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Dinámica estacional de la comunidad íctica en un lago subtropical del centro de México

Tesis Doctoral

Que presenta:

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Los estados de desorden son siempre
mucho más numerosos que los estados de orden.

De la Segunda Ley de la Termodinámica

CONTENIDO

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RESUMEN

La dinámica ambiental produce variaciones estacionales que afectan la estructura y función de las comunidades. Cuando esta dinámica no es muy marcada, se espera que no haya cambios significativos en la composición y estructura de las comunidades en el tiempo y el espacio, por lo que los atributos ecológicos de las especies tendrán mayor importancia, debido a las estrategias de sus ciclos de vida. Se hipotetiza que los lagos subtropicales con dimensiones pequeñas suelen ser ecosistemas que presentan características ambientales homogéneas, en parte por su importante capacidad de renovación hidráulica, debido a lo que se esperaría que la estructura de la comunidad de peces no cambie a lo largo del tiempo. Como modelo de estudio se utiliza el Lago Zacapu (área de 20 ha aprox.), poco profundo, considerado un lago subtropical monomíctico. Se realizo una estrategia de muestreo de dos años con colectas estacionales en cuatro puntos. Con este muestreo se desarrolló la siguiente investigación: 1) Se determinó la variación espaciotemporal de la estructura de la comunidad en términos de composición, diversidad y abundancia y se comparó con datos de 1995; 2) Se evaluó el ciclo reproductivo de las especies de peces vivíparos nativos, y se describió la variación anual; y 3) se describió la dieta y la estructura trófica mediante contenido estomacal e isótopos estables ($\delta^{13}C$, $\delta^{15}N$). Nuestros resultados muestran que 1) es un lago con características ambientales homogéneas espacialmente, en donde se encuentran 13 especies de peces, once nativas y dos no nativas. La subfamilia Goodeinae es la más representativa. Todas las especies colectadas en los muestreos de 1995 aún están presentes en el lago, indicando que la composición de la comunidad de peces presenta una estabilidad a través del tiempo. Sin embargo, la especie litoral dominante en 1995 fue reemplazado por una especie limnética en 2019-2020, y la diversidad y abundancia de peces sensibles disminuyó en muestreos recientes. 2) Las poblaciones de goodeidos tienen una mayor fertilidad en comparación con poblaciones de la misma especie en otros sistemas acuáticos, los machos maduran en tamaños más pequeños que las hembras, la proporción observada fue mayor en hembras y presentan dos picos reproductivos (primavera y otoño). 3) la estructura trófica permitió clasificar las especies en tres grupos tróficos: carnívoros, omnívoros-carnívoros y omnívoros-herbívoros, no se encontraron diferencias alimentarias significativas entre los diferentes sitios de colecta. En conclusión, la estructura de la comunidad íctica está influenciada por los factores bióticos como los atributos de las especies (ej. estrategias, tácticas reproductivas, estructura trófica) y los factores abióticos como la estabilidad ambiental que posee el lago, lo cual les permiten a las especies subsistir en el tiempo. Sin embargo, los cambios en los atributos estructurales de reducción de abundancias de algunas especies sensibles enfatizan la necesitada de implementar esfuerzos de conservación en este pequeño lago del centro de México.

Palabras clave: Ciclos reproductivos, estructura de la comunidad,
estructura trófica, lago, especies nativas.

ABSTRACT

Environmental dynamics produce seasonal variations that occur in the structure and function of communities. When this dynamic is low, it is expected that there will be no significant changes in the composition and structure of the communities over time and space, and the ecological attributes of the species will present more importance, mainly due to the strategies of their life cycles. The hypothesis is that subtropical lakes with small dimensions tend to be ecosystems that present homogeneous environmental characteristics, in part due to their significant capacity for hydraulic renewal, so it would be expected that the structure of the fish community would not be change over time. Lake Zacapu (area of 20 ha approx.), shallow, considered a monomictic subtropical lake, is used as a study model. A two-year sampling strategy was carried out with seasonal collections at four points and the following investigation was developed: 1) The Spatio-temporal variation of the community structure in terms of composition, diversity, and abundance was determined and compared with data from 1995; 2) The reproductive cycle of native viviparous fish species was evaluated, and the annual variation was described; and 3) diet and trophic structure were described by stomach content and stable isotopes ($\delta^{13}C$, $\delta^{15}N$). Our results show that 1) it is a lake with spatially homogeneous environmental characteristics, where 13 species of fish are found, eleven native and two non-natives. The Goodeinae subfamily is the most representative. All the species collected in the 1995 surveys are still present in the lake, indicating that the composition of the fish community is stable over time. However, the dominant littoral species in 1995 was replaced by a limnetic species in 2019-2020, and the diversity and abundance of sensitive fishes decreased in recent surveys. 2) Populations of goodeids have higher fertility compared to populations of the same species in other aquatic systems, males mature at smaller sizes than females, sex ratio favors the females, and they present two reproductive peaks (spring and fall). 3) the trophic structure allowed to classify the species into three trophic groups: carnivores, omnivores-carnivores, and omnivores-herbivores no significant differences were found in the diet of the species between sites. In conclusion, the fish community is structured by biotic factors such as the attributes of the species (e.g., strategies, reproductive tactics, trophic structure) and abiotic factors such as the environmental stability of the lake, which allow the species to subsist over time. However, changes in the community structural of reduction in the abundance of some sensitive species, emphasize the need to implement conservation efforts in this small lake in central Mexico.

Keywords: Reproductive cycles, community structure, trophic structure, lake, native species.

INTRODUCCIÓN GENERAL

La biodiversidad y el funcionamiento de los ecosistemas acuáticos dependen de la estructura y función del conjunto de especies que lo habitan, tanto en tiempo como en espacio (East et al., 2017). Los sistemas acuáticos se mantienen por factores bióticos (ej. competencia, depredación) y abióticos (ej. temperatura, oxígeno), los cuales en conjunto provocan cambios en la disponibilidad de recursos, estructuran las comunidades y la dinámica de la red alimentaria (Wang et al., 2016). La evaluación de la estructura y función de los sistemas acuáticos dulceacuícolas se aborda a continuación en el siguiente artículo de revisión.

