions between macrophytes and zooplankton. The findings suggest that comprehending the role and dynamics of each group is crucial for understanding the overall function of water bodies. Given the richness and distribution of both groups of organisms, Mexico presents a potential for further exploration of fundamental research questions and applications in ecology. The study highlights the need for more research on the impact of macrophyte removal on zooplankton communities, the role of macrophytes in mitigating anthropogenic stressors, the description of food webs, and different ecological interactions including allelopathy between primary and second producers. This work delves into discussing effective strategies for selecting editorial content and fostering collaborative efforts across different topics, all while considering the bibliometric results.

Keywords

Aquatic plants, rotifer, cladocerans, bibliometric analysis, citation.

Introduction

Importance of Zooplankton

Epicontinental aquatic systems such as lakes, reservoirs, and rivers harbor a vast array of biological diversity (Moss, 2018). An essential biological component of freshwater ecosystems is zooplankton which is of utmost importance as it serves as a building block for the sustenance of various trophic levels (Pace & Orcutt, 1981; Sommer, 2012; Kuczyńska-Kippen & Joniak, 2015). Zooplankton is a group of microscopic aquatic animals composed of invertebrates and heterotrophic (consumers) organisms, among which the following stand out for their frequency, species diversity, and biomass: rotifers, cladocerans, and copepods, among other groups such as protozoa and ostracods (Canfield & Jones, 1996; Sommer, 2012; García-Chicote et al., 2018). A great diversity of zooplankton species is recognized, including 850 species of cladocerans, 2,000 rotifers, and 2,800 freshwater copepod species (Boxshall & Defaye, 2007; Wallace et al. 2019).

Rotifers, together with microcrustaceans such as cladocerans and copepods, with sizes from 200 to 6,000 µm, have different feeding habits, most of them are consumers of algae, bacteria, and detritus; however, it is possible to find predators in these groups (Dumont & Negrea, 2002). These organisms have a central position in the aquatic trophic food web as primary consumers and, in addition, as a food resource for secondary consumers. Hence, they actively participate in various biotic interactions, which is why they have a great diversity of adaptations for optimal grazing (Lampert, 1997), predation avoidance, and intra and interspecific competition (DeMott, 1989; Diel et al., 2020); this has allowed the development of several areas of basic and applied research. Cladocerans, for example, have been used as an algal control tool to restore aquatic systems, mainly in temperate regions (Peretyatko et al., 2009). On the other hand, cladocerans and copepods have been used for live feed production in aquaculture (Piasecki et al., 2004; Pearson & Duggan, 2018).

Zooplankton has generated significant interest in scientific research, mainly in their use as indicators of water health status (Jeppesen et al., 2011; Chandel et al., 2023), this is due to their high sensitivity to natural and anthropogenic environmental changes and perturbations reflected in changes in their specific richness, densities, life history traits, and even morphological effects (Sarma & Nandini, 2006; Alvarado-Flores et al., 2022). Ecological indicators provide information for biodiversity conservation as well as to ensure the sustainable use of resources and ecosystem services associated with these systems (Jeppesen et al., 2011; Berta et al., 2018). Likewise, the sensitivity and short life cycles of zooplankton have led some rotifers and cladocerans species to be the focus of both descriptive and experimental ecotoxicological studies in the field (Peither et al., 1996; Friberg-Jensen et al., 2003) and laboratory (Rico-Martínez et al., 2016; Pérez-Morales et al., 2020; Guo et al., 2023).

In aquatic systems, zooplankton are widely distributed in the littoral, pelagic, and benthic zones (Wallace et al., 2019). However, it is possible to find a more significant number of species in the littoral zone, where the presence of macrophytes considerably plays an important role in mediating food web dynamics (Perrow et al., 1999; Duggan et al., 2001; Geraldes, 2004).

Importance of Aquatic Plants

The Neotropics are the regions with the most remarkable diversity of aquatic macrophytes (Murphy et al., 2019). Different types of macrophytes, such as submerged, floating, and emergent macrophytes, play an important ecological role associated with the physical, chemical, and biological characteristics of the water. Macrophyte-zooplankton interactions have been shown to be fundamental to the structure of aquatic communities as they influence higher trophic levels, which in turn are closely related to water quality (Perrow et al., 1999; Declerck et al., 2011).

Furthermore, they play an important role in cycling nutrients, providing habitats, purifying water, controlling diseases, and preserving cultural services (Thomaz, 2021). Applied approaches include controlling eutrophication caused by excessive loading of nutrients (Phosphorus and Nitrogen), the remotion of contaminants, and as food source for humans and livestock (Jeppesen et al., 2012; Singh et al., 2023). On the other hand, macrophytes could be of economic importance in cases such as species invasion, affecting navigation and excessive evapotranspiration, for example water hyacinth (*Eichhornia crassipes*) (Lugo et al., 1998).

Macrophyte diversity impacts invertebrate density and diversity, especially when considering plant structure. Morphologically complex macrophytes significantly affect animal populations and communities, for instance, in temperate zones, it has been observed that richer communities of larger-bodied organisms with higher densities of plant-associated cladocerans are present. In contrast, smaller-bodied zooplankton are typically found in subtropical water bodies (Merhoof et al., 2007; Thomaz & Cunha, 2010). The presence of macrophytes creates a rich substrate and abundant physical area through their leaves and roots, resulting in an increase of epiphytic algae and organic matter. This, in turn, attracts invertebrates for grazing and predators, leading to a higher diversity and abundance of animals in littoral zones (Dibble et al., 1996; Taniguchi et al., 2003).

In order to conserve biodiversity, it is essential to explore biological invasions. There is a global dispersion and introduction of macrophytes mainly for ornamental purposes (Lobato-de Magalhães et al., 2022; Bora & Padial, 2023). In certain ecosystems, invasive aquatic macrophytes have the ability to modify the complexity of habitats, which can lead to a reduction in water quality and availability (Thomaz & Cunha, 2010). This highlights the importance of monitoring and managing invasive species to prevent them from negatively impacting aquatic ecosystems. Mexico is no exception and the problem is that, for example, the water hyacinth has been affecting a large number of aquatic ecosystems, as well as 10 other species throughout the country, although there are few studies that investigate, in depth, its effect on the ecological dynamics between species, the availability and use of water, as well as solutions and alternatives for the restoration, management, and conservation of these systems (Gutiérrez et al., 1996; Lugo et al., 1998; Martínez-Jiménez & Balandra, 2022).

Interaction Between Macrophytes and Zooplankton

It is common practice to use macrophytes and invertebrates as bio-indicators of water quality due to the varying sensitivity of these organisms to pollution in their environments (Habib & Yousuf, 2014). The interaction between these two groups is crucial for several reasons. Macrophytes serve as a source of carbon and other nutrients that are taken up by heterotrophic bacteria, which in turn are consumed by the various zooplankton groups (Szabó-Tugyi & Tóth, 2020). This indirect source of food for zooplankton can be tapped during plant growth and even during their decomposition (Habib & Yousuf, 2014). In addition, the surface of macrophytes is exploited by periphyton for growth, which constitutes a food source for some members of zooplankton (Rautino & Warwick 2006).

The role of macrophytes in providing protection against predation for zooplankton has been questioned, as they seem to offer greater protection in temperate zones compared to tropical regions. In tropical areas, factors such as depth and behaviors like vertical or horizontal migration contribute to zooplankton survival. However, while it has been observed that zooplankton evade macrophytes, it has also been noted that macrophytes can serve as a habitat or refuge for cladocerans (Stansfield et al., 1997; Perrow et al., 1999; Montiel-Martínez et al., 2015; Arcifa et al., 2016). Moreover, macrophytes can influence the functional group richness and diversity of the invertebrate community, which in turn affects the abundance and distribution of zooplankton (Su et al., 2021; Wang et al., 2023). Some of the findings reveal an interesting chemical interaction in the food chain, macrophytes infochemicals trigger changes in demography growth of both phytoplankton and zooplankton; this can have a positive or negative effect depending on the species of macrophyte, finding species of rotifers, and cladocerans that grow particularly due to the presence of these (Duggan et al. 2001; Kuczyńska-Kippen & Nagengast, 2006; Espinosa-Rodríguez et al., 2016), however, is not clear and is missing empirical and experimental data for a better understanding.

The interaction between macrophytes and zooplankton is crucial for maintaining aquatic ecosystem balance and functioning, as it affects nutrient cycling, energy transfer, and overall ecosystem health (Mulderij et al., 2007). By conducting a bibliometric analysis based on the search of Mexican literature, this study aimed to describe the publication trends on the scientific research in recent years, as recorded in indexed journal databases. This analysis allowed us to identify the journals with the highest publication frequency, the leading institutions, and the primary topic addressed. Additionally, it highlights the most cited works, thematic trends, and reference patterns in the publications, along with the collaboration networks among authors. These findings, along with a discussion on the concepts, their importance, and the understanding of the macrophyte-zooplankton interactions, will be elaborated upon of this work.

Bibliometric Analysis

The study relied on bibliometric techniques to analyze the scientific output data obtained from the core collection of Web of Science© (WoS). The search method involved the utilization of the following keywords: “macrophyte* OR aquatic plant*”, which were subsequently refined by the term “zooplankton” and sorted by country (Mexico). This initial set of results was then subjected to a second logical operation, which was then applied using “zooplankton” filtered by “macrophyte* OR aquatic plant*”, followed by a final filter for the country. The results were from 1997 to 2023. The data from the documents obtained were exported as follows: the export selection was selected in the main WoS web page, then *Tab delimited file* was chosen, an emergent window asks for the records selection and it was marked *Full Record and Cited References* which includes the metadata of each document, finally, the text file was analyzed on R-language software using the Bibliometrix package (Aria & Cuccurullo, 2017). The package incorporates an interactive web interface (Biblioshiny) that permits an automatization of analysis, this involved the extraction and analysis of quantitative data related to the frequency and the impact of scientific publications. A three-field plot, including keywords, affiliation and source (journal) was obtained; a list of the most cited articles; a list of the topic tendencies during the last years; an occurrence network for dominant topics, and a network of collaboration within this two fields of study. A limitation of this package is the use of indexed databases, so those articles published under a different index database are omitted, and both the results and conclusions will be limited.

Discussion

In the period from 1997 to 2023 (26 years), a set of 30 documents were compiled. According to the bibliometric analysis (Table 1), there was no annual growth rate (0 %) in the topics related to macrophytes and zooplankton interactions. However, an average of approximately 10 citations per document was found, which could benefit the academic community in the dissemination of knowledge, for example, articles such as van Donk and van de Bund (2002), from 2002 to 2024 have a total of 435 citations, this article contributes to the impact of macrophytes on the plankton food web, showing a considerable gap in the scientific production and its impact worldwide. There has been a discussion (Leimu & Koricheva, 2005) on how different factors, such as the researcher's age, gender, the country where the research was conducted, the type and length of the article, the methodological strategies used, and the hypotheses proposed, can impact the citations of articles in the field of ecology.

Table 1. Main Information Data of Literature for Bibliometric Analysis.

Description	Results
MAIN INFORMATION ABOUT DATA	
Timespan	1997:2023
Documents	30
Annual Growth Rate %	0
Document Average Age	8.17
Average Citations per Doc	10.23
References	1453
DOCUMENT CONTENTS	
Keywords Plus (ID)	173
Author's Keywords (DE)	125
AUTHORS	
Authors	77
Authors of Single-authored Docs	0
AUTHORS COLLABORATION	
Co-Authors per Doc	3.73
International Co-authorships %	20
DOCUMENT TYPES	
Article	26
Article; Proceedings Paper	3
Review	1

In the three-dimensional analysis of the interrelationships between the keywords of scientific articles, university affiliations, and publication journals (Fig. 1), the central role of the National Autonomous University of Mexico (UNAM) stands out. Currently, UNAM is recognized as a foremost actor in scientific research, covering a variety of research topics and consolidating its role as a leader in the generation of scientific knowledge, followed by the National Polytechnic Institute (IPN). These and other institutions contribute to knowledge on topics of interest in the present work. Although Mexico has about 20,825 km^2 of hydrophytic cover including coastal systems, the information generated is still limited (Palacio-Prieto et al., 2000). Similarly, the diversity of zooplankton is high, and there is still a tendency to increase the study of zooplankton in freshwater systems of Mexico (Elías-Gutiérrez et al., 1997; Gómez & Morales-Serna, 2014; Sarma et al., 2021). This is why academics, researchers, and their students could utilize these topics in their future research projects and, as a consequence, publish information on them. Aside from the above, the information generated would also provide insight into problems arising from anthropogenic activities, such as the increase in eutrophication, xenobiotic contamination, and plant invasion, topics of great interest nowadays.

Regarding the diffusion of research publications, it is noteworthy that the academic journal Hydrobiologia (Impact Factor=2.6, Q1) has indicated a significant preference, followed by Allelopathy Journal (Impact Factor=0.96, Q3), and Ecohydrology & Hydrobiology (Impact Factor=2.6, Q2) in terms of publishing (Fig. 1). These results indicate the relevance of the journals as platforms for the publication of studies related to the topics of zooplankton and macrophytes suitable for members of the National System of Researchers of CONAHCYT who have the challenge of publishing their research (Silva Payró et al., 2016; Díaz-Martínez, 2020). This finding highlights the significant relevance of carefully selecting journals for disseminating scientific knowledge in the Mexican context. Each of these journals addresses diverse themes, which allows for a detailed understanding of the different fields of study that receive particular attention. These results contribute substantially to the understanding of the editorial dynamics in scientific research in Mexico and highlight the strategic importance of editorial decisions in the process of knowledge dissemination on topics of interest.

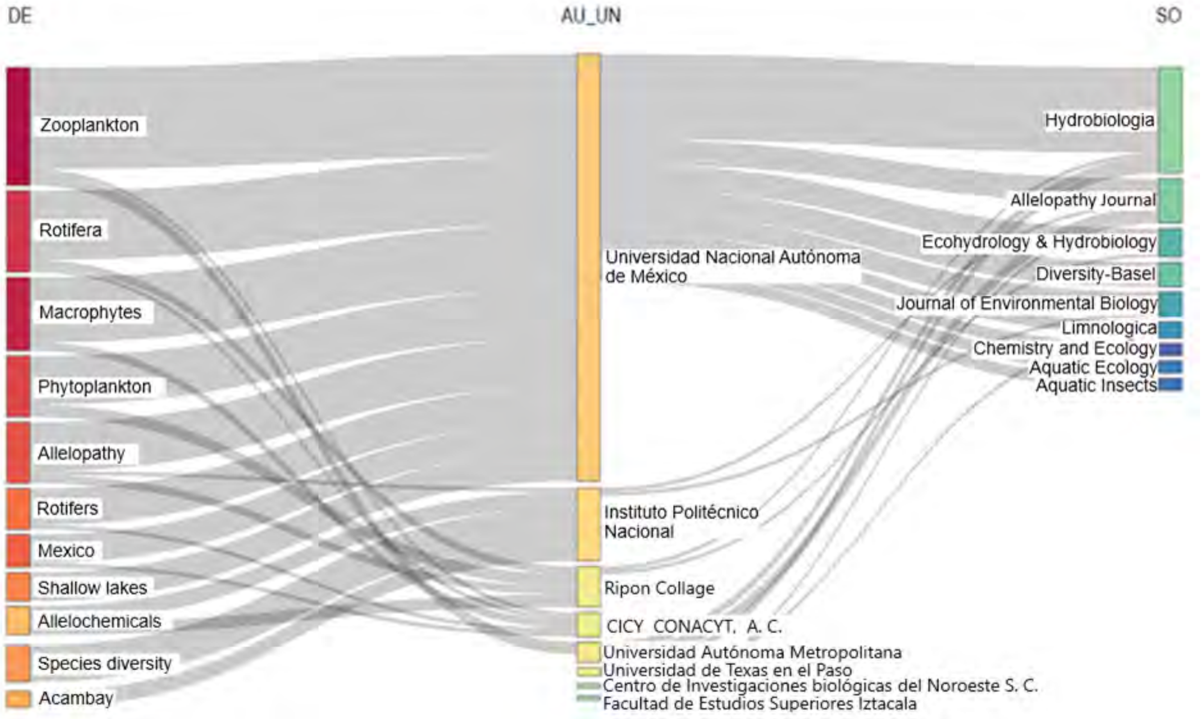

Figure 1. 3-field Graph, Showing the Interactions between DE: Keywords, AU_UN: Affiliation, SO: Source (Journal), Data from the Literature Indexed in WoS Related to Macrophytes and Zooplankton in Mexico.

A classification of the most cited scientific articles in the bibliometric analysis (Fig. 2) indicates that in 10 articles, the number of citations varies from 12 to 43 in accordance with WoS, reflecting the breadth and relevance of the Mexican contribution to the global scientific community, for example in a study related to citation of marine and freshwater articles and average of citation of 19.4 in a range of 1 to 373 (Nash et al*.,* 2017) was found. Mexican literature has made significant contributions in several areas, involving field and laboratory research. Studies have been carried out on the taxonomic description of species using traditional approaches (Elías-Gutiérrez et al., 1997). The use of isotopes has been added, for the study of biotic communities and their interaction with abiotic factors related to water quality (Zambrano et al., 2010; Muñoz-Colmenares et al., 2017). Research has been conducted on allochthonous fish and macrophyte species (Rocha-Ramírez et al., 2006). The potential impact of heavy metals on aquatic ecosystems can occur through several pathways, including the uptake of these metals by macrophytes. This may lead to their consumption by other aquatic organisms and aggravate the adverse effects of heavy metals on the ecosystem (De La Vega Salazar et al., 1997). Certain research gaps exist in the intriguing topic of fish-zooplankton predation mediated by macrophytes. Nonetheless, recent studies have addressed these gaps, revealing that free-floating macrophytes, such as water hyacinth, can serve as habitats for *Chydorus brevilabris* or refuges for *Simocephalus vetulus* (Montiel-Martínez et al., 2015).

It is worth noting that recent research has demonstrated the significant contribution of macrophytes to the diversity of invertebrates in aquatic ecosystems. In comparison to open water areas, macrophytes have been found to foster a greater taxonomical and functional diversity of invertebrates (Enríquez-García et al., 2009; González-Gutiérrez et al., 2016; Jiménez-Santos et al., 2019; Espinosa-Rodríguez et al., 2021). These findings highlight the importance of macrophytes in promoting biodiversity and the need to consider their presence when assessing the health and ecological dynamics of aquatic environments.