Ecological topics related to food webs: a review with emphasis on global freshwater fish communities

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Ecological topics related to food webs: a review with emphasis on global freshwater fish communities

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Abstract

Understanding the structure and dynamics of freshwater food webs remains a challenge for ecologists, mainly due to factors, mechanisms, and processes that maintain communities must be considered. This study aims to analyze the state-of-the-art food web on freshwater fish communities through a systematic literature review and applying the co-words bibliometric technique. Particularly, developed countries have increased the study of food webs in the last years. The evaluation of the different ecosystem components like phytoplankton, zooplankton, and aquatic macroinvertebrates are important to considered in food webs, and stable isotope analysis accompanied by stomach content as methodologies. Food web is usually represented by models (e.g., Ecopath with Ecosim) or diagrams (food networks connecting species). Further research is needed on describe food webs in freshwater system from developing countries.

Keywords: Communities, trophic structure, stable isotopes analysis, gut content, ecological network analysis.

Resumen

Comprender la estructura y la dinámica de las redes alimentarias en sistemas de agua dulce sigue siendo un desafío para los ecólogos, principalmente debido a los factores, mecanismos y procesos que deben tenerse en cuenta para que se mantengas las comunidades. Este estudio tiene como objetivo analizar el estado del arte en el tema de la red alimentaria en las comunidades de peces de agua dulce a través de una revisión sistemática de la literatura y aplicando la técnica bibliométrica de co-palabras. Particularmente, las redes alimentarias se han estudiado más en los países desarrollados en los últimos años. La evaluación de los diferentes componentes del ecosistema como el fitoplancton, el zooplancton y los macroinvertebrados acuáticos son importantes para considerar en las redes alimentarias y el análisis de isótopos estables acompañado del contenido estomacal como metodologías. La red alimentaria generalmente se representa mediante modelos (por ejemplo, Ecopath con Ecosim) o diagramas (redes alimentarias que conectan especies). Se necesita más investigación para describir las redes alimentarias en el sistema de agua dulce de los países en desarrollo.

Palabras clave: Comunidades, estructura trófica, análisis de isótopos estables, contenido estomacal, análisis de redes ecológicas.

Introduction

Food webs are one of the principals thematic in ecological science, the first depictions of community-wide feeding relationships were published in the early 20th century (Egerton, 2007). Yet, many people associate the dawn of food web ecology with Charles Elton (Elton, 1927). Through time, several authors have been added more specific ideas and important terms to Elton´s contributions: the flow of energy through ecosystems, trophic dynamic (Lindeman, 1942), food web complexity and stability (May, 1972), generalized food web models (Cohen, 1978), functional food webs (Paine, 1980), ecological network analysis (Polovina, 1984), stable isotopes perspectives of food web structure (Van der Zander and Rasmussen, 1999), trophic cascades (Carpenter, 1985), intraspecific trophic variation (Bolnick, 2003), keystone species (Libralato et al., 2006), between others.

Food web in communities describes either species and networks that represent interactions among a group of organisms, populations, or trophic units, the energy and biomass flow among compartments, species are represented by nodes, and trophic relationships are represented by links (Jordán and Scheuring, 2002). These depictions of feeding relationships can provide insight into almost every area of ecological research, ranging from population dynamics to the cycling of nutrients through ecosystems.

It is challenging to find a specific sub-discipline of ecology that is not related to, or relevant for, understanding of food webs, mainly due to having implications at the population (Winemiller, 1990), community (Paine, 1980), ecosystem (Carpenter et al., 2001) and evolutionary (Post and Palkovacs, 2009) levels. In this context, one of the taxonomic groups that must be considered is fish species because they are economically and ecologically important worldwide, mainly due to important food resources for humans; they also perform many functions within ecosystems (*bottom-up and top-down* theory, details coming later). Unfortunately, anthropogenic activities such as climate change, habitat degradation, pollution, the introduction of nonnative species, and overfishing are causing a decrease in fish populations (O'Reilly et al., 2015), leading many species to face extinction, thereby inducing cascade effects in ecosystems, for example, competition for resource between species (Devlin et al., 2017). Fish are mobile sources of critical nutrients like nitrogen and phosphorus (Samways and Cunjak, 2015); spatiotemporal variations in the production and biomass of fish create patterns in the freshwater and riparian food webs generally (García et al., 2015). Therefore, fish are represented on practically every trophic level, from herbivores to tertiary predators and decomposers (Delong et al., 2019). Some species are highly specialized to feed on items such as scales and fins, while others are generalists with broad diets, especially when exploiting abundant resources (Nelson, 2015). In addition, fish act as energy regulators between adjacent ecosystems by transforming and exporting energy from primary producers, and are the components of 90% of the nekton, as well maintaining energy reserves within food webs and are bioindicators (Dudgeon, et al., 2006).

Freshwater ecosystems including rivers, streams, lakes, wetlands, are critical for biodiversity, providing habitat for one third of all the vertebrate species, including approximately 40% of fish species, also they are some of the most important resources in the replenishment and purification of water sources used by humans (Lynch et al., 2016).

Despite covering only 0.01% of the Earth's total surface, they supply essential ecosystem services such as food, water, and energy provision to billions of people (Mota et al., 2014). Unfortunately, they are also one of the most highly degraded ecosystems, suffering from chemical contamination by waste and plastics, overexploitation of aquifers, eradication of wetlands, and others (Carpenter et al., 2011).

The objective of this research was to carry out a bibliometric review of the literature to understand better freshwater ecosystem food webs related to the fish community. The analysis of important topics in recent years provides an informative reference on the basic concepts and advantages in quantifying the food webs in communities and their applications to freshwater fish. Besides, we attempted to identify and comment on general gaps in the study of food webs in freshwater fish communities and give directions for further studies concerning this subject.

Methods

The research was focused on articles in the Scopus database and Web of Science-Thompson Reuters, these databases were selected because they are considered the largest abstract and citation database of peer-reviewed literature, with more than 60 million records, covering over 21,500 peer-reviewed journals from over 5000 international publishers in different scientific areas (Joshi, 2016).

In the first phase, articles were selected that used the terms *Freshwater* Fish* community** and *Food web** in the title, abstract, or keywords. As a result, an initial sample of 359 documents in Scopus and 972 documents in Web of Science was found. The topic of food webs has been aborded since the last century (Elton, 1927), however, this study aims to examine the most recent and innovative literature, a six-year timeframe was selected covering the period between 2015 and 2021, resulting in 164 documents in Scopus and 447 documents in Web of Science. The review was limited to “Article,” “Review,” and “Books” documents because they are the source of most up-to-date knowledge and probably have a greater impact on the field. The literature that only presented anthropology, archaeology, phytochemical, immunological data were excluded. Only articles with the language “English” were considered, since the dissemination of scientific knowledge is fundamentally done in this language and is a criterium used in various reviews (e.g., Thompson et al., 2012).

Results

Descriptive information: A total of 117 documents in Scopus and 388 documents in Web of science were obtained. After reading the abstracts and eliminating those that do not refer to freshwater fish and food webs, the final number of articles was 358 in both databases. The study of the freshwater fish communities and food web has been maintained a constant number of publications in Web of Science, with a decline in 2021, whereas Scopus databases showed in 2015 the lowest number of publications and increased in 2021 (Figure 1). The year with the highest number of articles was 2020, with 60 articles on Web of Science.

Figure 1

The publications are led by the Freshwater Biology journal, followed by Freshwater Science and Ecology, most of the journals are quartile one, only Ecology of Freshwater Fish and Journal of Great Lakes research are quartile 2. The highest impact factor is in Ecological monographs (10.31), following of Ecology (5.49) (Figure 2). The study fields of environmental science, ecology, freshwater ecology, and fisheries have extensive studies in freshwater fish communities and food web in Scopus database and Web of Science.

Figure 2

In this research, the results showed that the United States is the country that published the most articles about the food web in freshwater fish communities, followed by Canada and Germany (Table 1).

Table 1

The principal institutions are United States Geological Survey and United States Department of the Interior from USA (Table 2).

Table 2

Theories: Not all articles handle theories to test, some of them only mention fundamental concepts within the document. Twelve percent of the articles mention the Theory of *Bottom-up* and *top-down*, this is the main approach theory used to explain the study of the determinants of biomass pyramids (i.e., the patterns of the biomass of organisms at different trophic levels of an ecosystem) within and across ecosystems. This theory was first mentioned in 1986, established resource use *versus* consumer limitation (McQueen et al., 1986).

The “*trophic cascade”* is a concept considered by some authors in the documents reviewed (8% of the documents), this is for understanding trophic interactions, resulting in alternating abundance, biomass, or production across more than once trophic levels in an ecosystem (e.g., Leroux and Loreau, 2015; Rodríguez-Lozano et al., 2016). Trophic cascades have often been applied to explain indirect top-down effects in ecosystems. Broadly defined, trophic cascades refer to the indirect effects of an ecosystem perturbation (i.e., change in soil nutrients or predation rate) throughout an ecosystem (Carpenter et al., 1985).

The assembly rules are also included in some documents reviewed (5%), they have helped provide a means to generate realistic food web structures (Fath et al., 2007; Fath et al., 2019). They are used to describe general principles arising from mechanisms operating within the community and to which the assemble of a community conforms, for example relationship between community temporal dynamics and ecological stochasticity of an ecosystem, probably caused by anthropogenic activities (e.g., Li et al., 2021).

Approaches in consideration in the food web: Within the revised articles, some important topics are maintained that must be considered within the evaluations of food webs, for example, the diet of the species, trophic position, habitat use, the ecosystem functions as a biological, geochemical and physical process, like the decomposition, production, nutrients cycling and nutrient energy flows between species in the community, to determines how an ecosystem responds to perturbations and thus is key to understanding the ability to respond to perturbation without loss of essential functions (Ives et al., 2018).

The review of the studies indicates that fish play an important role in the trophic dynamics in freshwater ecosystems; through predation on zooplankton, planktivorous fish may promote cascading trophic effects (top-down) leading to increased phytoplankton biomass and reduced water clarity (Laske et al., 2017). Hence the literature has been centered on better understanding how the structure of the fish community may change depending on biotic and abiotic factors. Spatial and temporal variation in the relative abundance of dominant and other species likely is influenced by species differences in habitat selection, reproduction, and recruitment (e.g., Grubh and Winemiller, 2018). Fish community patterns were primarily attributable to seasonal changes instead of spatial gradient and habitat types (Sather et al., 2016). Various studies have suggested the importance of biotic interactions across habitats (littoral, benthic and pelagic zone).

Nowadays, one of the main focuses within the reviewed articles is the interactions of native and nonnative species, and several authors mention that invasive species are causing damage in native fauna (e.g., Pereira and Vitule, 2019). Introductions of nonnative species and their subsequent dispersal can change the structure and composition of entire communities (Gallardo et al., 2016). Moreover, present nonnative species simultaneously occupy different trophic levels and interact across trophic levels, leading to increased and often unforeseeable effects due to the prevalence among predators (Martins et al., 2021). The ecological consequences of nonnative freshwater fish introductions have been well documented (Cucherouset and Olden, 2011). However, most studies of the effects of nonnative fishes address solely direct effects rather than indirect interactions, such as cascading effects on other ecosystem compartments, that can alter ecosystem functioning in unpredictable ways.

The effects of nonnative fishes can cascade beyond conventionally defined habitat boundaries and have significant consequences for food web dynamics (Gallardo et al., 2016). However, such effects often are overlooked because researchers typically limit the scope of their studies to one system or even a single system component. For example, in some aquatic systems, lakes and rivers are physically connected, thereby generating the potential for several modes of interaction via resource use (Gou et al., 2018).

The design of the study, methodology: Different methodologies were used in the articles analyzed during the review process. The main methodology used was the Stable Isotope Analysis (SIA) of carbon ($\delta^{13}C$; information on food resources) and nitrogen ($\delta^{15}N$; information on trophic position). This methodology provides a powerful tool for measuring the trophic structure by describing the relative trophic positions of consumers within a community and the contributions of distinct basal resources (Svanbäck et al., 2015). This technique permits various fish tissues to be analyzed, but soft tissue, generally muscle, has typically been preferred. It is easy to collect and prepare material, and it provides the means to analyze several isotopic tracers (carbon $\delta^{13}C$, nitrogen $\delta^{15}N$, oxygen $\delta^{18}O$, sulfur $\delta^{34}S$).