Despite being a common practice in lake management in Europe and North America, the impact of the introduction and even removal of macrophytes on the taxonomic and functional groups of zooplankton has been little studied in Mexico. Recent research has shown that macrophyte removal has a significant influence on organisms over time, highlighting the need to better understand its effects (Espinosa-Rodríguez et al., 2021). The allelopathic effects of macrophytes in primary producers and their consumers is a topic that has been gaining attention currently. These effects can range from stimulating growth in *Simocephalus* spp. to interrupting growth in phytoplankton (*Scenedesmus acutus*) through interaction with *Egeria densa* (Espinosa-Rodríguez et al., 2016). The aforementioned contributions have provided valuable insights on diverse subjects, contributing significantly to the expansion of our knowledge at a regional as well as a global level.

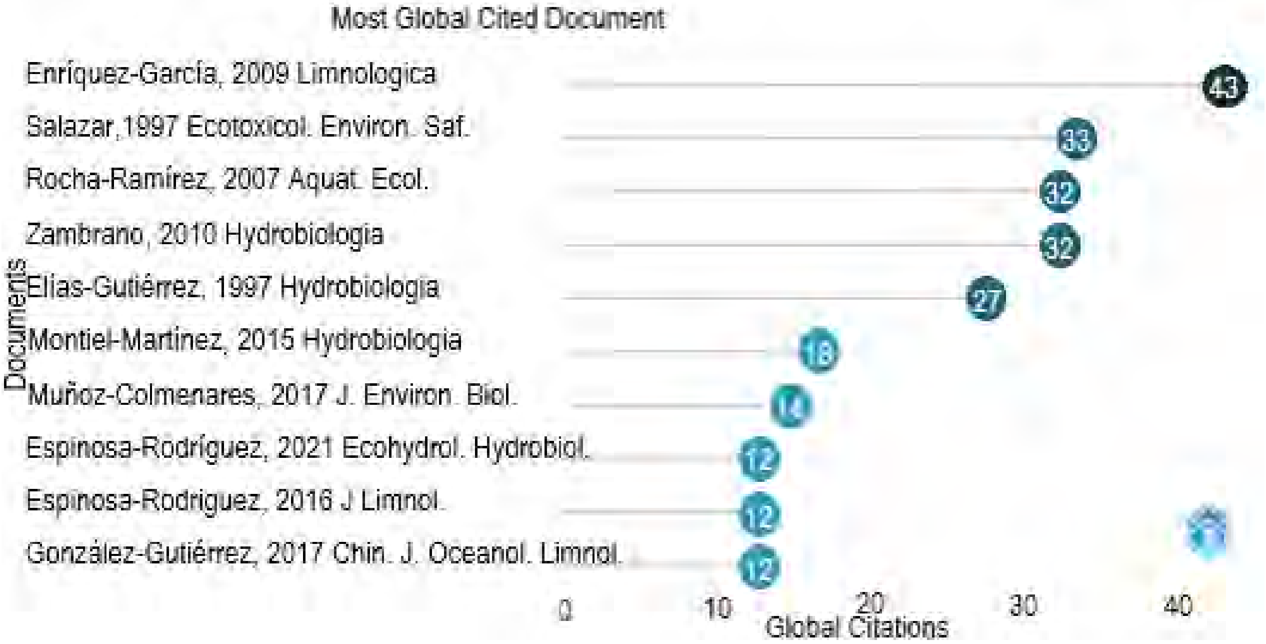

Figure 2. Documents with the Highest Number of Citations in the Area of Macrophytes and Zooplankton.

Figure 3 represents the Trend Topics through time and their temporal changes, 15 keywords with a high frequency of use and interest, mainly between 2010 and 2022. It is evident that certain topics were the subject of a more frequent study between 2010 and 2016 ("abundances" and "fish"), indicating a notable interest during that interval (articles from those years and the topics they address). Other topics, for their part, show an increase in their frequency of study between 2016 and 2018, suggesting a change in focus in research and an increase in the study and interest in the main topics of zooplankton and macrophytes ("*Daphnia*", "submerged macrophytes", "trophic state"). Additionally, a set of topics is identified that attracted notable attention between 2018 and 2022 ("diversity", "population growth", "zooplankton", "communities"), showing the progress in research where the interest in understanding natural phenomena passes through autoecology to the ecology of communities, suggesting interest in a holistic approach, not just a descriptive one. This temporal representation offers insight into research trends and changing focus on different topics across these observed periods.

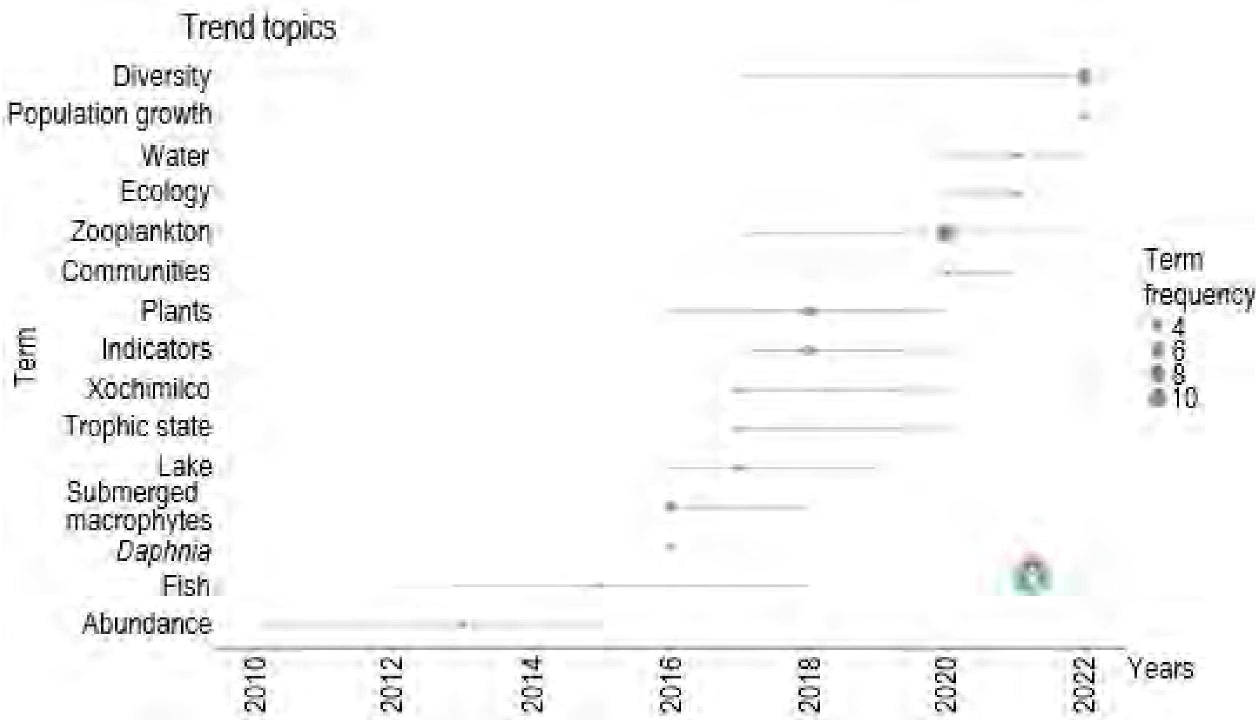

Figure 3. Topics and Their Trend in Relation to Publications Made in Mexico, Considering the Plus Keywords Provided in WoS Database.

The co-occurrence network analysis of the primary themes in Mexican literature related to zooplankton and macrophytes has revealed five distinct thematic groups (Fig. 4). The first group primarily focuses on zooplankton as a central theme. The second group highlights the interaction between fish and zooplankton evasion as relevant subtopics. In the third group, researchers address water diversity and quality, along with bioindicators, highlighting the link between these research areas. The fourth group mainly represents the predator-prey relationship in rotifers. Finally, the fifth group emphasizes the study of macrophyte coverage and geographic information systems, which is inclined towards technological approaches and integrated ecology. These findings provide a comprehensive understanding of the thematic interconnection in scientific research in conjunction with the above results, offering specific insights into biological dynamics in the aquatic environment.

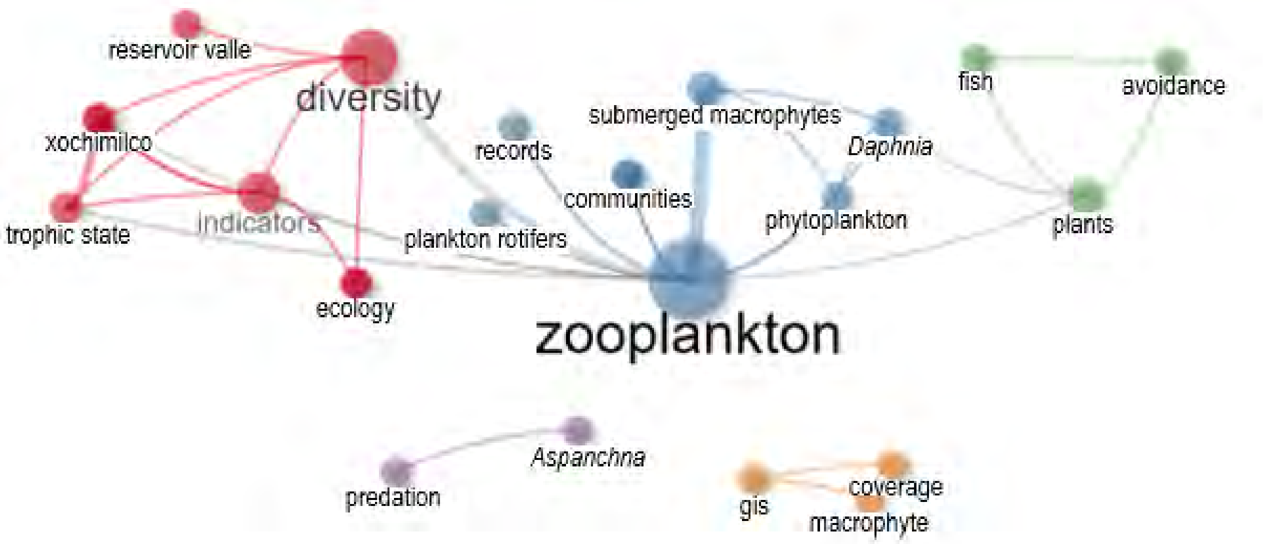

Figure 4. Network of Co-occurrence between the Dominant Themes of Focus in the Literature of Mexico.

The research on zooplankton and macrophytes in Mexican scientific literature shows a positive environment for collaboration, as evidenced by an average of 3.73 co-authors per document and 20 % of collaborations involving international co-authors (Table 1, Fig. 5). The collaboration network analysis reveals the presence of isolated clusters that reflect specialized scientific communities, varying in size from binary collaborations to groups with up to fifteen participants. Collaboration is crucial in scientific work, as well as in freshwater ecology, as it facilitates the convergence of diverse perspectives and skills, leading to the advancement of knowledge (Cullen et al., 1999). Identifying key actors and research producers in these groups enhances collaboration opportunities and promotes valuable synergy that contributes to the continuous progress of the scientific field. Collaboration among researchers establishes a breeding ground for exchange of ideas, access to funding, learning new skills, this promotes quality of results, which would be of great importance for this particular field of research conducted (Bansal et al. 2019).

Figure 5. Network Analysis of the Studies Distribution According to Authors in Mexican Literature in the Area of Macrophytes and Zooplankton.

Conclusion

This bibliometric work focused on the description of the ecological importance and scientific productivity related to the interaction of zooplankton and aquatic plants in Mexico, showing slow progress with limited diffusion of publication through the last decades with a limited finding due to indexation of articles. We found a current interest in research going from the autoecology and description approach to understanding the ecological interaction mechanisms at a community level in remarkable topics of diversity, water quality, predation, food webs, seasonal variation, allelopathy, and ecotoxicology with some opportunities in remote sensing, genomics, biogeochemical, climate change, biomanipulation, and conservation as challenges for future studies. The interaction between macrophytes and zooplankton has been observed to yield interesting and noteworthy phenomena. However, the current state of research and publication in this area needs collaborative and participative initiatives that can provide funding support. Such efforts will facilitate knowledge development, as well as the restoration and conservation of natural habitats. By enhancing our understanding of this phenomenon, we can better protect and conserve the environment.

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Authors' Contributions

JSMA conceptualization; JSMA drafting the initial manuscript; JSMA and FSMA methodology and data research; JSMA and FSMA data interpretation; JSMA and FSMA writing and editing the final manuscript.

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The Freshwater and Brackish Hydrozoans of Mexico: An Overview of their Diversity

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Abstract

Hydrozoans constitute a diverse cnidarian group with different morphologies and ecological strategies, occurring in all aquatic environments, including continental water bodies. The global diversity of freshwater hydrozoans has been scarcely addressed. The number of recognized species (~60) is substantially lower than other marine groups with continental representatives, such as sponges and crustaceans. The hydrozoan fauna of Mexico is relatively well known through inventories and recent studies on brackish and marine environments, although more effort is needed. Nevertheless, freshwater taxa are not included in the last checklists, leading to a gap in the understanding of the diversity of this group in Mexico. This chapter aims to provide an image of the diversity of freshwater and brackish-water hydrozoans in Mexico by reviewing 27 works that included hydrozoans recognized as inhabitants of these environments. Our search resulted in 15 taxa grouped into two subclasses, three orders, and seven families, of which Olindiidae was the richest. Seven taxa are recorded exclusively in freshwater environments, while eight are in lagoons, estuaries, or open oceans. Additionally, four hydrozoans are considered potentially invasive in other regions of the world, and few studies have monitored their populations in Mexico. Future perspectives in the study of freshwater hydrozoans include expanding research in freshwater environments and considering molecular tools for species identification.

Keywords

Medusozoa, Cnidaria, polyp, estuarine environment, biodiversity, Hydrozoa.

Introduction

The members of the class Hydrozoa constitute a diverse cnidarian group, including approximately 3,774 accepted species (Schuchert, 2024), which usually present a life cycle with a succession of different stages, including a larval, a benthic asexually reproducing polyp, and a sexually reproducing medusa (Santander et al., 2022). Nevertheless, several variants of this cycle exist in which the medusa may be absent or vice versa (Boero et al., 1992; Miglietta & Cunningham, 2012; Bentlage et al., 2018). Hydrozoans occur in diverse aquatic ecosystems, going from freshwater to hypersaline environments, and from the surface to the deepest regions of the oceans (Jankowski, 2001; Bentlage et al., 2018). Of the total hydrozoan species, few are representative of freshwater or brackish environments (Jankowski, 2001; Jankowski et al., 2008). For instance, only seven genera of Hydrozoa develop exclusively in freshwater environments, *i.e*., *Hydra* Linnaeus, 1758, *Craspedacusta* Lankester, 1880, *Limnocnida* Günther, 1893, *Astrohydra* Hashimoto, 1981, *Velkovrhia* Matjasic & Sket, 1971, *Halmomises* von Kennel*,* 1891, and *Calpasoma* Fuhrmann, 1939, comprising around 60 species (Deserti et al., 2023; Schuchert, 2024). On the other hand, there are more representatives of the brackish environments, such as some members of the orders Limnomedusae (*e.g.*, *Vallentinia* Browne, 1902, *Olindias* Müller, 1861, *Gonionemus* A. Agassiz, 1862), Anthoathecata (*e.g*., *Moerisia* Boulenger, 1908, *Odessia* Paspalew, 1937, *Cordylophora* Allman, 1844) and Leptothecata (*e.g*., *Blackfordia* Mayer, 1910) (Schuchert, 2024).

The success of freshwater and brackish hydrozoans involves diverse adaptations throughout their evolutionary history, such as the presence of solitary reduced polyps in Limnomedusae (an order of the subclass Trachylinae where most of its members lack this stage) (Bentlage et al., 2018), and the development of adhesive structures to attach to macroalgae or seagrasses, commonly occurring in estuaries (Ahuatzin-Hernández et al., 2020). Unfortunately, their study has been scarce compared to those inhabiting marine ecosystems (Jankowski, 2001; Deserti et al., 2023), so taxonomy, evolutionary history, and ecological aspects of some of these taxa are poorly known (Jankowski, 2001). The knowledge regarding freshwater hydrozoans from Mexico is limited since most studies focus on new records or behavioral experiments (*e.g*., Moreno-Leon & Ortega-Rubio, 2009; Rivera-de la Parra et al., 2016). Despite more effort needed, brackish species are better known in the country since they are included in taxonomical and ecological studies conducted in estuaries or coastal lagoons (*e.g*., Álvarez-Silva et al., 2006; Ahuatzin-Hernández et al., 2020; Ocaña-Luna et al., 2021).

The number of studies concerning brackish-water environments in Mexico in the last years is comprehensive, likely due to some advantages of these environments, such as easy access and cheaper sampling costs (*e.g*., Sarma et al., 2000; Hendrickx et al., 2007; Castellanos-Osorio, 2009; Benítez-Díaz Mirón et al., 2014; Ahuatzin-Hernández et al., 2020). A similar scenario happens with the freshwater biota of Mexico, which shows a progressive advance in the knowledge of the main taxonomic groups over the years (Calderón-Gutiérrez et al., 2017; Álvarez et al., 2023; Cervantes-Martínez et al., 2023). However, hydrozoans are not considered in these works, which could be associated with the benthic behavior of some tiny taxa (*Hydra*) and the seasonal fluctuation between polyp and medusae stages (*e.g.*, *Craspedacusta*, *Moerisia*). Moreover, recent inventories about the medusozoans of Mexico do not include freshwater taxa, which represents a gap in the knowledge of this group (Segura-Puertas et al., 2003; Gasca & Loman-Ramos, 2014; Estrada-González et al., 2023).

Faunistic inventories are fundamental to improving the knowledge of the biodiversity of a region, which is necessary for applying good management of natural resources and conservation strategies (Cervantes-Martínez et al., 2023; Deserti et al., 2023). This task represents a challenge for a megadiverse country such as Mexico, so integrating dispersed literature about a taxonomic group allows us to improve the knowledge about that taxon, identifying gaps in the information, and recognizing future research fields. Herein, we gathered available published literature about freshwater and brackish-water hydrozoans from Mexico in order to provide a comprehensive picture of the state of the art and their biodiversity.

The information was integrated by reviewing available published literature, considering academic databases, such as Scholar Google, Scopus/Elsevier, ScieLO, and Web of Science/Clarivate, using keywords such as “Hydrozoa”, “freshwater”, “brackish-water”, “Mexico”, “medusa”, “polyp”, “anchialine fauna”, “Cnidaria”, both in Spanish and English. The information was assessed using the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-analysis) protocol (Page et al., 2021). The name of the taxa was cross-checked with WoRMS (marinespecies.org; April 2024) and GBIF (Global Biodiversity Information Facility) to retrieve additional occurrences and correct synonyms, invalid species, and typing errors. In addition, we identified non-native species based on the information provided in the literature, which could be useful for future monitoring of the impacts that these species could exert on native populations.

Species Diversity

We found 27 works containing information about freshwater or brackish hydrozoans, resulting in 15 taxa grouped into two subclasses, three orders, and seven families (Table 1). The order Anthoathecata grouped nine taxa, distributed into five families, whereas Leptothecata was represented by one species. The order Limnomedusae was represented by five species grouped into one family. Seven of the 15 taxa were exclusively recorded in freshwater bodies, representing ~11.6 % and ~50 % of the worldwide and Neotropical freshwater known hydrozoans, respectively (Deserti et al., 2023; Schuchert, 2024). Five of the seven freshwater taxa were recorded in the polyp stage and two in the medusa stage. Family Olindiidae was the richest, matching previous studies (Jankowski, 2001) and supporting the hypothesis of independent origin in freshwater hydrozoan groups. This hypothesis states Olindiidae as the most diverse freshwater cnidarian group (Jankowski et al., 2008), suggesting an older origin of this taxon as representative of freshwater medusozoans. *Pachycordyle* Weismann, 1883 was not considered in the literature of the Neotropical region (Deserti et al., 2023), so we add this genus to the knowledge of the diversity of this group. This taxon was recorded in a reef lagoon in the Mexican Caribbean (Ramos & Segura-Puertas, 2004).

Table 1. Freshwater and Brackish-water Hydrozoans Recorded in Mexico. P=Polyp, M=Medusa, F=Freshwater, B=Brackish, O=Ocean.

Taxa	Morphology	Environment	Locality	Invasiveness	References
Subclass Hydroidolina Collins, 2000 Order Anthoathecata Cornelius, 1992 Suborder Aplanulata Collins, Winkelman, Hadrys & Schierwater, 2005 Family Hydridae Dana, 1846					
Hydra sp.	P	F	San Luis Potosi, State of Mexico		Osorio-Tafall, 1943; Zagmajster et al., 2011; Rivera-de la Parra et al., 2016
Hydra vulgaris Pallas, 1766	P	F	State of Mexico, Aguascalientes, Chihuahua		Marroquín-Cardona et al., 2009; Oseguera et al., 2016; Armas-Chávez et al., 2022; GBIF
Hydra viridissima Pallas, 1766	P	F	Nuevo León, State of Mexico, México City, Michoacán		Deserti et al., 2023 (Retreived from iNaturalist); Retrieved from iNaturalist through GBIF
Hydra oligactis Pallas, 1766	P	F	State of Mexico		Deserti et al., 2023 (Retreived from iNaturalist)

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Suborder Filifera Kühn, 1913					
Family Bougainvilliidae Lütken, 1850					
Nemopsis bachei L. Agassiz, 1849	M	B/O	Laguna Madre and Open Ocean (Tamaulipas),		Mendoza-Becerril et al., 2009; Gutiérrez-Aguirre et al., 2015
Pachycordyle sp.	M	B	Puerto Morelos (Quintana Roo)		Ramos and Segura-Puertas, 2004
Family Cordylophoridae von Lendenfeld, 1885					
Cordylophora caspia (Pallas, 1771)	P	F	Mandinga Lagoon (Veracruz), Nuevo León	X	Rioja, 1959; Guajaro et al., 1987; López-Ochoterena and Madrazo-Garibay, 1989
Family Hydractiniidae L. Agassiz, 1862					
Cnidostoma fallax Vanhöffen, 1911	M	B	Acapulco Bay (Guerrero)		Guerrero-Ruíz et al., 2015
Suborder Capitata Kühn, 1913 (sensu stricto)					
Family Moerisiidae Poche, 1914					
Moerisia inkermanica Paltschikowa-Ostroumowa, 1925	M	F	In Ballast Water of Tankers Loaded at Cayo Arcas Oil Terminal (Campeche)	X	Ahuatzin-Hernández et al., 2024
Order Leptothecata Cornelius, 1992					

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Family Blackfordiidae Bouillon, 1984					
Blackfordia virginica Mayer, 1910	M	B	Tampamachoco and Pueblo Viejo Lagoons (Veracruz), Lagunar System Chantuto-Panzacola (Chiapas)	X	Esquivel et al., 1980; Álvarez-Silva et al., 2003, 2006; Ocaña-Luna et al., 2021
Subclass Trachylinae Haeckel, 1879					
Order Limnomedusae Kramp, 1938					
Family Olindiidae Haeckel, 1879					
Craspedacusta sowerbii Lankester, 1880	M	F	Sinaloa, Nuevo León	X	Guajardo et al., 1987; Moreno-Leon and Ortega-Rubio, 2009
Cubaia aphrodite Mayer, 1894	M	B	Ascensión Bay, Puerto Morelos, Bojórquez lagoon, Mahahual reef, Chinchorro Bank (Quintana Roo)		Canché-Canché and Castellanos-Osorio, 2005; Segura-Puertas and Damas-Romero, 1997; Suárez-Morales et al., 1999; Gasca et al., 2003; Ramos and Segura-Puertas, 2004
Octobulbacea brachymera (Bigelow, 1909)	M	O	Open Ocean (Tamaulipas), Acapulco harbor (Guerrero)		Bigelow 1909; Gutiérrez-Aguirre et al., 2015
Olindias tenuis (Fewkes, 1882)	M	B	Ascensión Bay, Bojórquez Lagoon (Quintana Roo)		Canché-Canché and Castellanos-Osorio, 2005; Segura-Puertas and Damas-Romero, 1997
Vallentinia gabriellae Vannucci Mendes, 1948	M	B	Costal Lagoon in Progreso, Bocas de Dzilam (Yucatan), Puerto Morelos, Bojórquez Lagoon (Quintana Roo)		Foster, 1973; Segura-Puertas and Damas-Romero, 1997; Ramos and Segura-Puertas, 1997; Ahuatzin-Hernández et al., 2020

Eight brackish hydrozoans were recorded either in lagoons, estuaries, or open ocean, mainly in the Gulf of México and the Mexican Caribbean. Coastal environments of Mexico are characterized by the strong influence of freshwater, mainly in the coastal lagoons of the Yucatan peninsula (Herrera-Silveira & Morales-Ojeda, 2010; Camacho-Ibar & Rivera-Monroy, 2014), causing mixing zones where marine and freshwater biotas are found. The eight brackish taxa were recorded in the medusa stage, likely due to most studies conducted in coastal environments focusing on zooplanktonic organisms, so benthic representatives fell out of the scope of the traditional zooplanktonic methods.

Most brackish medusae reported here belong to Limnomedusae and Anthoathecata, being characterized by a metagenetic life cycle, alternating a benthic polyp and a free-swimming medusa. In Limnomedusae, a mostly neritic group of the subclass Trachylinae, a reduced polyp is present, which represents an adaptation to inhabit coastal environments. This fact is evident since other trachylines inhabiting the open ocean develop from zygote to medusa via a free-swimming larva, lacking the polyp stage (Bentlage et al., 2018; Ahuatzin-Hernández et al., 2023). The polyp represents a derived character (novelty) in the evolution of Hydrozoa (Cartwright & Nawrocki, 2010), providing several advantages in the adaptation and colonization of new habitats, either by producing cysts resistant to environmental changes (longer life spans) or attaching to vagile substrates, driving long distances (dispersal).

Fifteen states of Mexico, either in continental or coastal environments, recorded hydrozoans. The states of Mexico and Quintana Roo showed the richest composition, while nine states only presented one taxon (Fig. 1). The diversity of freshwater hydrozoans of Mexico is poorly known. For instance, conventional inventories of medusozoans leave out the freshwater representatives (Segura-Puertas et al., 2003; Gasca & Loman-Ramos, 2014; Estrada-González et al., 2023), and those works addressing the freshwater diversity of Mexico don't consider hydrozoans in their scope (*e.g.*, Álvarez et al., 2023; Cervantes-Martínez et al., 2023; Gómez-Marín et al., 2024). This fact contrasts with investigations on coastal hydrozoans, which have been constant in recent years (*e.g.*, Canché-Canché & Castellanos-Osorio, 2005; Ahuatzin-Hernández et al., 2020; Mendoza-Becerril et al., 2020). The gap in the knowledge of freshwater hydrozoans biases the understanding of the diversity of both medusozoans and continental biota in Mexico, so more research in this sense is needed.

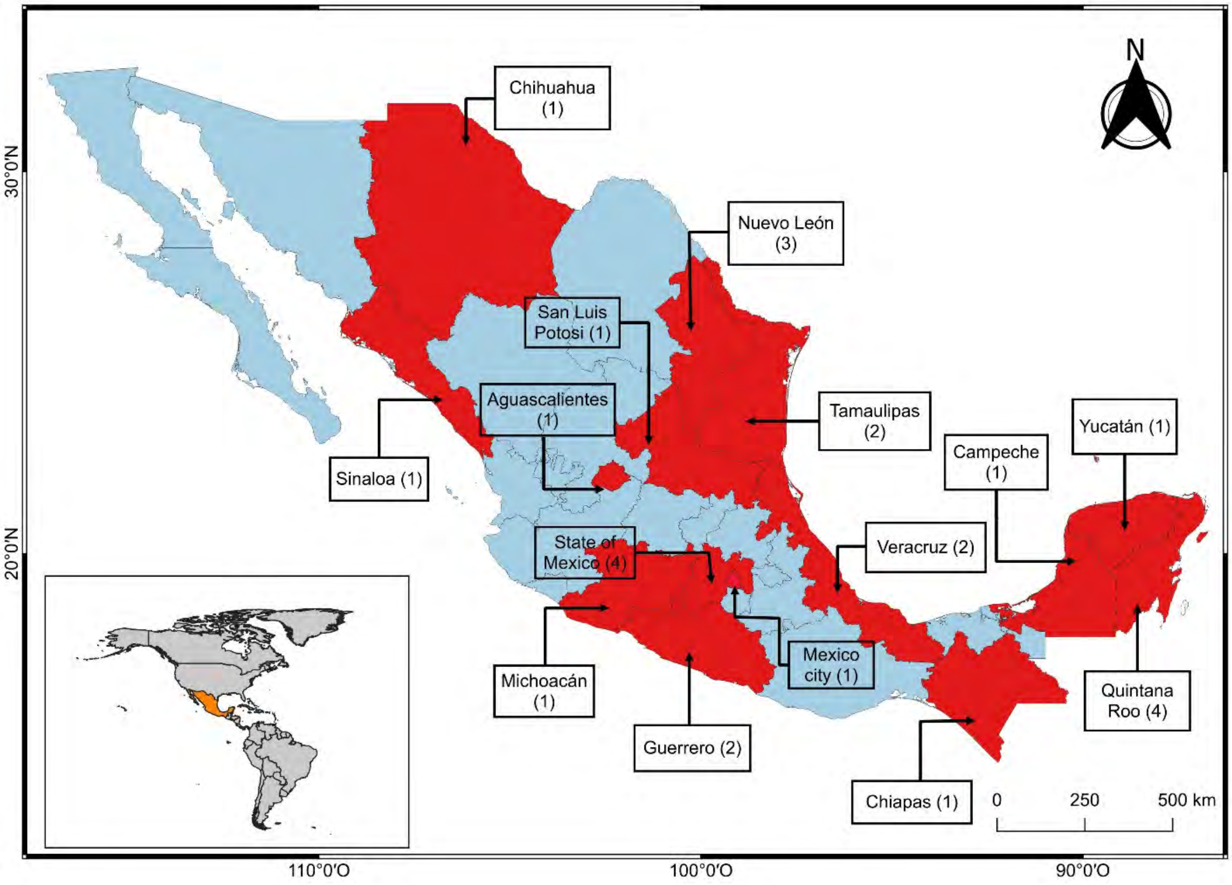

Figure 1. Mexican States with the Presence of Freshwater or Brackish-water Hydrozoans. The Number of Species per State Is Indicated in Parentheses.

Invasive Species

Four of the 15 hydrozoans are considered non-native based on literature records, *i.e.*, *Cordylophora caspia* (Pallas, 1771), *Moerisia inkermanica* Paltschikowa-Ostroumowa, 1925, *Blackfordia virginica* Mayer, 1910, and *Craspedacusta sowerbii* Lankester, 1880. In the case of *M. inkermanica*, and *B. virginica*, recorded in brackish environments, the introduction in other regions of the world is attributed to maritime transport through the ballast water or biofouling (Nowaczyk et al., 2016; Ahuatzin-Hernández et al., 2024). The presence of these and other non-native species in the aquatic environments of Mexico encourages attention to the application of protocols that regulate the management of this type of water since it is one of the main vectors of invasion (Okolodkov et al., 2007; Okolodkov & García-Escobar, 2014).

On the other hand, the introduction pathways might be different regarding *C. caspia* and *C. sowerbii*, both recorded in continental water bodies. In this sense, a migratory route hypothesis by aerial dispersion due to bird migration is supported by observational evidence in *C. sowerbii* (Marchessaux et al., 2021). In this case, the role of the polyp stage, which is drought-resistant, is crucial for the long-transport success. A similar scenario may happen with *C. caspia*, recorded in freshwater and brackish-water environments of Mexico on multiple occasions (Rioja, 1959; Guajaro et al., 1987; López-Ochoterena & Madrazo-Garibay, 1989), which suggests its establishment in the country, yet more research on the distribution of this species in Mexico is needed. Of the species treated here, only *C. caspia* is reported in the lists of non-native aquatic species of Mexico (Okolodkov et al., 2007). Therefore, this study adds three species to the knowledge of non-native hydrozoans in the country and encourages us to continue exploring continental and brackish-water ecosystems where other unrecorded species may occur.

What do We Know about the Freshwater Hydrozoans of Mexico?

The knowledge about the freshwater hydrozoans of Mexico is scarce in many senses. The known number of species is likely underestimated due to the lack of research on this group. In addition, the taxonomy and evolution of the known taxa is also limited. In recent years, studies considering molecular data have shown that species previously considered cosmopolitan (*Hydra*, *Craspedacusta*, and *Cordylophora*) represent groups of species geographically delimited (*e.g*., Martínez et al., 2010; Schwentner & Bosch, 2015; Oualid et al., 2019; de Paula et al., 2024). However, studies conducted in Mexico regarding these taxa do not include molecular data or a suitable morphological analysis, so their taxonomic identity is uncertain.

The most studied genus of Mexico from freshwater environments is *Hydra*. Studies use it as a biological model to understand the effects of predation and the characterization of mycotoxins (Marroquín-Cardona et al., 2009; Rivera-de la Parra et al., 2016). Nevertheless, little is known about the relationship of this and other freshwater taxa with environmental variables. This fact leads to a gap in the knowledge of the ecology of these taxa. Thus, in the case of invasive species, their monitoring and prediction of further impacts on native populations is complicated.

More efforts are needed to improve the knowledge about the freshwater hydrozoans of Mexico. First, studies considering integrative taxonomy approaches are crucial to assigning an accurate identity to the Mexican taxa. Only then aspects related to the ecology of the species might shed light on their trophic relationships. Finally, these research lines could be integrated into an evolutionary frame to address issues such as biogeography, evolution, and distribution expansion by climate change through distribution models.

Conclusions

The diversity of freshwater hydrozoans in Mexico has been overlooked over the years. In contrast, brackish hydrozoan diversity is better known due to constant research efforts in coastal environments. Four species are considered non-native; however, few works have monitored their distribution patterns and potential impact on native populations. Future perspectives on freshwater hydrozoans encompass global and local challenges. Hence, more research efforts are needed locally since other unrecorded species might occur in unexplored continental ecosystems. Due to a metagenetic life cycle involving benthic and planktonic stages, studies should include methodologies considering both types of environments.

Relevant topics with little information about Mexican freshwater hydrozoans include taxonomy, ecology, and potentially biotechnology. For example, *Hydra*, *Craspedacusta*, and *Cordylophora* have proved cryptic speciation, but Mexican records usually assign specimens to the type species, which are currently considered species complexes (Martínez et al., 2010; Schwentner & Bosch, 2015; Oualid et al., 2019; de Paula et al., 2024). The feeding and trophic ecology of *Hydra* has been studied in Mexico and other regions of the world (Rivera-de la Parra et al., 2016; Deserti et al., 2017; Morales et al., 2018). However, these aspects remain unexplored for the rest of the freshwater hydrozoans of Mexico, which are fundamental to knowing their ecology, mainly for those non-native ones. Finally, *Hydra* is one of the most widely implemented taxa as a biological model, being the basis of several studies concerning toxicology, regeneration, proteomics, and aging (*e.g.*, Mocz, 2007; Galliot, 2013; Tomczyk et al., 2015; Murugadas et al., 2019), yet these approaches have not been implemented in the Mexican species. Addressing these lines would be crucial since it might change our view about the diversity of this group, recognizing new cryptic species distributed in the country, the potential impacts of those non-native ones, and their use as sources of natural compounds.

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Authors' Contributions

JMAH and LVLD conceptualized the idea. JMAH reviewed the literature and conducted the analysis. Both authors read and approved the final version of the manuscript.