Furthermore, this technique has been developed to investigate the consequences of nonnative fish species introductions on trophic structures (Sagouis et al., 2015). They provide a powerful approach to predicting the invasion impacts of nonnative species and the degree of dietary competition pressure felt by native species (Hill et al., 2015).

The gut content analysis usually complements the stable isotope methodology (e.g., Laske et al., 2018). The gut content analysis consists of dissecting the fish stomach, and prey items are identified to the lowest taxonomic level possible. A prey accumulation curve must be elaborated for the fish species to determine whether the number of analyzed stomachs that accurately described the diet (Márquez-Velásquez, et al., 2019). Two indices were mainly mentioned in the reviewed articles to evaluate the contribution of each prey item to the diet of the fish species, the index of relative importance (IRI) (Yáñez-Arancibia et al., 1976) and prey-specific index of relative importance (PSIRI) (Brown et al. 2012). In addition, other two important index are the diet overlaps between taxa, which is possible to assess by the Horn´s index and trophic niche width calculated using the standardized Levin´s index (Krebs, 1989).

The use of multiple approaches allows more robust assertions about the trophic patterns and trophic interactions among species (Weidner et al., 2017). Stable isotopes and gut content analyses complement each other to gain more insight into the feeding relationships of fish species and the degree of dietary resource sharing (Mwijage et al., 2018). Gut content may underestimate niche widths if there is limited diet information for each individual in the population, for example, if stomach size is small or resource competition constrains the number of preys consumed per individual (Svanbäck et al., 2015). The use of stable isotopes is important, especially when characterizing the diet and feeding interaction of predatory fish species that sometimes have high prey regurgitation and stomach vacuity (Hill et al., 2015).

Aquatic components from the system: Phytoplankton and zooplankton biomass and composition were evaluated as complementary components in several documents reviewed (e.g., Kovalenko et al., 2019), considered important drivers of the aquatic ecosystem function. The phytoplankton assemblage composition is essential to predict food web responses to stressors, including increased nutrient loading, changes in surface temperature, and thermocline depth (Vesterinen et al., 2016). The zooplankton moderate effects of fish on phytoplankton biomass (Beaver et al., 2019). Another important group in food webs are the macro-invertebrates, they are considered a good biological indicator in aquatic systems and play an important role in trophic transfer within and across ecosystems, linking energy flow from basal food sources to upper trophic levels such as fish and eventually respond to a wide range of anthropogenic impacts (Dedieu et al., 2015). Phytoplankton, zooplankton, and macroinvertebrates can affect the food web by periphyton assimilation, species identity, functional feeding groups, and seasonal and spatial environmental variations, mainly due because their functional role in linking the energy flow from basal food sources to higher trophic levels (Guo et al., 2018).

Mathematical modeling: In the selected works reviewed, the trophic structure is usually represented by models (Ecopath with Ecosim) or diagrams (food networks connecting species), but it can also be assessed by a more simplified approach based on the use of trophic guilds (Konan et al., 2015).

The Ecopath and Ecosim (EwE) modeling approach was primarily developed to answer ‘what if…’ questions that could not be addressed with single-species assessment models (Christensen and Walters, 2004). The Ecopath model can be seen as a toolbox offering a large collection of methods to analyze various ecological phenomena, for example, it has been widely used to analyze the trophic structure and energy flow between all species occurring in the aquatic ecosystems and predict trends in their development (Deehr et al., 2014). It is recognized as a core new-generation tool for studying aquatic ecosystems worldwide (Ortiz et al., 2015). The EwE modeling complex consists of a suite of three main sub-models: (1) Ecopath, static and descriptive, (2) Ecosim, dynamic and predictive, and (3) Ecospace, spatially explicit, dynamic, and predictive (Christensen and Walters, 2004). Ecosim uses the outputs of Ecopath to produce time-dynamic simulations of changing trophic interactions with changes in the ecosystem due to anthropogenic or environmental disturbances (Moutopoulos et al., 2018). Ecosim may be used to fit model predictions to time-series data and explore different fisheries management or climate change scenarios (Christensen and Walters, 2004).

On other hand, diagrams analysis considers interaction strength may identify species whose impacts on their communities are disproportionately large relative to their abundances (Reis et al., 2020). The diagrams analysis provides an effective method to understand and describe the topological structures, dynamic characteristics, and the complexity of functions between species within the food web (Jiang and Zhang, 2015). In addition, an ecological network analysis is an important tool to understand whole-system interactions in the food web, which include the energy-matter flow of who eats whom, and non-feeding pathways to detritus (Fath et al., 2007; Fath et al., 2019). Other modeling options have been also used in food webs are for example STELLA (Spieles and Mitsch, 2003), EcoNet (Kazanci, 2007), and statistics packages for the program R (e.g., enaR, Borrett and Lau, 2014).

Current limitations: Determining the disturbances' effects on the biotic communities represents a major challenge in most of the reviewed articles. To understand the effects of climate change at an ecosystem level, ecologists need to better understand their impact across the trophic structure; the disturbances occur over long-temporal scales, and it is difficult to isolate the effects of these interlinked stressors. Given changing environmental conditions and anthropogenic impacts on freshwater communities, understanding the adaptive capacity of food webs supporting important resources, such as commercial fisheries are vital to ecological and economic stability.

Although the effects of environmental variability on the trophic structure of fish assemblages have been investigated, most works are based on short-term sampling focusing mainly on local factors (e.g., temperature, turbidity, and salinity) (Nelson et al., 2015). However, many ecological processes and environmental phenomena occur on a long-term time scale or are cyclical processes, requiring several years or even decades of continuous monitoring and investigation to understand their influences on the biota.