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Aquatic Macroinvertebrates Diversity in the Grijalva and Usumacinta Rivers, Mexico

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Abstract

Aquatic macroinvertebrates are important and abundant components of the aquatic ecosystem, they transfer energy to higher trophic levels and can be used as bioindicator of aquatic ecosystem condition. The diversity of macroinvertebrates was determined through multihabitat diurnal sampling in three sections and five sites per section in the Grijalva and Usumacinta rivers, covering dry, rainy, and northern wind seasons. 75,482 individuals were recorded corresponding to 79 families, 128 genera, and 140 species, six species of mollusks, 11 of insects, and four of crustaceans for the Grijalva, and 17 of mollusks, 44 of insects, and 9 of crustaceans for Usumacinta were exclusive. The invasive mollusks *Tarebia granifera, Corbicula fluminea,* and *Melanoides tuberculata* accounted for 89.8 and 60.1 % of the abundance for the Grijalva and Usumacinta rivers. The maximum diversity values were in Lacantún section (Usumacinta) (H’=4.49, J’=1.14, D=1 and Margalef 22.76), and seasonally in northern winds (H’=3.42, J’=0.85 and Margalef 15.19), meanwhile, dominance was in dry (D=0.93). The dominant trophic groups were scrapers (74 %) and filter feeders (11 %), with maximum values in the Ostitán section (Grijalva) in rainy season. The collectors (10 %) were present in four sections, with the maximum value in the Tres Brazos section (Usumacinta) in the dry season. However, environmental variation reflects changes in the diversity of macroinvertebrates due to the function of these tropical rivers and their dependence on natural variation, hydraulic connectivity, and flow regulation. It is the first study that addresses the diversity of macroinvertebrates (three taxonomic groups) in two of the largest rivers in the country with contrasting ecohydrological conditions.

Keywords

Macroinvertebrates, diversity, wetlands, Grijalva-Usumacinta basin

Introduction

Aquatic macroinvertebrates (mollusks, crustaceans, and insects) are an important component in aquatic ecosystems for their abundance, in addition to being the intermediate link between primary producers and consumers, where their role as transformers and integrators of organic matter is relevant in the energy flows of the river systems (Barba-Macías et al., 2000). Mollusks, a group of marine origin, have a wide distribution and are associated with different types of habitats such as soft bottoms, logs and aquatic vegetation (Naranjo-García and Olivera-Carrasco, 2014). Furthermore, it is well known that, some bivalves are consumed in the lower basin of the Usumacinta River (Pantanos de Centla Biosphere Reserve), such as *Potamilus alatus* (Say, 1817), *Cyrtonaias tampicoensis* (Lea, I., 1839), *Pyganodon grandis* (Say, 1829), *Rangia cuneata* (Sowerby ł, 1832), and *Pomacea flagellata* (Say, 1829). Other species such as *P. flagellata, Vitta usnea* (Röding, 1798), *Neritina virginea* (Linnaeus, 1758), *Biomphalaria obstructa (havanensis)* (Morelet, 1849), and *Rangia cuneata* are used as indicators of moderately or uncontaminated environments (Naranjo-García & Meza-Meneses, 2000). While, the invasive species *Melanoides tuberculata* (Müller, 1774), *Tarebia granifera* (Lamarck, 1816) and *Corbicula fluminea* (Müller, 1774) have been recorded with high abundances and probably generate an imbalance in the biodiversity of the aquatic environments that they colonize (Naranjo-García & Meza-Meneses, 2000; Cruz-Ascencio et al., 2003; Albarrán-Melzer et al., 2009; Sánchez et al., 2012; Barba-Macías & Trinidad-Ocaña, 2017).

On the other hand, 89 % of the recorded crustacean species are of marine origin, 10 % are freshwater, and 1 % are terrestrial (Álvarez et al., 1996). Crustaceans inhabit a variety of substrates such as muddy bottoms, logs, submerged, floating, and emerging aquatic vegetation. These organisms play an important role in energy transfer to higher trophic levels (Barba-Macías et al., 2000). Species such as: *Macrobrachium* spp. (Camacho-Sánchez, 2007), *Hyalella azteca* (Keithly et al., 2004), *Mysidopsis bahia* (Raz-Guzmán, 2000) are used as indicators of water quality (Álvarez et al., 1996; Cumberlidge et al., 2009; Schertzinger et al., 2018). Furthermore, within this group, penaeid shrimp, carideans, and crabs are important in commercial and coastal fishing, and contribute 1.4 % of national production (CONAPESCA, 2013).

Aquatic insects are distributed in a wide variety of ecosystems, such as streams, rivers, lakes, etc., and their distribution depends on the concentration of dissolved oxygen and water temperature (Bass, 1995; Castella et al., 2001; Li et al., 2001; Sullivan et al., 2004), and water chemistry, including pH, salinity, and concentrations of ions or elements, as well as the presence of riparian vegetation (Subramanian et al., 2005). This group has been widely used as a bioindicator, where various authors with studies in temperate and tropical regions have found that the diversity and richness of species decreases in areas impacted by human activities (Stone & Wallace, 1998; Ometo et al., 2000; Benstead et al., 2003), in addition to presenting channels with a lack of boulders and the presence of terrigenous sediment, which drastically reduces the availability of niches and, as a consequence, a decrease in diversity (Allan et al., 1997). There are also other factors that, to a lesser extent, explain the structure and composition of the aquatic entomofauna, such as seasonal patterns (Miserendino & Pizzolon, 2003; Waite et al., 2004; Sporka et al., 2006; Joshi et al., 2007).

The Grijalva-Usumacinta basin (GUB) is characterized by its high-water wealth and biodiversity, in addition to contributing 30 % of the country's total surface runoff (García-García and Kauffer-Michel, 2011; Cruz-Paz et al., 2018). Previous studies have focused on the Usumacinta basin: mollusks and crustaceans (Trinidad-Ocaña et al., 2018) and insects for mountain areas of Tabasco (Benítez-Abud et al., 2016). However, the increase in anthropogenic activities causes greater pressure on the system due to the modification of land use (Kolb & Galicia, 2012), with the consequent decrease in riparian vegetation and an increase in the discharge of untreated wastewater, these affect water quality (Laino-Guanes et al., 2016). Therefore, records of invasive non-native species are increasingly frequent in the Grijalva-Usumacinta basin (Cruz-Ascencio et al., 2003; Rangel-Ruiz et al., 2011; Barba Macías et al., 2014).

This contribution analyzes the diversity of aquatic macroinvertebrates in two basins with contrasting hydrological conditions, a dammed river (Grijalva), and one with free flow (Usumacinta) and if there are significant differences between sites and between basins, depending on the state of the ecological quality of the banks and the natural flow of the river expressed in better hydrological conditions, high values of riparian quality, high species richness, abundance, and biomass in relation with altered and unaltered river functionality.

Materials and Methods

Study Area

The study area includes hydrological region number 30 (RH30) formed by the Grijalva and Usumacinta rivers, both rivers make up the largest hydrological basin in México (Conagua, 2014). Its runoff area is 112,500 km^2 and represents 4.2 % of the continental national territory (Andrade-Velázquez & Medrano-Pérez, 2020), with a discharge of 4,500 m^3/s, occupying second place in discharge to the Gulf of México after the Mississippi with an annual discharge of 18,000 m^3/s (Yàñez-Arancibia et al., 2009; Sánchez et al., 2015). Both rivers are transboundary, they originate in Guatemala and cross the states of Chiapas and Tabasco in Mexico and converge on the coastal plain of Tabasco providing conditions for extensive wetland areas that mainly make up the Pantanos de Centla Biosphere Reserve (Barba-Macías et al., 2006; Conagua, 2014). The climate of the region is generally composed of three climatic groups: the warm-humid ones with approximately 93.5 % of the territory are temperate-humid with 6.3 % and a small portion of dry climate (Conagua,2014).

The Usumacinta River annually transports around 59,397 hm^3 (including the contribution of the San Pedro River), its flow represents the largest contribution of water to the Laguna de Términos and the Pantanos de Centla Biosphere Reserve (PCBR) (Soria-Reinoso et al., 2022), this river does not have dams. While the Grijalva River is one of the largest rivers in the country, it annually transports a volume of 27,013 hm^3 and, in the rainy season, its flow increases. For this reason and to take advantage of the waters flow of this river, it was dammed with a system of four hydroelectric dams at the end of the 60's (Netzahualcóyotl, La Angostura, Chicoasén and Peñitas) (Conagua, 2014).

Three study areas were selected for each river, considering its main environmental, hydrological and ecological characteristics according to regulatory appendix F of the Ecological Flow Standard (MNX-AA-159-SCFI-2012), where Flow Study Units were determined. Ecological, which consists of the scale of analysis in the territory of the basin. These evaluation units refer to surface water bodies (rivers, lakes, lagoons, or other wetlands) or part of them in the same hydrological basin and that have the same hydrological regime to which an environmental objective is assigned. These were validated by a panel of experts before the selection of reference areas. The areas chosen in the Usumacinta River were Lacantún, Jonuta, and Tres Brazos, while for the Grijalva River they were Amacohite, Ostitán, and Chilapa, in each study area five sampling sites were selected.

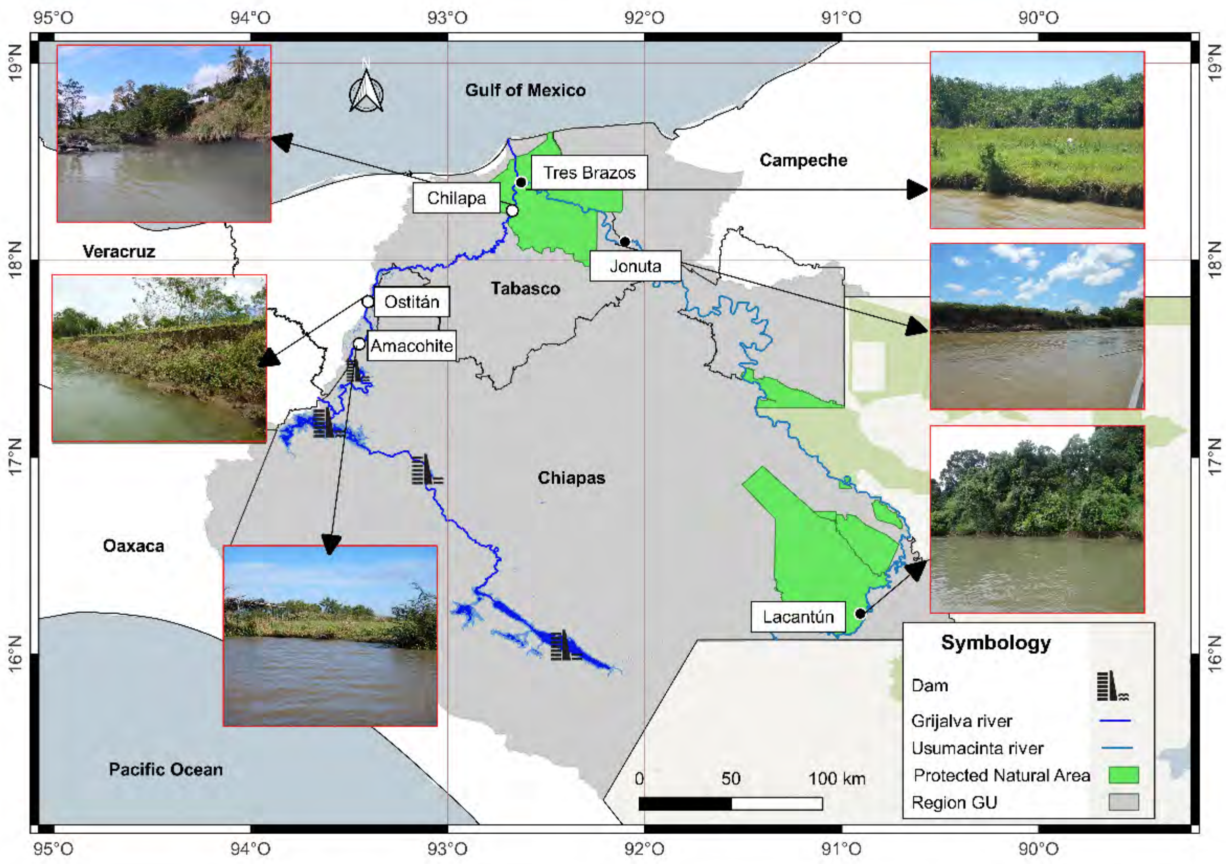


Figure 1. Sampling Sections of Grijalva and Usumacinta Rivers (Modified from Miranda-Vidal et al., 2023).

Ecological quality of the riverbanks at each selected site was evaluated using the Riverbank Quality Index (RQI) according to Miranda-Vidal et al. (in press), where seven attributes described in the protocol were evaluated; 1) riparian space (width) occupied by vegetation associated with the river, 2) longitudinal continuity of vegetation, 3) composition and structure of woody vegetation, 4) natural regeneration, 5) condition of banks, 6) transversal connectivity, and 7) vertical connectivity (González del Tánago et al., 2006; González del Tánago & García del Jalón, 2011) (Annex. 1).

Sampling

Samples were collected in the rainy season (wettest period of the year; 950 mm of precipitation), "northern winds" (locally known as "nortes", a condition where polar masses cross the Gulf of Mexico; 660 mm) and dry season (driest and hottest period of the year; 270 mm) (Ayala-Pérez et al., 2021; Cardoso-Mohedano et al., 2022) of an annual cycle of 2017-2018. At each site, the physicochemical parameters of the surface water were recorded using a Hanna HI9829 multiparameter for: temperature (°C), pH, dissolved oxygen (DO) (mg/L), conductivity (mS/cm^{-1}), total dissolved solids (TDS) (mg/L) and salinity (ups).

Aquatic macroinvertebrates were collected following the Macroinvertebrate Sampling Protocol in continental waters for the application of the Ecological Flow Standard (NMX-AA-159-SCFI-2012). The biological collection material was carried out through a multihabitat approach with various collector equipment's. For infauna, a nucleator with an area of 0.0044 m^2 was used (in rivers and shallow wetlands) and a Petite Ponar dredge with an area of 0.025 m^2 in rivers more than 2.5 m deep. Epifauna was collected with different types of nets: dip net with a mesh size of 500 microns and an area of 0.082 m^2, Renfro beam trawl net with a mesh size of 1 mm and an area of 2 m at the mouth with trawls of 25 m in length covering an area of 50 m^2, seine net 15 m in length, with a mesh size of 1 cm on the sides covering four meters on each side and a 2 mm mesh size in the center in a length of 7 m and a drop of 2.20 m covering 62 m^2. The use of each sampling equipment must be in accordance with the depth of the body of water and the conditions present in each location; at least three replicas must be taken per equipment used. All organisms were preserved in a plastic bag with 96 % alcohol.

Analysis

The organisms were identified, counted and weighed; identification was carried out to the lowest possible taxonomic level with various taxonomic keys for mollusks using Burch and Cruz-Reyes (1987), Thorp and Covich, (1991) and Hershler and Thompson (1992). For crustaceans were used: Bousfield (1972), Chace (1972), Felder (1973), Williams (1984), Pennak (1978), Throp and Covich (1991), Raz Guzmán et al. (1992), and Raz-Guzmán and Sánchez (1996). The insects were identified using the keys from: Wiggins (2000), Merritt et al. (2008), and Bueno-Soria (2010).

These organisms were assigned to food groups according to their trophic specialization. Eight trophic groups were determined following categories proposed by Cummins and Klug (1979), Merritt and Cummins (1996), Liévano and Ospina (2007) and Tomanova et al. (2006). From these, Herbivores (H) that feed on aquatic vascular plants or filamentous algae, Omnivores (Om) that feed on diverse types of food, Collector-Shredders (C-Sh) that feed on coarse particulate organic matter, Scrapers (Ra) that are herbivores and feed on algae or microbes attached to rocks or other substrates, Gatherers (Ga) that consume fine particulate organic matter, Filter feeders (Ff) which is a special group of collectors that filter in the water column, Predators (P) that feed on other living organisms and Shredders (Tr) are organisms that cut or chew pieces of living or dead plant material, including all plant parts like leaves and wood.

Abundance and weight data were standardized to density (org/m^2) and biomass (g/m^2). Diversity indices H' Shannon (Shannon and Wiener, 1963), species richness (D) of Simpson (1949) and evenness (J') of Pielou (1966) were applied; the indices were calculated with the statistical package PAST version 2.17c (Hammer et al., 2001).

Results

Environmental Description

Riparian quality of the Usumacinta River showed a gradient of riverbank quality ranged from very good (scores of 139) at the Lacantún site to Tres Brazos (classified as poor score 41), while at Grijalva, the evaluation of riverbank quality ranged from moderate with scores of 70 and 73 (Chilapa and Amacohite sites, respectively), to poor in Ostitán site (score of 58) (Annexe 1). In Grijalva, sampling sites revealed that the attributes of the riverbank are degraded and altered in their functioning. Temperature was uniformly in both basins with values between 23 and 30°C, the minimum value being recorded in the Amacohite section. Sections corresponding to Grijalva basin (GB) recorded lower values of conductivity and total dissolved solids than those of Usumacinta basin (UB), but the minimum record was from the Amacohite section for conductivity (166.69 mScm^{-1}) and 132.62 ppm to total dissolved solids (TDS) for the Chilapa section. Because they are freshwater environments, salinity is very low with records less than 1 ups. Dissolved oxygen registered values greater than 4 mg/L in the sections of both basins, the minimum value being recorded in the Jonuta section which registered 4.29 mg/L in the dry season (Table 1). However, data recorded corresponds to acceptable values for aquatic life.

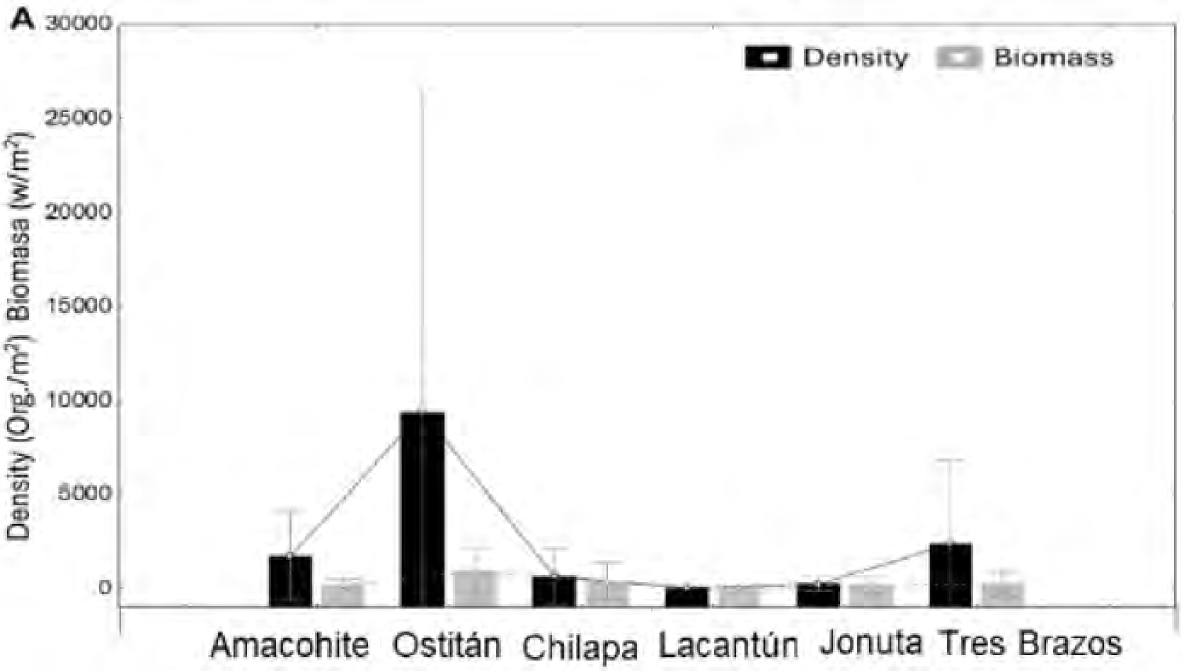
Table 1. Average Value of Physicochemical Parameters per Section and Season Sampling Areas of the Usumacinta and Grijalva Basin. R: Rainy, N: Northern Winds, D: Dry, Tr: Transparency, T: Temperature, OD: Dissolved Oxygen, TDS; Total Dissolved Solids.

Basin	Section	Season	Depth (m)	Tr (m)	T (°C)	pH	OD (mg/L)	Salinity (ppm)	Conductivity (mScm-1)	TDS (ppm)
Grijalva	Amacohite	N	1.73	0.62	23.35	4.49	5.15	0.1	166.69	138.89
		R	1.73	0.62	30.02	7.24	4.81	0.17	368.20	184.80
		D	1.72	0.62	27.97	10.14	8.33	0.17	361.70	180.90
	Ostitán	N	1.3	0.68	26.37	9.55	6.5	0.12	319.40	159.70
		R	1.23	0.68	29.87	7.39	4.93	0.2	360.20	219.20
		D	1.27	0.68	27.96	11.61	8.11	0.18	372.93	186.43
	Chilapa	N	2.53	0.33	25.4	7.55	4.64	0.15	265.25	132.63
		R	2.53	0.33	31.49	7.58	5.34	0.17	471.10	235.60
		D	2.53	0.33	27.58	9.73	8.05	0.11	429.60	214.60
Usumacinta	Lacantún	R	1.08	0.36	24.99	8.24	7.02	0.2	417.37	208.75
		D	0.57	0.58	26.26	9.76	10.01	0.32	653.26	326.66
	Jonuta	N	0.77	0.26	29.76	8.26	6.3	0.15	385.50	193.00
		R	1.8	0.54	28.68	7.99	5.66	0.16	384.50	192.25
		D	1.1	0.55	27.93	8.48	4.29	0.19	660.50	330.00
	Tres Brazos	N	1.9	0.3	30.31	7.99	6.73	0.24	377.13	188.75
		R	1.86	0.43	28.81	7.74	4.64	0.18	575.75	326.87
		D	1.83	0.58	28.65	8.64	4.3	0.94	1488.14	744.00

Aquatic Macroinvertebrates

A total of 75,482 individuals corresponding to 79 families, 128 genera, and 140 species were collected. GB recorded 44 families, 60 genera, and 66 species, nine species of crustaceans were recorded (4,918 indiv.), 33 insect genera were recorded (317 indiv.), and for mollusks with 24 species (50,110 indiv.). While in UB 69 families, 111 genera and 117species were recorded, 14 species of crustaceans were recorded (4,525 indiv.), 67 genera of insects (1243 indiv.) and 36 species of mollusks were recorded (14,369 indiv.). Species recorded exclusively in each basin were in GB 6 species of mollusks, 11 of insects, and 4 of crustaceans, while in UB there were 17 species of mollusks, 44 of insects, and 9 of crustaceans.

Regarding the density of macroinvertebrates, 70 % of the density was from the Grijalva basin and 30 % from the Usumacinta basin. Spatially, maximum values of density and biomass in Grijalva were in the Ostitán section (99.4 indiv./m^2 and 9.7 g/m^2); while in Usumacinta, they were in the Jonuta section 24.8 indiv./m^2, and 6.9 g/m^2 respectively (Fig. 2A). Temporally, maximum values of density and biomass in Grijalva were 112.5 indiv./m^2 in the rainy season, and 10.9 g/m^2 in northern winds, respectively; for Usumacinta, maximum temporal values were in the dry season, 31.9 indiv./m^2 and 5.3 g/m^2 respectively (Fig. 2B).



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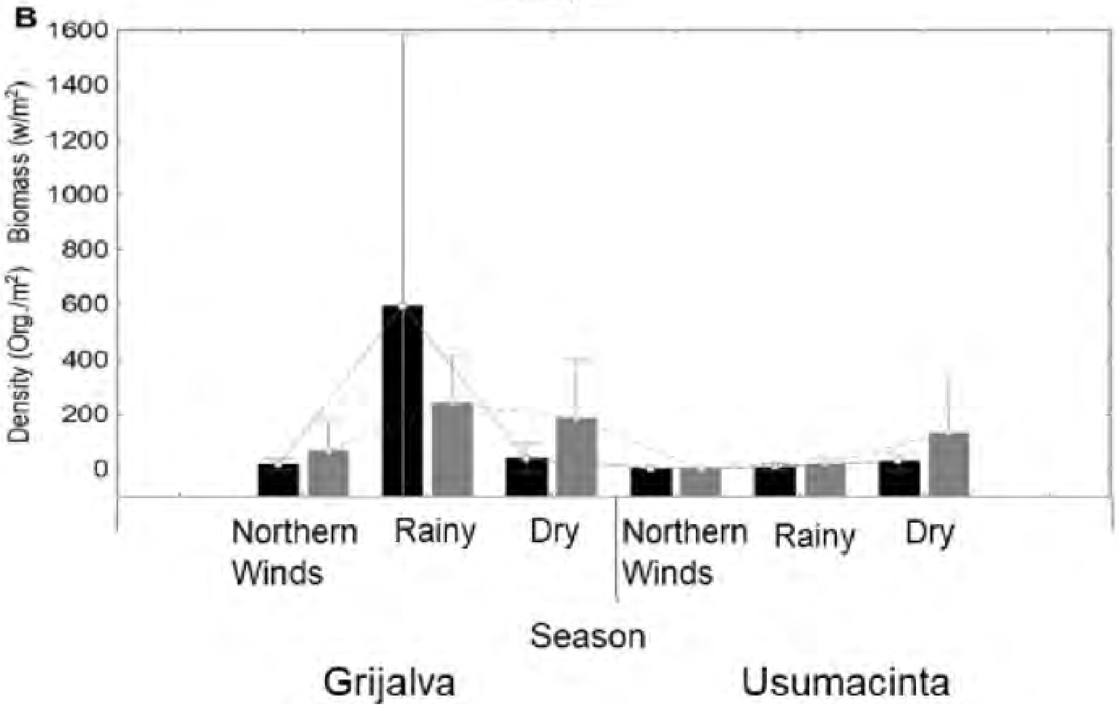

Figure 2. Mean and Standard Deviation of Density and Biomass of Aquatic Macroinvertebrates, Spatial (A) and Temporal (B) Distribution in Grijalva and Usumacinta Basins.

Table 2. Density and Biomass of AA<Aquatic Macroinvertebrates on Grijalva and Usumacinta Basins (*Exotic Species, CG=Grijalva Basin, CU=Usumacinta Basin, D=Density, B=Biomass). Many Species Recorded Densities Less than One Individual per Square Meter

Group/Species	GB		UB		Group/Species	GB		UB	
	D	B	D	B		D	B	D	B
Mollusks					*Berosus* sp.			0	0
Anodonta sp.			46	4	*Brachycerus* sp.	1	0	1	0
Aroapyrgus clenchi			141	1	*Camelobaetidius* sp.	1	0		
Aroapyrgus sp.			281	1	*Campsurus* sp.			1	0
Biomphalaria helophila	1	0	57	1	*Cheumatopsyche* sp.	0	0	0	0
Biomphalaria obstructa	1	0	69	1	*Chimarra* sp.			0	0
Biomphalaria subprona			1	0	*Chironomus* sp.	28	0		
Cochliopina francesae			47	0	*Chrysops* sp.			0	0

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Cochliopina infundibulum			5	0	*Coryphaeschna* sp.			1	0
Corbicula fluminea *	2,520	3,400	75	141	*Crambus* sp.			0	0
Cyrtonaias tampicoensis	0	38	5	113	*Cybister* sp.			0	0
Drepanotrema lucidum			2	0	*Desmopachria* sp.	0	0		
Eupera cubensis	101	1	169	3	*Dythemis* sp.			0	0
Hebentancylus excentricus			426	2	*Ellipes* sp.			0	0
Helisoma duryi					*Enallagma* sp.	18	0	6	0
Hydrobia sp.			675	2	*Enochrus* sp.	0	0		
Lamellaxis micra	0	0			*Ephoron* sp.	28	0	233	1
Littoraria nebulosa			0	0	*Eretes* sp.			1	0
Lucidella lirata	2	0	6	0	*Erpetogomphus* sp.			1	0
Margaritifera auricularia	2	103			*Gelastocoris* sp.			0	0
Mayabina polita	0	0			*Glossosoma* sp.	0	0		
Mayabina sp.			111	2	*Graptocorixa* sp.			36	0
Megalonaias sp.			0	0	*Gyretes* sp.			0	0
Megapitaria sp.			252	6	*Helichus* sp.			0	0
Melanoides tuberculata *	39	1	355	49	*Helobata* sp.			0	0
Mytilopsis leucophaeta	14	2	835	20	*Helochares* sp.			0	0
Neritina usnea	478	102	2,359	440	*Heptagenia* sp.			1	0
Neritina virginea	0	0	14	0	*Hetaerina* sp.	1	0	3	0
Physa sp.	35	0	209	1	*Heterelmis* sp.			1	0
Planorbella duryi	0	0	141	1	*Hexatoma* sp.			1	0
Polymesoda caroliniana	28	248			*Hydrometra* sp.	0	0		
Pomacea flagellata	6	14	332	812	*Hydrophilus* sp.			1	0
Potamilus alatus			4	14	*Lacophilus* sp.			1	0
Psoronaias crocodilarum	15	630	30	429	*Lachlania* sp.			0	0
Pyganodon grandis			14	9	*Leptohyphes* sp.	7	0	1	0
Pyrgophorus parvulus	3	0			*Leptonema* sp.	7	0	0	0

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Pyrgophorus coronatus	20	0	2,799	15	*Leptysma* sp.			0	0
Rangia cuneata			1	0	*Libellula* sp.	1	0	4	0
Stenophysa impluviata	0	0	6	0	*Limnogonus* sp.	0	0		
Subulina octona	1	0	10	0	*Maccaffertium* sp.			0	0
Succinea undulata	0	0	15	0	*Macrelmis* sp.			12	0
Tarebia granifera *	54,199	2,782	9,293	2,090	*Metrobates* sp.	0	0		
Texadina sphinctostoma			1464	5	*Microcylloepus* sp.			1	0
Crustaceans					*Neptopsyche* sp.			1	0
Armases cinereum			4	1	*Notonecta* sp.	0	0	3	0
Callinectes sapidus	0	0			*Omophron* sp.			0	0
Callinectes sp.			0	0	*Orchelimum* sp.			1	1
Cymadusa compta			40	0	*Palaemnema* sp.			0	0
Discapseudes mexicanus			2,774	7	*Paracleodes* sp.			0	0
Ericthonius brasiliensis			5	0	*Paraponyx* sp.	0	0	0	0
Hyalella azteca	0	0	4	0	*Pelocoris* sp.			12	1
Macrobrachium acanthurus	410	32	240	19	*Petrophila* sp.	0	0		
Macrobrachium carcinus	25	4	22	3	*Phyllocycla* sp.	0	0	20	4
Macrobrachium hubbsi	27	2			*Polyplectropus* sp.			0	0
Macrobrachium olfersii	113	11	642	286	*Probezzia* sp.			0	0
Minuca sp.			4	2	*Progomphus* sp.	14	0	2	0
Uhlorchestia uhleri			1	0	*Ranatra* sp.	0	0	1	0
Pachygrapsus transversus			1	1	*Rhagovelia* sp.	2	0	37	0
Potimirim mexicana	109	3	60	2	*Rhantus* sp.			0	0
Pseudothelphusa hartmanni	0	7			*Simulium* sp.	1	0	0	0

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Rhithropanopeus harrisii			1	0	*Stenus* sp.	3	0		
Uca pugilator	0	0			*Tabanus* sp.			0	0
Insects					*Tanysphyrus* sp.	2	0		
Aeshna sp.			0	0	*Thraulodes* sp.			4	0
Ambrysus sp.			3	0	*Tortopus* sp.			1	0
Anacroneuria sp.			2	0	*Traverella* sp.			1	0
Anaxipha sp.			2	0	*Trepobates* sp.	0	0	3	0
Aphylla sp.	0	0	2	0	*Triacanthagyna* sp.			0	0
Argia sp.	0	0	1	0	*Tricorythodes* sp.	11	0	2	0
Baetis sp.	9	0	58	0	*Tropisternus* sp.	0	0	2	0
Belostoma sp.	2	0	5	0					

Regarding the groups, mollusks represented 93 %, crustaceans 6 %, and insects 1 % of the total average density. Considering the density by basin, mollusks represented 98 % and crustaceans and insects 1 % respectively in the Grijalva basin (GB), while in the Usumacinta basin (UB) mollusks represented 83 %, crustaceans 15 %, and insects 2 %. Regarding biomass, in CG it registered 62 %, while CU 38 %. In both basins, mollusks represented more than 90 % of the total biomass.

Dominant species by density in the GB, were mollusks: *Tarebia granifera* with 77% while in biomass, they were *C. fluminea* (46 %) and *T. granifera* (38 %). For crustaceans, the dominant species in density were *Macrobrachium acanthurus* (28%), *M. olfersii* and *Potimirim mexicana* with 19 % respectively. *M. acanthurus* represented the largest biomass of crustaceans in the basin with 53%. In insects, the dominant species in density were *Chironomus* sp. and *Ephoron* sp. with (20 %) respectively, and *Enallagma* sp. (13 %), while the highest biomass was for *Progomphus* sp. and *Ephoron* sp. (18 %) respectively, followed by *Chironomus* sp. (16 %). In UB, the dominant species in density for mollusks were *T. granifera* (45 %), *Pyrgophorus coronatus* (13 %), and Neritina usnea (11 %). Regarding biomass, the dominant species were *T. granifera* (50 %) and *Pomacea flagellata* with 19 %. In crustaceans, the dominance in density was for *Discapseudes mexicanus* with 73 % of the density, while in biomass it was *M. olfersii* with 88 %. Regarding insects, the dominant species in density were *Ephoron* sp. (49 %), and *Baetis* sp. (12 %), while the species *Phyllocycla* sp. (45 %), and *Ephoron* sp. (13 %), were for biomass (Table 2).

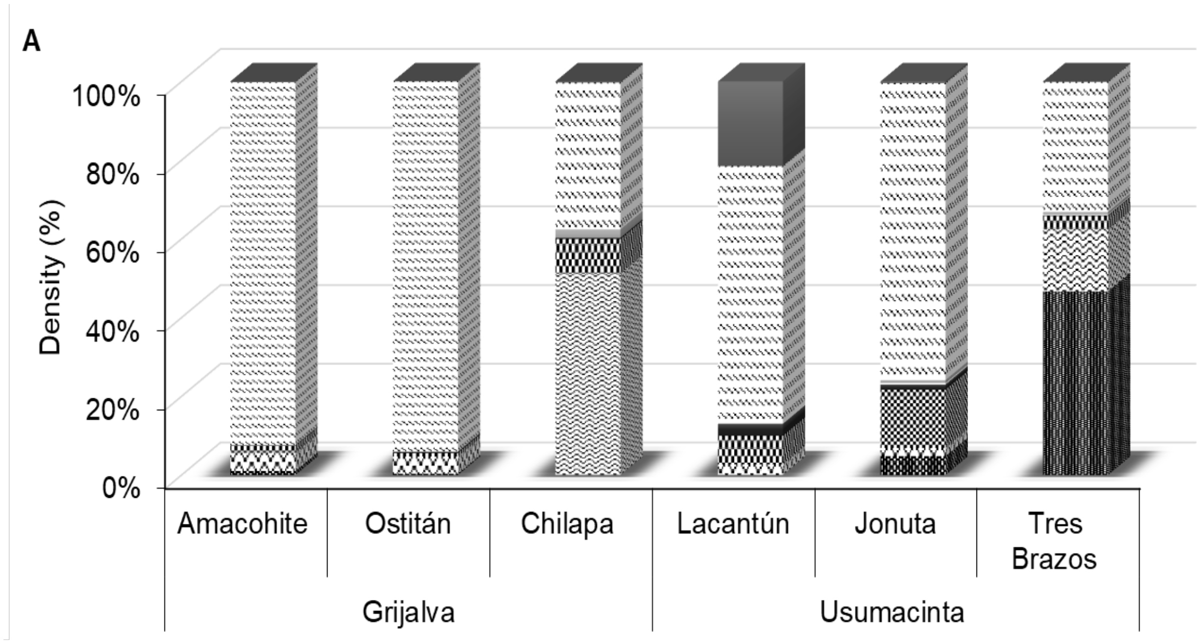
Diversity indices by basin, UB presented maximum values, spatially maximum diversity values were in the Lacantún section in upper basin (H'=4.49, J'=1.14, D=1 and Margalef=22.76). Temporally, maximum values were in the Northern winds (H'=3.42, J'

=0.85 and Margalef=15.19) and in the dry season (D=0.93) (Table 3). Maximum values of diversity in GB were in lower basin section Chilapa (H'=1.78, J'=0.48 y D=0.71), seasonally maximum values were in dry season (H'=2.28, J'=0.79, D=0.58 y M=8.73) (Table 3)

Table 3. Spatial and Temporal Diversity of Aquatic Macroinvertebrates in Grijalva and Usumacinta Rivers.