Future directions: The study of food webs in freshwater fish communities has grown in recent years in developed countries, based in the increase of the number of publications (Figure 1). However, we consider that certain questions can help us expand our knowledge about the relationship between food webs, freshwater communities' structure, and ecosystems' functioning. Further research is needed on what traits best describe food webs in a freshwater system. In this sense, there are important advances in the homogenization of criteria in the main use methodologies as stable isotopes analysis inconjunct with stomach content and mathematical models. However, it could be interesting to incorporate the molecular-based approaches, which have made DNA techniques more available to ecologists for reconstructing consumers' diets, identifying species interactions, showing how food webs are structured. By amplifying genes and comparing sequences to existing DNA libraries of known species. Few studies have examined food web involving interacting species across several trophic levels, established their interactions are critical to restoring function to degraded freshwater ecosystems. It is important to consider the evaluation of food webs in tropical and subtropical lakes and hots spots with endemic species. The articles reviewed in this study focused mainly on big lakes and rivers in template areas, less in-stream, ponds and in tropical and subtropical areas.

Conclusions: This research is focus on food webs on freshwater fish communities, this issue being more examined in developed countries in the last years. There is a concern about the methodologies that could be used to evaluate a project, targeted not only in international researchers but also to grad students in higher education institutes.

Considering its deeper multidisciplinary nature, the articles included in this systematic literature review were published in a great diversity of journals, analyzing various themes such as ecology, environmental sciences, fisheries, and water resources.

The studies on significant aspects such as the changes in abundance, species richness, size distribution, life history of the species, feeding habits (diet), space use, and trophic dynamics will improve the understanding of the changes in food webs in freshwater fish community structure and dynamics, and the potential cascading effects (bottom-up and top-down). Evaluating periphyton, phytoplankton, and zooplankton is vital to understand the roles and the limitations of the species, finding their position in the trophic cascade (filter-feeding herbivorous fish, predator control, omnivorous fish). Stable isotope analyses of carbon and nitrogen together with gut content analysis provide a powerful approach to predicting the invasion impacts of nonnative species and the degree of dietary competition pressure felt by native species. Thereby enhancing the chances of preserving the freshwater ecosystems with high diversity.

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Figures

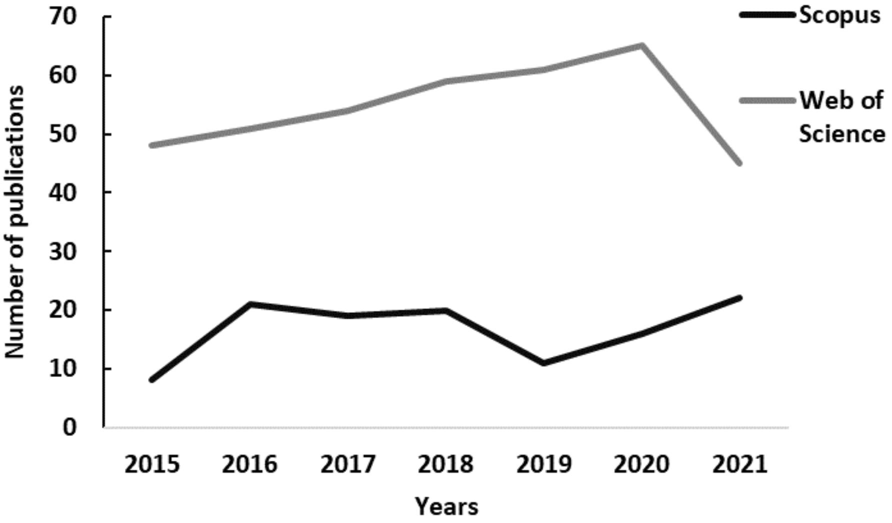

Figure 1. Total of articles published during 2015 to 2021 in Scopus databases and Web of Science.

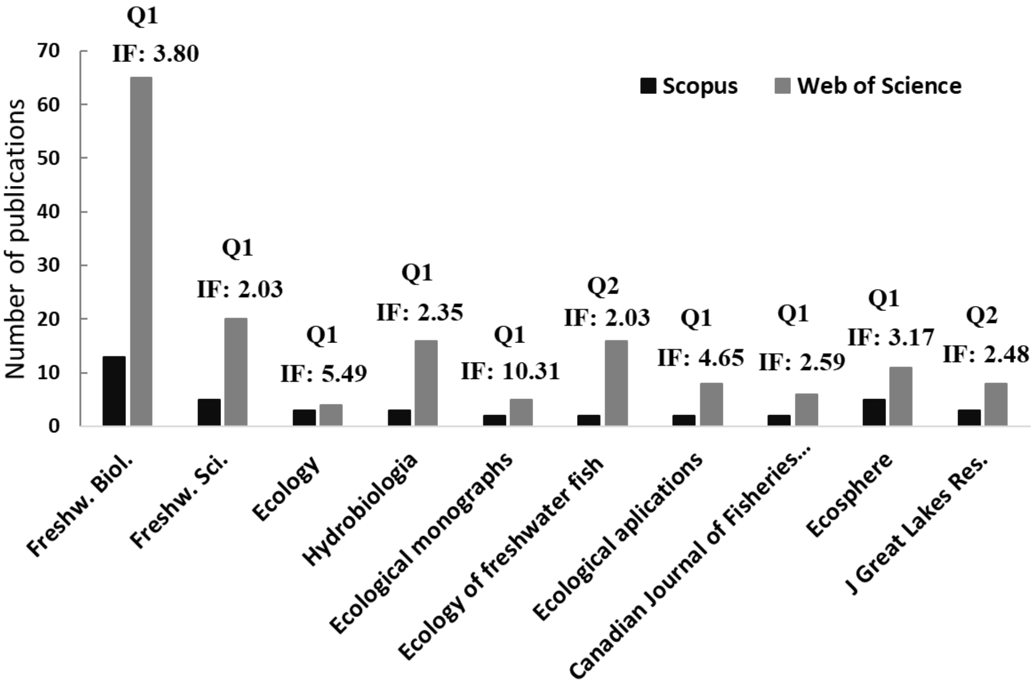

Figure 2. Main journals with their impact facor and quartils, per number of articles published in Scopus database and Web of Science. FI = impact factor, Q= Quartils.

Tables

Country	Number of articles in Scopus	Number of articles in Web of Science
United States	45	78
Canada	20	56
Germany	11	28
China	5	28
England	10	23
Australia	7	22
Spain	5	20
México	2	6

Table 1. Main countries with a number of articles published by Scopus database and Web of Science.

Scopus Institution and country	**Number of publications**	**Web of Science Institution and country**	**Number of publications**
United States Geological Survey (USA)	15	United States Department of the Interior (USA)	27
Aarhus University (Denmark)	9	United States Geological Survey (USA)	25
CNRS Centre National de la Recherche Scientifique (France)	9	CNRS Centre National de la Recherche Scientifique (France)	23
University of Washington, Seattle (USA)	8	University of California System (USA)	21
University of Wisconsin-Madison (USA)	8	CNRS Institute of Ecology Environment INEE (France)	14
The University of British Columbia (Canada)	7	Aarhus University (Denmark)	12

Table 2.- Principals institutions and their origin country, and the number of publications per database (Scopus and Web of Science)

Las comunidades en sistemas dulceacuícolas, principalmente en cuerpos de agua pequeños, son focales para determinar cuáles son los factores que las están estructurando, e idóneos para explorar los efectos ambientales sobre los patrones de ensamblaje de la comunidad, debido principalmente a que albergan niveles altos de diversidad y presentan diferentes funciones ecosistémicas importantes (Biggs et al., 2017). En ese sentido, el lago Zacapu, es utilizado como modelo de estudio en el presente trabajo. Es un lago volcánico ubicado en el centro-occidente de México, en el estado de Michoacán. Tiene una superficie aproximada de 20 ha (Ayala-Ramírez et al., 2007), mantenido por la contribución de numerosos afluentes de manantiales. Las condiciones físicas y químicas del agua en el lago (por ejemplo, temperatura del agua, oxígeno disuelto) son homogéneas en todo el ecosistema (Moncayo-Estrada, 1996; Valencia-Vargas y Escalera-Vázquez, 2021), debido a que existe una gran capacidad de renovación hidráulica, por el flujo continuo de agua de los numerosos manantiales (Domínguez-Domínguez et al., 2008). Las características generales del sistema de estudio son abordadas en el siguiente artículo de divulgación.

Small Lake, High Biodiversity

Arely Ramírez-García, Rodrigo Moncayo-Estrada y Omar Domínguez-Domínguez

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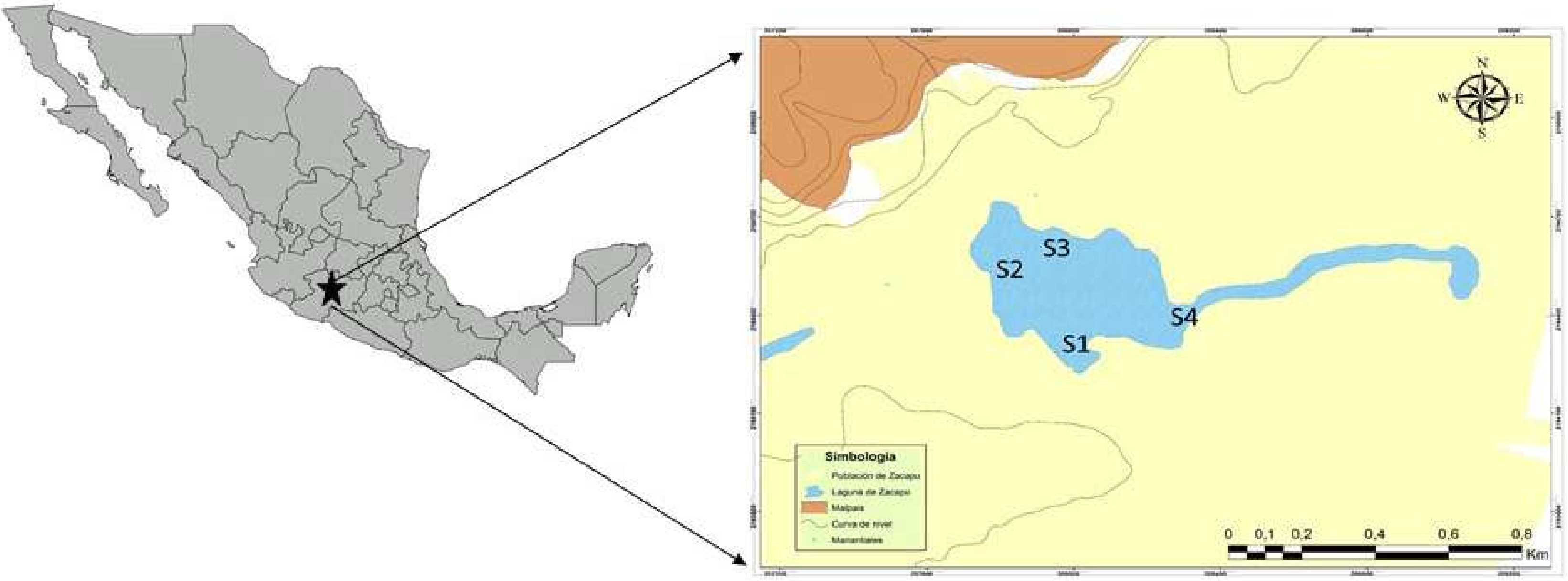

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NEWS FROM GOODEID COUNTRY

Small Lake, High Biodiversity: Lake Zacapu, México

by

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Dr. John Lyons

John Lyons is a lifelong fish fanatic who has been fortunate to translate his passion into a career as a professional ichthyologist and fisheries scientist. He has been observing, catching, keeping, and cooking and eating fish for well over 50 years, and has kept *Goodeids* almost exclusively for the last decade. When not focused on fish and their habitats, he likes reading, history, and travel.

The spread of non-native species, Some small lakes have high biodiversity and are a refuge for species that have disappeared from larger water bodies. However, often they are surrounded by urban areas and exposed to high levels of human impacts. In addition, many small waters have been poorly studied and may not have water management plans. Yet, their fishes are important elements of both the aquatic and human communities and could serve as biological indicators of human-induced changes in lake ecosystems. Further, knowledge of species interactions could help in developing management decisions and conservation policies. Lake Zacapu, México, is just such a lake.