Basin / Section	**Grijalva**			**Usumacinta**		
	Amacohite	**Ostitán**	**Chilapa**	**Tres Brazos**	**Jonuta**	**Lacantún**
Shannon_H	0.98	0.79	1.78	2.93	2.52	4.49
Equitability_J	0.28	0.22	0.48	0.73	0.58	1.14
Simpson_1-D	0.28	0.25	0.71	0.93	0.77	1.00
Margalef	7.09	6.25	6.77	8.00	13.21	22.76
Season	**Northern Winds**	**Rainy**	**Dry**	**Northern Winds**	**Rainy**	**Dry**
Shannon_H	1.70	1.06	2.28	3.42	2.73	3.07
Simpson_1-D	0.70	0.36	0.79	0.89	0.88	0.93
Equitability_J	0.56	0.27	0.58	0.85	0.63	0.70
Margalef	5.18	7.10	8.73	15.19	11.74	10.97

The dominant Trophic groups were the scrapers (74 %) and the filter feeders (11 %) present in all the sampled sections, presenting the maximum values in GB in the Ostitán section and the rainy season. Collectors (10 %) were present in four sections, having the maximum value in UB in the Tres Brazos section in the dry season (Fig. 3).



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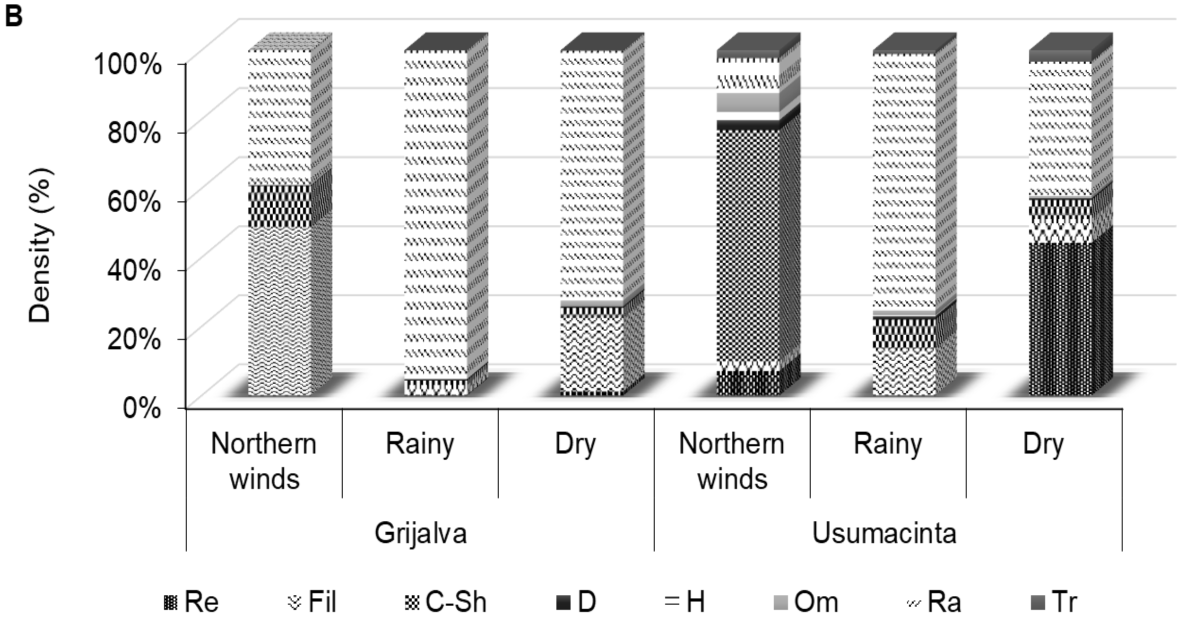

Figure 3. Spatial (A) and Temporal (B) Distribution of Trophic Groups in Grijalva and Usumacinta Rivers. Collector (Re), Filtering (Fil), Collector-shredders (C-Sh), Predator (D), Herbivores (H), Omnivores (Om), Scrapers (Ra) and Shredders (Tr)

Trophic groups per basin, presented significant differences with respect to density, mollusks ($p \leq 0.001$), these differences occurred between Filter feeders BG over scrapers BU and filter feeder's BU over scrapers BU. Regarding crustaceans ($p \leq 0.05$), these presented differences between gathering in BU over omnivores in BU and shredders in BU over omnivores in BU, and insects ($p \leq 0.001$) the differences were presented between shredders in BG over predators BG, shredders BU over predators BG, and with a $p \leq 0.05$ gathered BG over predators BG, shredders BU predators BU, predators_BG: predators_BU and shredders BU: shredders _BG.

Discussion

In the Grijalva River, it has been identified that main causes of modification of the river ecosystem are the construction of hydraulic infrastructure, urban growth, and pressure on aquatic resources related to primary activities (Sánchez et al*.,* 2015; Sandoval-Rivera et al., 2022). This pattern of riparian quality form regular to poor, is a common condition that has also been observed in other basins (Escalona-Domenech et al., 2022). On the other hand, variation of parameters of temperature, salinity, and TDS in Grijalva, because of urbanization, changes in the use of land, modification of drainage networks, discharges of untreated water from the cities of Villahermosa and Tuxtla Gutiérrez, agricultural activities, oil industry and sugar mills (Ramos-Herrera et al., 2012; Marin, 2014; Musálem-Castillejos et al., 2018).

While in the Usumacinta River, the ecological condition of the river bank from very good to poor, could be explained by its location, since areas in Montes Azules Biosphere Reserve (MABR) in the state of Chiapas (Salinas-Rodríguez et al., 2021; Soria-Reinoso et al., 2022), so the riparian vegetation still presents natural conditions (Ochoa-Gaona et al., 2018), to Jonuta classified as good, this could be because there are unsustainable practices in the area (such as subsistence agriculture, use of agrochemicals, extensive plantations such as oil palm and in the lower areas of Tabasco, extensive livestock farming) (Salcedo-Garduño et al., 2019; Camacho-Valdez et al., 2022), and the Tres Brazos site, located in the Pantanos de Centla Biosphere Reserve in Tabasco, presented a poor riparian state. Due to economic activities such as agriculture, fishing, and livestock are developed in the area, coupled with presence of the oil and gas industry (Barba-Macías et al., 2006; Barba et al., 2018). These activities put the PCBR and its environmental services at risk and keep them under constant pressure (Barba Macías et al., 2014, 2015, 2018; Puc-Carrasco et al., 2016; Ochoa-Gaona et al., 2018).

Temporal variability of the physicochemical parameters of the water occurred due to the dynamics of tropical rivers, which depend on precipitation and flow rates (Soria-Reinoso et al., 2022), combined to this, human settlement and land use change in this river generate alterations in the physicochemical conditions of the water, mainly in dry season, when the volume of water decreases and, therefore, the concentration of discharges increases, increasing the concentration of contaminants and decreasing water quality (Salcedo-Garduño et al., 2022). It should be noted that in the Grijalva River, the depth did not show variation throughout the climatic seasons, which could be explained by the management that the dams carry out on the flow, since it is a characteristic of the reservoirs to compensate for low flows during the dry season and regulate high flows in the rainy season (Wang et al., 2016).

Tropical seasonality differs from the temperate zone whereas temperature differences in tropical streams are usually very subtle (≈10°C), where taxonomic composition, richness, and trophic guilds are driven by the seasonality through the contrasting (rainy and dry seasons) (Cortés-Guzmán et al., 2021).

Aquatic macroinvertebrate species richness was considerably lower in Grijalva (66 spp.) compared to those in the Usumacinta River (117 spp.). It is the first study that groups three phyla (mollusks, crustaceans, and insects) and therefore, the importance of the information generated. For group of mollusks, 24 species are recorded in the Grijalva River, compared to Mellano-Hernández et al. (2015) who reported 17 species of Gastropods and six species of Bivalvia, with *P. coronatus, M. impluviata, L. tenuipes, M. polita, and Pomacea flagellata* being dominant in abundance. For the Usumacinta River, in this study, 36 species of mollusks were recorded having a similarity with those reported by Trinidad-Ocaña et al. (2018) recording 35 species.

For the group of crustaceans in Grijalva, nine species were recorded, according to Álvarez et al. (2005), 72 species of crustaceans are registered for the State of Tabasco, of which

44 were counted for decapods and peracarids; It is considered that there is an underestimation of the records for invertebrates and especially crustaceans and insects since most of the studies have been carried out with species of commercial importance (Sánchez & Barba, 2005). For the Usumacinta River, 14 species were recorded, compared to what was reported by Trinidad-Ocaña et al. (2018) with 13 species. Insects in the Grijalva basin were recorded with 33 genera and for the Usumacinta River, 67 genera were recorded, which compared to Castillo et al. (2018) the value is lower than what they report (127 genera). This may be due in part to the fact that for some individuals of some orders, identification at the genus level was not possible.

73 % of total density was in the Grijalva River, due to a high number of exotic mollusk species, *Tarebia granifera,* with 65 % of total density (both rivers). This is the first study which groups three phyla (mollusk, crustaceans and insects), past reports are about a single zone *p.e.* Lacantún (Cortés-Guzmán et al., 2021), or just Insects (Castillo et al., 2018), or mollusk and crustaceans in Usumacinta (Barba-Macías et al., 2018). In Lacantún section 63, the genera of benthic macroinvertebrates were recorded from 39 families and ten orders of those 24 genera (40 %) have been previously reported from the Usumacinta River Basin (Castillo et al., 2018). In the Grijalva river, 17 species of Gastropod and six species of Bivalvia were recorded, being dominant in abundance *P. coronatus, M. impluviata, L. tenuipes, M. polita* and *Pomacea flagellata* (Mellano-Hernández et al., 2015),

Macroinvertebrate diversity was higher in the Usumacinta River, in the Lacantún section, and in northern winds, in Grijalva, the diversity was higher in the Chilapa section in the dry season. Spatial distribution of density by the taxonomic group in Grijalva, crustaceans and insects were higher in Chilapa, and mollusk in Ostitán, in Usumacinta mollusks and insects were higher in Jonuta, and crustaceans in Tres Brazos. Temporal distribution was in Grijalva, mollusks and insects higher in rainy, crustaceans in northern seasons, meanwhile, in Usumacinta highest density values were in dry season.

Scrapers group were dominant in all sections, with highest density values in Ostitan GB, in the rainy season, collectors were present in four sections with highest values in Tres Brazos in the dry season, differences between sections and rivers can be explained by differences in hydrological regime. The Usumacinta River is free-flowing with a maximum 220 discharge (averaged 3,632 m^3/s) in the rainy season and a minimum (723 m^3/s) in the dry season. This reflects the relationship between the rainfall regime in the rainy season with flow volume. The Grijalva River flow drastically modified, showed a decrease in volume to less than a half; being notorious in dry season with an increase in 156 (m^3/s) of natural volume (Miranda-Vidal et al., 2023). Free-flow of the Usumacinta River has flow regimes well marked by seasonality (rainy and dry), with natural conditions of hydrological connectivity and flow regimes (Salinas-Rodríguez et al., 2021). These conditions facilitate the lateral and longitudinal migration of fish and their permanence in the aquatic systems of the floodplain (Castillo, 2011). In addition, hydrological connectivity is very important for the dynamics of aquatic and riparian vegetation (Mendoza, 2014), because it promotes the dispersal of seeds, fruits, or parts of the plant in the rainy season which enables individuals to develop for repopulation and, in addition, facilitates the flow and transfer of nutrients (Ochoa-Gaona et al., 2018).

Loss of seasonal flow variation in the Grijalva river compromised the seasonal variation of geomorphology creation and maintenance, reflected in the homogeneity of riparian and aquatic habitats (Wang et al., 2016). Furthermore, hydrological connectivity was altered for various aquatic species that require extreme flows to complete their life cycles (Metcalfe et al., 2013). With such alteration to the flow, temporal pulses, and homogenization of levels (depth), the entry and permanence of invasive species are facilitated (Ormerod et al., 2011). Reduced flow favors soil and water salinization and decreases the inflow of freshwater to the sea, as in the mouth of the Grijalva River where the salt wedge has reached up to 46 km upstream (Alcérreca-Huerta et al., 2019). This threatens fluvial ecological processes and the permanence of freshwater species, especially in the RBPC (Mata-Zayas et al., 2017).

On the other hand, maximum values of richness and abundance recorded in the Usumacinta River could be so since it still has good natural conditions of flow and hydrological connectivity, so the heterogeneity of the landscape as a riparian condition represents an important role for aquatic macroinvertebrates. A similar situation occurs with fish diversity, Soria-Barreto et al. (2018) reported 172 species, through a search of bibliographic information and sampling carried out from the Lacantún River in Chiapas to the Centla Swamps in Tabasco and the Palizada River in Campeche. Contrary to the Grijalva River, only 92 species of fish have been listed (Gómez-González et al., 2015).

Conclusions

Present work enriches information on the diversity and trophic groups of aquatic macroinvertebrates in the Grijalva River and Usumacinta River, one of the most important rivers in México, and due to their high water and natural wealth, they not only gather a large part of the biodiversity, but they also contribute 30 % of the country’s total surface runoff.

Analysis of study and temporal zones for each basin allows us to demonstrate difference in macroinvertebrate diversity that exists between them. The Grijalva River had the highest density values represented by the exotic mollusk *Tarebia granifera* with 77 %. Other exotic species were *Melanoides tuberculata* and *Corbicula fluminea*. The Usumacinta River had the greatest richness and diversity of macroinvertebrates. Presence of trophic groups such as fragmenters and collectors are strongly related in the Usumacinta areas with better water quality. This relationship could be because the habitat where they are found has greater vegetation cover. However, trophic groups such as predators and scrapers are strongly associated with the Grijalva areas with lower water quality values and with evident human intervention.

Results confirm that rivers with natural flow regimes and high riparian quality values have greater diversity and trophic levels. The Usumacinta River has a natural seasonal flow corresponding to maximum and minimum flood seasons, providing various resources (habitat, food, shelter, connectivity) to aquatic populations. In addition, it provides various services such as supply and cultural services by obtaining water and food from the river and providing areas for sport fishing and recreation.

However, given the extension, complexity of the landscape, and the hydrological characteristics of the basin, it is necessary to carry out studies at a finer scale such as sub-basins and geomorphological units in such a way that the biogeographic and diversity patterns are explained, not only of macroinvertebrates, but of all the aquatic species that inhabit them.

Riparian habitats of the Usumacinta and Grijalva rivers are compromised by various anthropogenic activities and need urgent attention. Studies are needed to exhaustively evaluate the management of tropical forests to prolong and maintain the ecosystem services that the basins still have and focused on trophic groups, since this constitutes an approach to the ecology of the macroinvertebrate community where greater studies are necessary to understand the effects of changes in aquatic habitats on functional aspects of the community and its relationship with the quality of habitats and their environmental services.

Authors' Contributions

EBM, JJF, sampling design, obtaining financing. EBM, JJF, CTO, FJMV sample collection, species identification, analysis. EBM, JJF, CTO, drafting of the document

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Annexe 1. Environmental Characteristics of the Selected Sites in the Usumacinta River; Season (D): Dry, (R): Rainy; Habitat: EMV (Emerged Vegetation, Trees and Shrubs *Phragmites australis, Typha dominguensis*), FFV (free floating vegetation, *Salvinia minima, Eichhornia crassipes)*. SAV (Submerged Vegetation *Vallisneria americana, Cabomba palaeformis*) HA: Human Activities, MI: Marine Influence, RQI: Riparian Quality (Miranda-Vidal et al., 2023).

Section	Depth (m)	Habitat	HA	RQI	MI	Reference Image
Lacantun 90°54’20.083”W 16°12’30.938”N	0.57 (D) 1.08 (R)	EMV Substrate Boulders and Sand, Moderate Current.	Agriculture, Fishing Harvest, Forest Tourism	Very Good	No	
Jonuta 92°05’59.676” W 18°05’42.492” N	0.90 (D) 1.80 (R)	EMV, FFV, Substrate Sand, Gravel, or Mud, and Moderate Current.	Agriculture, Livestock Fishing	Moderate	No	
Tres Brazos 92°37’38.267”W 18°23’50.702” N	1.83 (D) 1.96 (R)	EMV, SAV, Substrate Sand, Silt, and Clay, Strong Current.	Agriculture Livestock Fishing Tourism	Poor	Yes	

Annexe 2. Environmental Characteristics of the Selected Sites in the Grijalva River; Season (D): Dry, (R): Rainy; Habitat: EMV (Emerged Vegetation, Trees and Shrubs *Phragmites australis, Typha dominguensis*), FFV (free floating vegetation, *Salvinia minima, Eichhornia crassipes*). SAV (Submerged Vegetation *Vallisneria americana, Cabomba palaeformis*) HA: Human Activities, MI: Marine Influence, RQI: Riparian Quality (Miranda-Vidal et al., 2023).