Lake Zacapu is located in central-western Mexico in the Lerma-Chapala river basin, has a surface area of 216 hectares (534 acres), and is 1,980 meters (6,494 ft) above sea level *(Figure 1).* It is a Protected Natural Area because it hosts several endemic and native fish and amphibian species, provides ecosystem services to the surrounding human communities, and possesses cultural regional importance. In 2005, a management plan was developed and implemented, but despite that human impacts are still present, including wastewater discharges, water extraction, non-native species, overfishing, and wetland destruction. We have developed a project to assess the condition of the lake and its fish community. Our principal objectives are to: (1) describe spatial and temporal variation of the fishes in relation to environmental variables in the lake; (2) evaluate aspects of the biology of the fishes including feeding, reproduction, and competition; and (3) use this information to evaluate the effectiveness of the management plan and provide recommendations to relevant decision and policy makers. We hope that recommendations will be included in a revised management plan to improve long-term conservation of the lake and its fishes.

Based in part on funding from the North American Branch of the Goodeid Working Group of the American Livebearers Association, sampling of Lake Zacapu fishes will take place between May 2019 and May 2020 on four occasions (dry season = January and May and rainy season = July and October) at four sampling sites. The sites are distributed along the shoreline and chosen to represent differ-

Scientific Name	Common Name	IUCN Red List/NOM-059	Native/ Non-Native
Goodeidae			
Alloophorus robustus	Bulldog Goodeid	Vulnerable/IUCN	Native
Skiffia lermae	Olive Skiffia	Endangered/IUCN Threatened/NOM-059	Native
Hubbsina turneri	Highland Splitfin	Critically Endangered/IUCN Danger of Extinction/NOM-059	Native
Zoogoneticus quitzeoensis	La Luz/Tarascan Splitfin	Endangered/IUCN Threatened/NOM-059	Native
Xenotoca variata	Jeweled Splitfin	Least Concern/IUCN	Native
Goodea atripinnis	Blackfin Goodea	Least Concern/IUCN	Native
Allotoca zacupuensis	Catarina Allotoca	Critically Endangered/IUCN	Native
Poeciliidae			
Poeciliopsis infans	Lerma livebearers	Least Concern IUCN	Native
Atherinopsidae			
Chirostoma humboldtianum	Shortfin silverside	Vulnerable/IUCN	Native
Cyprinidae			
Algansea tincella	Spottail Chub	Least Concern/IUCN	Native
Notropis grandis	Zacapu Shiner	Endangered/IUCN	Native
Cyprinus carpio	Common Carp		Non-Native
Ctenopharingodon idella	Grass Carp		Non-Native

Table 1 Fish species from Lake Zacapu

ent habitats in the Lake (Moncayo-Estrada, 1996). With the help of local fishers and researchers from the Regional Center of Aquaculture and Fisheries Research of Pátzcuaro (CRIAP by its Spanish acronym), fish are sampled with a seine net of 25 m long and 1.8 m high, with a 5 mm mesh opening *(Figure 2)*. Each captured fish is identified, weighed, and counted and then released at the site of capture.

We have found that Lake Zacapu hosts 13 fish species in four families—11 natives and 2 non-natives *(Table 1)*. Five are of conservation concern according to the International Union for Conservation of Nature (IUCN) and Mexican Federal laws (NORMA 059-SEMARNAT). There is as well one endemic salamander, an axolotl *(Ambystoma andersonii)*. Thus far, we have a collected a total of 4,072 specimens weighing 70.887 kg (156.28 lbs) in total. *Goodeidae* (7 species) is the richest family, followed

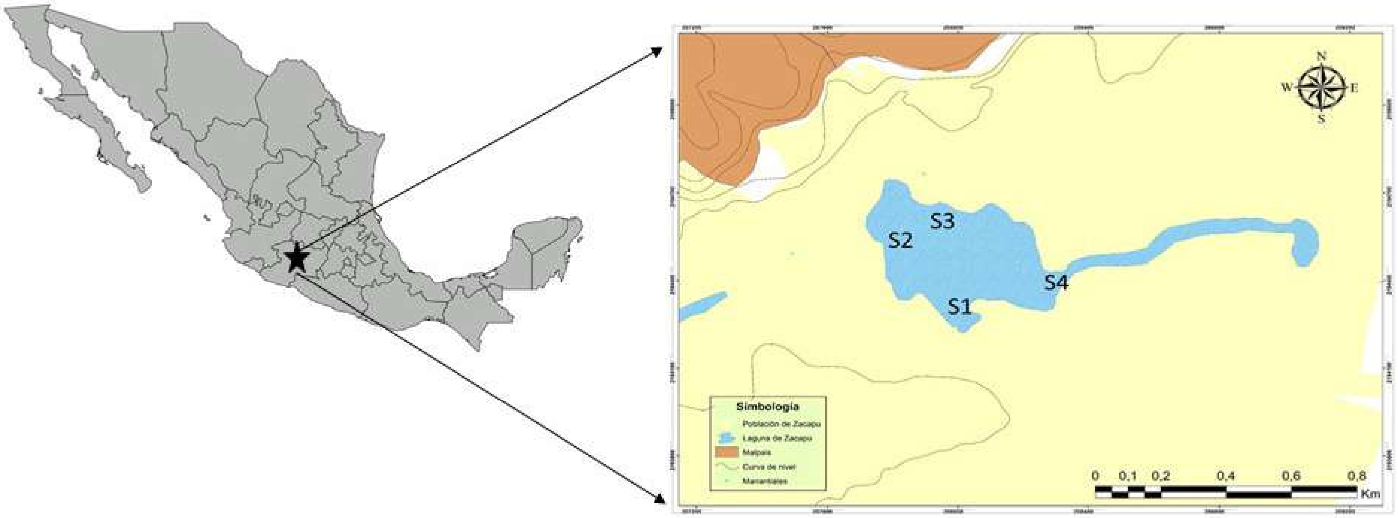

Figure 1 Location of the Lake Zacapu and Sampling Sites (S1–S4).

by *Cyprinidae* (Minnows) (4 species). The silverside *Chirostoma humboldtianum (Figure 3)* is the dominant species with the highest abundance and biomass, followed by the Goodeid *Xenotoca variata.* These values differ from previous studies in which the *Cyprinid Notropis grandis* and the Goodeid *Goodea atripinnis* were the dominant species. The Goodeid *Hubbsina turneri (=Girardinichthys ireneae)* already extinct in larger water bodies to the east (Lake Cuitzeo and Cointzio Reservoir), is now found only in Lake Zacapu and cataloged as Critically Endangered by IUCN and Endangered by Mexican Federal laws *(Figure 4).* The Goodeid *Allootoca zacapuensis* and *Notropis grandis* are endemic to this lake and classified as Critically Endangered and Endangered by the IUCN, respectively. The Goodeids *Skiffia lermae* and *Zoogoneticus quitzeoensis* are considered Endangered by the IUCN and Threatened by the Mexican Federal Government.