Section	Depth (m)	Type of Habitat	HA	RQI	MI	Reference Image
Amacohite 93°26’56.016” W 17°34’40.449” N	1.47 (D) 1.62 (R)	EMV, Substrate Boulders, Gravel, and Sand, Moderate Current.	Agriculture, Fishing Aquaculture Livestock, Forest	Moderate	No	
Ostitan 93°24’14.918” W 17°47’30.883” N	1.05 (D) 1.07 (R)	FFV, Substrate Sandy and with Moderate-slow Current.	Agriculture, Fishing Livestock, Forest River Transport	Poor	No	
Chilapa 92°40’19.311” W 18°15’14.303” N	2.16 (D) 2.53 (R)	EMV, FFV, Substrate Mud and Silt, with Strong Current.	Agriculture, Fishing Livestock	Moderate	Yes	

Fishing Among Socioecological Challenges: The Case of the Zimapán Dam

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Abstract

The Global Climate change crisis urgently demands a deeper and more comprehensive understanding of aquatic systems. In this study, we analyzed the Zimapán Dam, a relatively recently created ecosystem distinguished by its high complexity and distinct anthropization, where fishing is intricately connected with ecological, environmental, and social factors. We updated the list of fish species present in the dam and analyzed daily registers of the “13 de Junio” Fishing Cooperative, aiming to comprehend the dynamics of fishing activity. Additionally, semi-structured interviews were conducted with fishers to capture their perceptions of the situation, identify underlying causes, and explore potential solutions. The fish community is composed of eight species and two subspecies identified as exotics. On average, during the study period, the catch per unit effort of tilapia was 10 kg per fisher per day. The fishing activity has experienced notable variations over time, lacking evident consistency and was influenced by various factors. Several causes for the decrease in fishing and the gradual abandonment of the activity due to lack of profitability were pointed out by the interviewees, primarily the presence of black bass. This study underscores the need for integrated approaches and collaborative solutions addressing both the ecological problems and social dimensions of fishing. Ecosystems like the Zimapán Dam will become increasingly important in the context of global change; therefore, understanding them as key ecosystems on which we will depend in the near future is essential.

Keywords

Anthropization; Black Bass; Exotic species; Hydroelectric Dam; Tilapia.

Introduction

Throughout the Anthropocene, human activities have caused impacts on the environment, altering atmospheric, geological, hydrological, and ecosystem processes at multiple scales, ranging from local to planetary (Ruddiman, 2013). Nowadays, we are witnesses of the ecosystem disruptions resulting from the transformation of natural and social processes, such as land use change, transformation and degradation of the ecosystems, and alterations in biogeochemical cycles. In fact, ecosystems are no longer conceivable without human influences (Schmitz, 2016). There is a growing concern about the capacity of ecosystems to maintain their function in the context of global change. According to the Global Risks Report (World Economic Forum, 2019), water bodies are acknowledged as one of the systems experiencing the most significant social, political, and economic pressure globally, as nearly all human activities are intimately linked with water. For instance, estimates indicate that humanity expropriates more than half of the accessible drinking water (Gleick & Palaniappan, 2010).

Aquatic ecosystems are particularly affected, and it is estimated that aquatic populations have decreased by 76 % in epicontinental bodies of water since 1970 (WWF, 2014). Epicontinental water bodies are key to ensuring the water supply for human population and the sustainable development of nations (Bunn, 2016). The viability of these water bodies in the future is crucial and depends on the control that can be exerted over the sources impacting them, which, in turn, relies on an adequate understanding of their functioning (Sage, 2019). This situation is particularly concerning in Mexican aquatic ecosystems.

In our country, 77 % of the human population resides in areas where only 33 % of renewable water is found (Arreguín-Cortés et al., 2020). According to the Atlas of Water Vulnerability to Climate Change (Arreguín-Cortés et al., 2015), the most critical basins and aquifers in terms of population and economic activities are over-conceded and overexploited respectively. Besides the scarcity of availability, pollution represents another limiting factor; in Mexico, 70 % of bodies of water show some degree of contamination (Conagua, 2018). For example, 49 % of rivers and streams are categorized with a high or very high degree of ecohydrological alteration (Garrido et al., 2010). According to Sánchez (2017), in Mexico, more than 80 % of municipal wastewater generated by public-urban use is discharged into water bodies without any treatment. Likewise, 82 % of industrial wastewater is discharged untreated (Bunge, 2010). This, coupled with the expected impact of climate change on precipitation patterns, contributes to the challenges. The country’s situation is projected to become critical by 2025 (Ávila, 2008).

Additionally, introduced species are among the main effects of human alteration of aquatic systems. Exotic species can reduce native fish populations (Rahel, 2000), modify community dynamics (Minns & Cooley, 1999), alter trophic structure stability (Vander Zanden & Rasmussen, 1999), and even lead to the extinction of native species (Lodge, 1993). The potential consequences on native fauna and ecosystems are severe, especially in areas of high diversity (Zambrano et al., 2006). In Mexico, exotic fish species are established in virtually all bodies of water in the central region of the country and are one of the most significant factors contributing to the loss of native species (Zambrano & Hinojosa, 1999; Contreras-MacBeath et al., 2014). Numerous effects generated by exotic species have been identified, such as changes in community structure, competition for food resources (Zambrano et al., 2010), modification of native species populations, trophic cascades, and algal blooms (Figueredo & Giani, 2005), increased turbidity (Miller & Crowl, 2006), and reduction of trophic pathways (Córdova-Tapia, 2011). Currently, some negative effects of these species are known, but many details about how they integrate into food webs and their ecological implications remain unclear. Both pollution and the introduction of exotic species act synergistically on epicontinental water bodies, generating direct and indirect changes in the quantity and quality of existing resources, which in turn can lead to changes in community structure and ecosystem functioning (McCormick et al., 2009).

Water-related issues in Mexico are becoming increasingly problematic. Climate change, water scarcity, exotic species, and poor water quality are persistent and worsening problems. Major cities will have less water, water quality will deteriorate, and conflicts over water will increase. Moreover, poverty and social inequality will rise, making the situation even more complex (Ávila, 2008). In summary, it is expected that in the coming years, Mexico will experience a loss of water security, affecting many people and exacerbating poverty and inequality, while also endangering the country's ecosystems. We are facing a water crisis, both nationally and globally, posing a significant challenge for limnology. Therefore, in recent years, research efforts have been directed towards understanding how ecosystems can continue to provide goods and services under different anthropization scenarios (Naeem et al., 2012). In summary, this crisis urgently demands a deeper and more comprehensive understanding of aquatic systems. In this regard, limnology plays a crucial role in identifying solutions for sustainable water management in a context of scarcity and global change.

Zimapán as an Example of a Highly Anthropized Complex System

The Fernando Hiriart Balderrama "Zimapán" hydroelectric dam is situated in the "El Infiernillo" Canyon, marking the conclusion of a complex system comprising twelve dams along the Moctezuma River sub-basin in the Pánuco River region (Fig. 1). Its primary tributaries are the Tula River, carrying wastewater from the metropolitan area and traversing the Mezquital Valley, known for its intense agricultural activity. This river also passes through the Miguel Hidalgo Refinery "Tula" and the Tula Thermal Power Plant. The other main tributary is the San Juan River, collecting wastewater from the industrial zone of San Juan del Río, as well as from the wine and cheese industry in Querétaro, and the community of Tequisquiapan, known for its goldsmithing. Thus, this dam is strongly influenced by human activities throughout the basin.

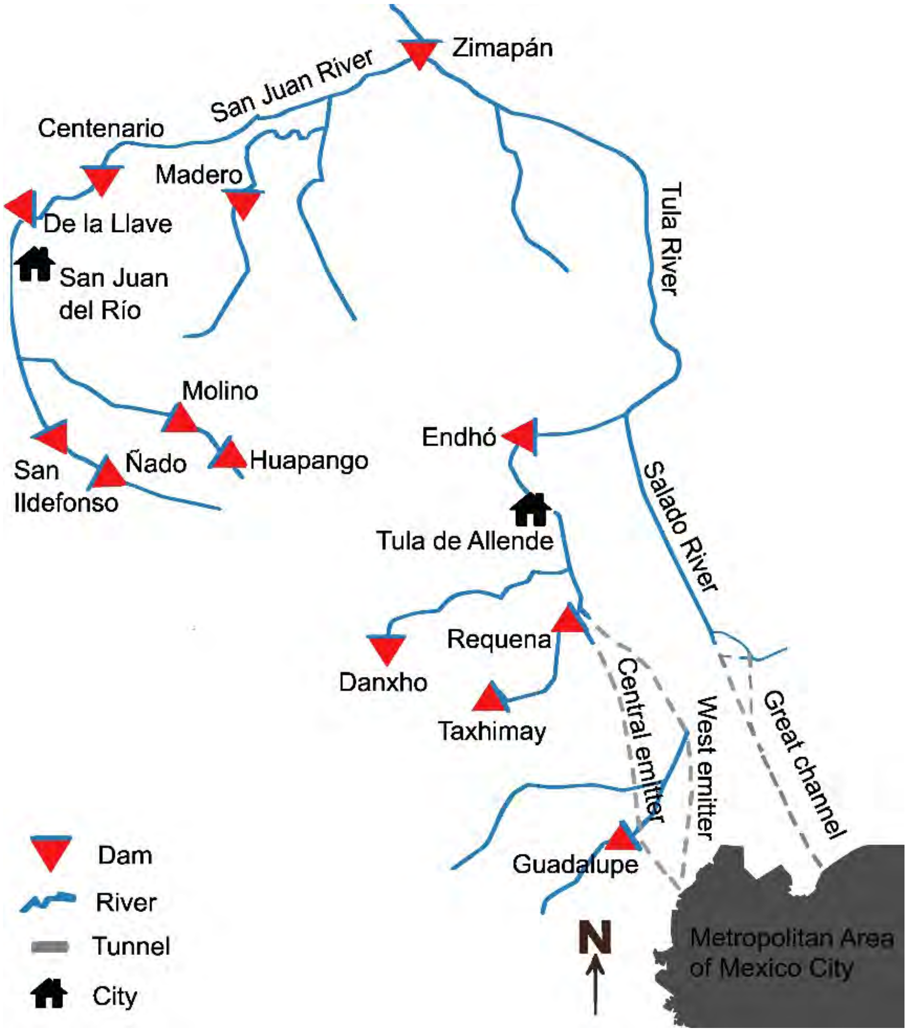

Figure 1. Hydrological System of Rivers and Dams that Converge in the Zimapán Dam. Based on Cortes-Silva et al., 2006.

Zimapán was built between 1990 and 1995 by the National Commission of Electricity (CFE) with the goal of generating electricity, featuring a 200 m high curtain dam forming a reservoir of 1,500 million m^3 of water in 2,300 ha. The dam's construction impacted the lives of twelve Otomi ejidos (community-owned lands) residing along the riverbanks, as well as 2,290 ha of cultivated and fruit-bearing lands (López-Hernández et al., 2021). The relocation of families living on the dam's edges, such as Vista Hermosa and Rancho Viejo, led to a radical shift from traditional agriculture to fishing, a new activity posing a challenge for these communities (López-Hernández et al., 2007). Despite the challenges, fishing cooperatives were formed in Hidalgo and Querétaro, initiating fishing activities in 1998, which has since become the primary source of income in the area. To this end, two exotic species, tilapia (*Oreochromis* sp.) and carp *(Cyprinus carpio*), were introduced. The dam has been subjected to multiple introductions of exotic species over the years; for instance, according to personal communications the fishermen, in 2005, largemouth bass (*Micropterus salmoides*) were illegally introduced to promote sport fishing. Since 2013, fishing efforts were organized within 13 associative groups, comprising 192 fishermen from Querétaro and 455 from Hidalgo. Fishing is conducted using gill nets in accordance with established regulations, and an annual closed season is implemented from April 21 to June 20 (SAGARPA, 2011).

A recurring environmental problem affecting fishing activity is the entry of wastewater from the Tula and San Juan rivers due to improper hydrological management and extraordinary floodings of untreated wastewater. In 2002 and 2021, extraordinary floods of untreated water were recorded due to the retention incapacity of the Requena and Endhó dams, which resulted in massive fish deaths in 2002; and a few months after the entry of water in 2021, there was a massive proliferation of *Lemna gibba* directly affecting fishing activities. In recent years, there has been a growing concern among fishing cooperatives as the catch has been decreasing to a point where it is considered an unprofitable activity (López-Hernández et al., 2021).

The situation is concerning since in the riverside populations of the Zimapán Dam, fishing is the dominant economic activity, followed by agriculture in localities such as Tziquia and Tzibantzá (Querétaro), where water is extracted from the reservoir for drip irrigation of crops such as tomatoes, pumpkins, chili peppers, beans, and corn (López-Hernández et al., 2021). Livestock breeding is also practiced, mainly goats and sheep, and there is migration to nearby cities for jobs in the primary sector (SAGARPA, 2011). This situation led the Tecozautla Municipality, starting 2021, to promote the cultivation of tilapia through a scheme where the fish are placed in floating enclosures with the aim of increasing the size by three inches before their release on the dam.

Zimapán is a relatively recently created ecosystem, distinguished by its high complexity and distinct anthropization, where fishing is intertwined with ecological, environmental, and social factors. Given the growing anthropization trend in Mexico's water bodies, Zimapán represents a paradigmatic example of an ecosystem highly modified by human activities. Nonetheless, these complex systems are precisely the ones that pose new challenges for limnology and the approach to studying these water bodies. Within the framework of this study, an updated list of fish species present in the dam was compiled. Daily registers of the “13 de Junio” Fishing Cooperative, the largest in the dam, were analyzed, aiming to understand the dynamic of the fishing activity from the beginning of June 2021 through August 2023. Additionally, semi-structured interviews were conducted with fisherman from various communities aiming to encapsulate their perceptions regarding the situation, identify underlying causes, and explore potential solutions. With this information, the goal is to delve deeper into understanding how these various issues interplay and shape a complex socio-ecological situation.

Materials and Methods

The Zimapán Dam is situated between coordinates 20°35’-20°40’N and 99°22’-99°37’W, at an elevation of 1,870 m above sea level, and has an extension of approximately 2,300 ha. The dam represents the territorial confluence of Hidalgo and Querétaro states, extending into the municipalities of Zimapán, Tasquillo, and Tecozautla in the western part of Hidalgo, as well as in the municipality of Cadereyta de Montes in Querétaro (Figure 2). The region’s climate is classified as BSh, indicating a dry and semi-arid profile with an average annual temperature of 19.1°C. The prevalent vegetation in the area corresponds to xerophytic shrubland. The National Fisheries Institute identifies the reservoir as suitable for tilapia fishing, based on physicochemical conditions and the availability of food resources, both natural and artificially induced (López-Hernández et al., 2007).

Figure 2. Location of the Zimapán Dam and Neighboring Municipalities.

Six field trips were conducted to cover an annual cycle and consider different seasons of the year (October and November 2022, February, May, August, and November 2023). To assess species richness, various fishing techniques were employed during four days during each visit. Five trap nets were set on the dam's shore, fixed to nearby rocks and left for six-hour periods. Casting nets with a diameter of three metres and mesh size of one inch were thrown from the quay and boats. Two sets of gill nets of 100 metres in length and five metres deep, with different mesh size openings (2, 3, 3.5, 4, and 4.5 inches) were installed and checked every 24 hours. Simultaneously, the species captured by commercial fishermen, who delivered their catches to the cooperative collection center, and those caught by sports fishermen at the dam were noted.

To analyze the fishing dynamics, a collaboration with the "13 de Junio" cooperative, was established. Access to the daily fishing logbook was obtained, going from June 2021 to August 2023, with a total of 4,923 records. This detailed record contains daily information on each fisher, including the daily kilograms captured of each species (tilapia, carp, and silver carp). It's important to highlight that the data in this logbook are considered of high quality as it's the same logbook used for fish commercialization. Using this information, the catch per unit effort (CPUE) was calculated, a metric allowing evaluation of fishery behavior (Díaz & Goenaga, 2003). The CPUE calculated represents the daily kilograms obtained by a fisherman over each week of the year. Additionally, the weekly number of fishermen delivering products to the collection center was examined to understand whether the quantity of active fishers' changes over time.

To comprehend the fisher's perception of the socio-environmental vulnerability of the fishing situation in the Zimapán Dam, semi-structured interviews were conducted. The main objective of these interviews was to clarify the economical relevance of fishing and acquire information about the evolution of the fishing situation over time. During these interviews, inquiries were made about the main issues identified by them, seeking information on potential solutions to improve the fishing activity. This approach provided a complete and detailed perspective of the locals' view, adding valuable insights complementing the technical and quantitative analysis of fishing at the Zimapán Dam.

Results

The fish community in the dam consists of eight species distributed among three taxonomic orders: Cypriniformes, Perciformes and Siluriformes (Table 1). The order Cypriniformes is represented by a single family: Cyprinidae, with three species: *Hypophthalmichthys molitrix* (Silver carp), *Ctenopharyngodon Idella,* (Grass carp) and *Cyprinus carpio* (Common carp) with two subspecies: *Cyprinus carpio specularis* (Mirror carp) and *Cyprinus carpio koi* (Koi carp). The order Perciformes is represented by two families: Centrarchidae and Cichlidae. The family Centrarchidae includes *Lepomis macrochirus* (Bluegill) and *Micropterus salmoides* (Largemouth bass). The family Cichlidae contained *Oreochromis* spp. (Tilapia) and *Herichthys carpintis* (Pearlscale cichlid). In the order Siluriformes, the family Ictaluridae was represented by a single species, *Ictalurus punctatus* (Channel catfish). The eight species and two subspecies identified are exotic species originating from various regions: America, Asia, and Africa. The Pearlscale cichlid is native to the Gallinas River basin and the upper Tamasopo River basin in Mexico.

Table 1. Fish Species and their Records in the Zimapán Dam.

Order	Family	Species/Subspecies	Local name	Body shape
Cypriniformes				
	Cyprinidae			
		Cyprinus carpio (Linnaeus, 1758)	Carpa común	
		specularis	Carpa espejo	
		koi	Carpa koi	
		Hypophthalmichthys molitrix (Valenciennes, 1844)	Carpa plateada	
		Ctenopharyngodon idella (Valenciennes, 1844)	Carpa herbívora	
Perciformes				
	Centrarchidae			
		Lepomis macrochirus (Rafinesque, 1819)	Mojarra azul	
		Micropterus salmoides (Lacepède, 1802)	Lobina	
	Cichlidae			
		Oreochromis spp. (Günther, 1889)	Tilapia	
		Herichthys carpintis (Jordan & Snyder, 1899)	Mojarra tampiqueña*	
Siluriformes				
	Ictaluridae			
		Ictalurus punctatus (Rafinesque, 1818)	Bagre	

The catch per unit effort (CPUE) analysis revealed that tilapia reached its peak during the month of November 2022, with an average of 23 kg/fisher/day (Fig. 3A). Similarly, carp recorded its highest average value in January 2023, achieving a CPUE of 9 kg/fisher/day (Fig. 3B). On average, during the study period, the CPUE was 10 kg/fisher/day for tilapia and 5 kg/fisher/day for carp. The fishing dynamics of both species were influenced by various factors, including environmental conditions, seasonal changes, ecological interactions, and social dynamics. In October 2021, fishing was suspended preventively due to an extraordinary influx of wastewater into the reservoir. Throughout 2022, there was an uncontrolled proliferation of *Lemna gibba*, commonly known as duckweed. Duckweed is a fast-growing aquatic plant that quickly covers the water surface, blocking sunlight and hindering the growth of other photosynthetic organisms (Arroyave, 2004). This proliferation affected fishing activities during six months. After overcoming the contingency, the highest record of catch per unit effort was observed in November of the same year. However, this efficiency was followed by a rapid decrease in the following weeks.

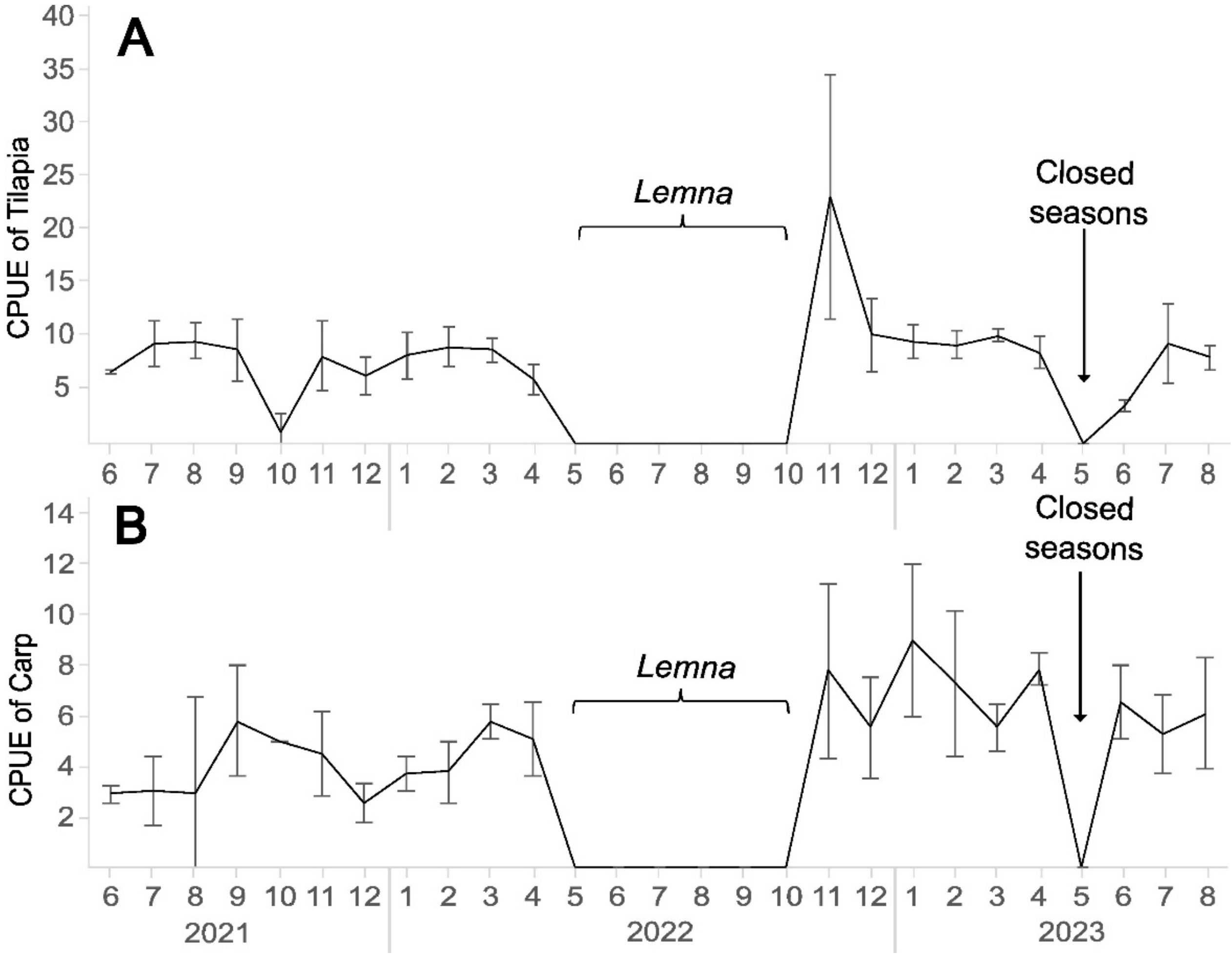

Figure 3. Mean and Standard Deviations of the Catch per Unit Effort (CPUE) for (A) Tilapia (*Oreochromis* sp.) and (B) Common Carp (*Cyprinus carpio*). The CPUE is Expressed as the Average Daily Catch in Kilograms per Fisher.

The fishing activity of the "13 de Junio" Fishing Cooperative has experienced notable variations over time, lacking evident consistency (Fig. 4). November 2022 stands out as the period of highest activity, with the participation of over 40 fishers. In contrast, during July 2023, the historical minimum activity was recorded, with only three fishers. On average, fishing activity remained at approximately 15 fishermen throughout the study period. Noteworthy is the dynamic of peaks where an increase in the number of fishermen is followed by a sharp decline in participation. This phenomenon is clearly observed in June 2021, at the conclusion of the annual closed season. Similarly, the pattern is also present after the contingency related to *Lemna gibba*, and after the closed season in June 2023.

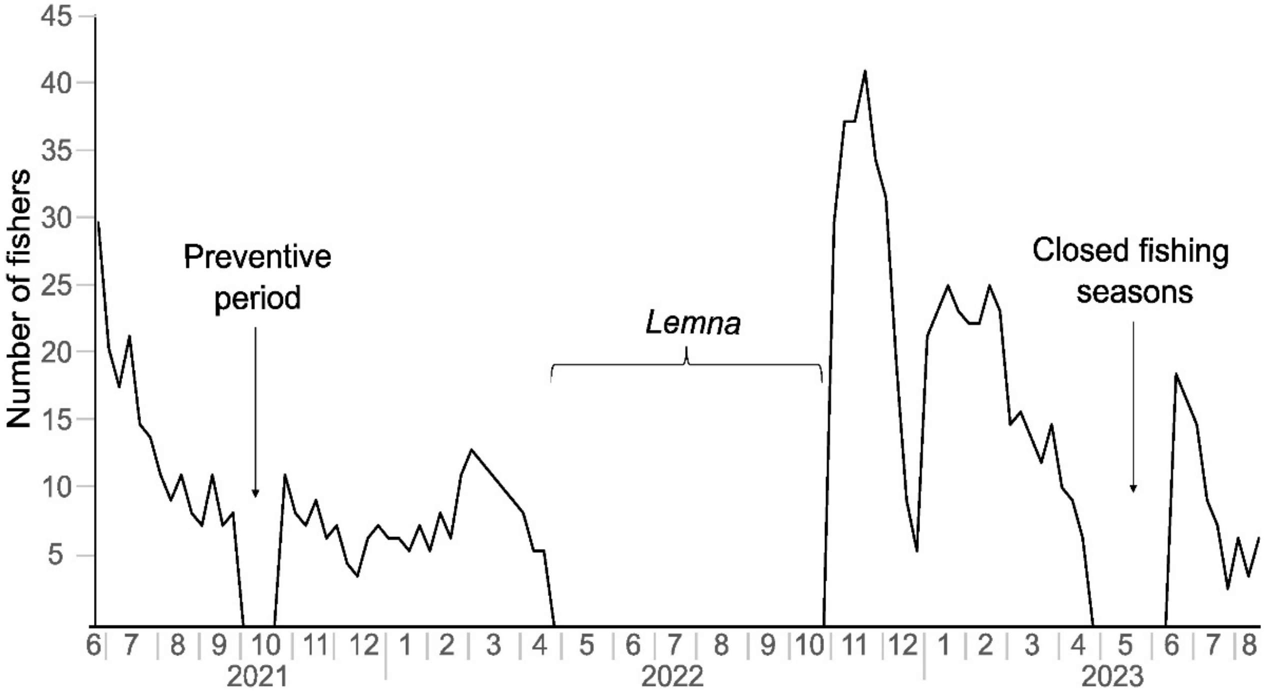

Figure 4. Behavior of Fishing Activities in the "13 de Junio" Cooperative.

In total, 43 interviews were conducted. Out of these interviews, 28 (65 %) corresponded to men, and 15 (35 %) to woman. Regarding the highest level of education among fishermen, 2 (5 %) have university education, another 2 (5 %) completed high school, 21 (49 %) attended middle school, 17 (39 %) have elementary education, and 1 (2 %) are in a situation of illiteracy. On the other hand, 31 (74 %) of the interviewees stated that fishing was their main economic activity, while 11 (26 %) indicated having another occupation besides fishing.

Several causes for the decrease in fishing and the gradual abandonment of the activity due to lack of profitability were pointed out by the interviewees. The introduction of carnivorous species, particularly the largemouth bass, a consequence of sport fishing, was often referred to as a significant problem. Around 50 % of the interviewees mentioned that the largemouth bass feeds on tilapia, identifying that before its introduction, more tilapia was fished. "[...] initially, there wasn't a fish that eats on tilapia… and when we opened it (the bass), there were fish in its stomach. I imagine they eat them because the fishing has been decreasing little by little, and yes, we attribute it to that, to the bass". Despite efforts in tilapia fingerling restocking, fishers expressed concern about the lack of recovery in the captured quantities. It was mentioned that the largemouth bass, being carnivorous, could be negatively affecting the success of restocking. "[...] the bass is carnivorous, so, we believe that it also eats a lot of what is being stocked and also small fish. We have even caught bass weighing 4 kg with a tilapia weighing half a kilogram in its belly". Furthermore, concern was highlighted regarding the increasing population of largemouth bass and the lack of economic benefits for commercial fishers. Restrictions on catching and commercializing largemouth bass were mentioned as a limitation. "We can only catch tilapia, not bass. They said we can't catch bass". "Yes; the stocking of tilapia. But this goes hand in hand with the utilization of bass or the reduction of its population. It's useless to restock if you have an excess population of bass".

Only 10 % of the fishermen acknowledge overexploitation as a cause of the decrease in catch. "The cause is that the reservoir was excessively exploited from the beginning". "I think the causes might have been that, at the time when there was good fishing, maybe we didn't know how to control it. I think we might have overexploited it then". A lower percentage (8 %) of the interviewees considered water quality an issue, highlighting the decrease in oxygen in the reservoir. "Because yes, we have noticed, especially with the cages, we take measurements, and we realize that oxygen is already very low sometimes and other times it's not".

Around 15 % mentioned that fishing has become unsustainable, jeopardizing the economic security and causing the abandonment of fishing in Zimapán, some people are migrating in search of better opportunities. "Well, fishing is really low at the moment. That's why we are leaving, because we must look for another job because if we don't, if we just rely on this, we won't survive". "Very critical and very difficult. No more. That's why there's not many fishers, because, well, it's not worth it anymore. We have to find elsewhere because fishing won't do". Regarding possible solutions, 23 % of the interviewees saw tilapia restocking as an alternative to increase daily catches. "Well, now we are restocking in higher quantities. Maybe it's what affected us, at the beginning, when we started fishing, we didn't repopulate, we just fished".

Discussion

The Zimapán hydroelectric dam stands out as a paradigmatic case of a complex system heavily influenced by human activities. Within this context, fishing, which initially emerged as an activity after the relocation of Otomi communities, has evolved into the primary source of income in the area. However, fishing in the Zimapán dam faces significant challenges, a product of the complex interaction between ecological, environmental, and social factors.

Exotic species represent a major concern for the conservation of aquatic ecosystems as they often displace native species, particularly in polluted habitats (Bourret et al., 2008). The fast loss of species and habitats in Mexico's central region, identified as a key ichthyic endemism center in the country (Miller, 2009), has raised concerns regarding the need to protect and conserve areas and species of ecological importance (Gutiérrez-Yurrita et al., 2013). In this regard, Mexico's National Strategy on Invasive Species is a comprehensive plan established by the Mexican government to address the management of invasive species. Its main objective is to prevent the introduction and spread of exotic species that may pose a threat to biodiversity and native ecosystems (CONABIO, 2010).

The species introduction phenomenon can trigger irreversible damages (Strayer, 2010). However, the continuous introduction of exotic species into artificial reservoirs is mainly attributed to socioeconomic factors (De la Lanza-Espino & García-Calderón, 2002). This circumstance presents a dilemma regarding the encouragement of the expansion of exotic species in these water bodies, posing a rising potential risk. In the Zimapán dam, 8 exotic species were recorded coexisting within the reservoir, raising interesting questions for future exploration about ecological interactions and the factors enabling their coexistence.

The introduction of largemouth bass as a measure to promote recreational fishing to diversify economic activities might be among the main causes of the decrease in tilapia population, thereby generating a socioecological conflict between both fishing practices. The presence of largemouth bass is identified by commercial fishermen as a key factor in the decline of catches. Furthermore, the coexistence of other exotic species suggests the possibility of competition for food resources and habitat, both with the native species (Pearlscale cichlid) and also tilapia (Córdova-Tapia et al., 2015). The presence of carnivorous species, such as largemouth bass and catfish, poses an additional challenge to the survival of tilapia fingerlings and juveniles.

The results reveal significant variability in fishing activity, characterized by peaks of participation followed by abrupt declines. These patterns highlight the susceptibility of fishing in Zimapán due to economic, ecological, environmental, and social factors. The interaction among species introduction, recreational fishing, and wastewater discharges could be generating complex and synergistic dynamics (Simberloff et al., 2013).

In 2021, precautionary measures after a flood caused by Hurricane Grace resulted in four weeks without records (from September 27th to October 24th) due to the severe flooding affecting Hidalgo state from the overflowing Tula River. In 2022, a few months after the floodings, *Lemma gibba*. In April of the same year, fishing was suspended due to the mandatory closed season. However, upon its conclusion in June, it was impossible to resume fishing activities as a great part of the reservoir was covered by *L. gibba*, making it impossible to set nets. Several months of that year were dedicated to removing it. Once the dam was cleared at the end of October, fishing activities resumed. November was the month with the highest presence of fishers, followed by a rapid abandonment. In 2023, the lowest number of active fishermen was recorded.

Interviews with the fishermen reveal a growing concern about the profitability of fishing. This concern is supported by the results of the analysis of catch per unit effort (CPUE), showing that, on average, fishermen obtain around 10 kg of tilapia/day and 5 kg of carp/day. The selling prices of tilapia is 40 Mexican pesos per kilogram (2.3 USD), while carp sells for one Mexican peso per kilogram (0.05 USD). Consequently, the average daily income of fishermen is 405 Mexican pesos (23.7 USD). However, this income is affected by associated expenses, such as transportation from their homes to the dam and the cost of gasoline for the boat used during checking of the nets (190 per day, 11.3 USD). Therefore, on average, a fisher earns 215 Mexican pesos (12.8 USD) per day of work. This situation generates uncertainty about the economic sustainability of fishing activities and poses a challenging outlook for the fishermen, raising legitimate concerns about the future of this activity at Zimapán Dam.

The restocking of tilapia emerges as a potential solution, according to the perception of some fishers, to increase daily catches and strengthen fishing activity at Zimapán dam. Even so, this approach faces significant challenges arising from the increased population of largemouth bass and the restrictions associated with their capture. The coexistence of these factors raises questions about the long-term viability of this strategy. It is imperative to reconsider fishing management strategies at Zimapán, considering not only tilapia stocking but also critically evaluating the continuous introduction of exotic species into bodies of water for socioeconomic purposes. This needs a relevant debate about the appropriateness of such practices given their long-term ecological impact (Simberloff et al., 2013).

The complex interaction between the introduction of several exotic species, the adaptation of local fishing to changing conditions, and the exploration of economic alternatives such as tourism, emphasizes the need to comprehensively understand the ecological and socio-economic dynamics of artificial reservoirs. This scenario underscores the importance of developing sustainable management strategies and biodiversity conservation. This could involve the implementation of sustainable land use practices, pollution reduction, population regulation of species like largemouth bass, effective fishing regulation, and the promotion of community participation in decision-making.

Conclusions

Fishing at the Zimapán dam faces multifaceted challenges, from environmental issues to socioeconomic challenges. The water crisis, human impact, and a lack of sustainable management threaten the long-term viability of this activity, indicating complex problems occurring at different spatial and temporal scales. This study highlights the need for integrated approaches and collaborative solutions addressing both the ecological problems and the social dimensions of fishing in the ecosystem. Ecosystems like the Zimapán Dam will become increasingly important in a context of global change; therefore, understanding them as key ecosystems upon which we will depend in the near future is essential. We consider that such ecosystems will become more frequent, posing significant challenges for a field like limnology.

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Authors' Contributions

RCB, MLH, and FCT conducted fieldwork. RCB and FCT performed data analysis. RCB, KERV, MLH, MAGP, and FCT wrote and reviewed the manuscript.

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Conclusions

This book presents limnological research with various lines of progress, focused on continental environments in Mexico, showing certain trends in specific areas such as water quality, characterizing its ionic properties, contrasting between different aquifer systems, but above all, highlighting the environmental problems presented by aquatic resources; A relevant topic that stands out in recent research in Mexico is the study of plankton, which is not restricted only to its characterization or identification at a taxonomic level in the traditional way, but also the studies focus on highlighting its importance in the dynamics of ecosystems, energy transfer, and community structure, the tendency in these investigations is to carry out molecular and genetic studies with emphasis on ecological studies and species evolution, as well as adaptation to adverse scenarios such as Climate Change. On the other hand, the use of zooplankton species as indicators of environmental risk stands out, as well as a review of the studies focused on ecological interactions between zooplankton and macrophytes and one of the groups of great ecological importance and little studied in Mexico, the hydrozoans of continental waters.

Thus, this publication is an excellent reference for limnological research carried out in Mexico, not only for the topics and lines of research addressed, but also for the quality of the information presented and the effort made to achieve knowledge with solid arguments and scientific-academic support, which will undoubtedly support researchers and science students for current and future projects.

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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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