We plan to collaborate with local communities and government to conserve these species. Results from this study will help to establish a comprehensive analysis of this small subtropical lake with two marked climatic seasons. We will identify the variations in life strategies of the species which could reflect their local adaptation, monitoring the responses of the fish to identify those susceptible to anthropogenic impacts and contributing to their conservation. With the historical and current data, we will provide information and recommendations to respective authorities and local people about the management plan for Zacapu Lake. In addition, we want to help establish sampling protocols that could be used to evaluate fish communities in different water bodies and in different areas of Mexico.

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Figure 2
Zacapu team, fishers, and CRIAP fishing in Lake Zacapu with a seine net

Figure 3
Chirostoma humboldtianum, the most abundant species during the study

Figure 4
Hubbsina turneri, a Critically Endangered species by the IUCN

ENFOQUE DE LA TESIS

En el presente trabajo se analizó la dinámica temporal (decadal y estacional) y espacial de la estructura y función de la comunidad íctica en un lago subtropical mexicano. La hipótesis general se plantea de la siguiente manera: la dinámica ambiental produce variaciones estacionales más que espaciales, que afectan la estructura y diversidad de las comunidades ícticas, la cual estará determinada por factores y procesos bióticos y abióticos, donde los atributos de las especies tendrán gran importancia. Para responder a esta hipótesis se planteó el siguiente objetivo general: evaluar la dinámica de la comunidad íctica y su función en el lago de Zacapu, relacionando los factores asociados a la estructura y función de la comunidad a escala temporal y espacial.

Para poder abordar esta hipótesis y objetivo general se generaron cuatro capítulos, descritos de la siguiente manera:

Capítulo I

El uso de diferentes artes de pesca permite tener una aproximación más cercana de la distribución, abundancia y riqueza de especies en un ecosistema, indicando que no está sesgada por el método de captura. Con base a esto, en el primer capítulo se planteó como objetivo comparar la efectividad de cuatro trampas diferentes. Se evaluó la información que brindan sobre la comunidad de peces, estableciendo similitudes y diferencias en la eficiencia de la pesca entre los modelos de trampa. Como hipótesis se estableció que las trampas con mayor abertura de entrada serán las que obtengan la mayor riqueza y abundancia de especies.

Capítulo II

En el capítulo II se analizó si los patrones de la estructura de la comunidad de peces están determinados por factores bióticos o abióticos. Se dispuso de datos cualitativos y cuantitativos de la ictiofauna del lago Zacapu de 1995, y se realizaron colectas siguiendo el mismo protocolo de muestreo de 1995 (Moncayo-Estrada, 1996). Este capítulo plantea los siguientes objetivos: (1) evaluar los cambios temporales en dos décadas y entre estaciones en términos de estructura de la comunidad (abundancia de especies y diversidad), e (2) identificar patrones de asociación entre la estructura de la comunidad de peces y variables fisicoquímicas. Como hipótesis planteamos que debido a que los factores abióticos son homogéneos de manera espacial, pero fluctúan de manera estacional en el lago de Zacapu, se espera que la estructura de la comunidad de peces no cambie con el tiempo en diferentes décadas, y este relacionada con los cambios estacionales de los factores abióticos.

Capitulo III

En el capítulo III se incorpora el análisis del aspecto funcional. Tuvo como objetivo evaluar el ciclo reproductivo de las especies de goodeidos, describiendo la variación anual a escala temporal de la proporción de sexos, talla de primera madurez, índice gonadosomático, fertilidad y factor de condición de las especies que habitan en el lago de Zacapu. Utilizando un enfoque teórico de la teoría de la historia de vida, la que permite identificar rasgos invariantes y variables ambientales que caracterizan el ciclo reproductivo de las especies. Hipotetizamos que la homogeneidad ambiental permitirá que las especies nativas presenten una combinación de rasgos de historia de vida (madurez temprana, altas tasas de fertilidad) que favorece un alto éxito reproductivo en el lago de Zacapu comparado con otros cuerpos de agua.

Capitulo IV

Finalmente, el cuarto capítulo está integrado por la descripción de dieta y la estructura trófica mediante el análisis del contenido estomacal e isótopos estables de carbono y nitrógeno. Como objetivo del capítulo se describe la dieta de las especies de peces en el lago, y se documentó su posición trófica en la red alimentaria de manera temporal (dos estaciones) y espacialmente (4 sitios). Hipotetizamos que, debido a la homogeneidad espacial ambiental del lago, se espera que la estructura trófica de la comunidad íctica sea homogénea, sin embargo, la variación estacional influirá en la estructura de las cadenas tróficas.

Por otro lado, y para complementar la discusión general de la tesis, se evaluaron algunos componentes de la red alimentaria, los grupos de fitoplancton y zooplancton, en términos de diversidad, riqueza y composición, los resultados son abordados en la discusión general y los resultados mostrados en el anexo I. También se integran en la discusión general los resultados de los aspectos reproductivos de algunas especies ovíparas del lago anexo II.

Todas las técnicas de muestreo de campo realizadas y los protocolos de manejo de peces fueron revisados y aprobados por la Secretaría de Medio Ambiente y Recursos Naturales de México (SEMARNAT- SGPA/DGVS/00012/19), Secretaría de Medio Ambiente, Cambio Climático y Recursos Naturales (SEMACCDET-OS. 0084/2019), y la Secretaría de Agricultura y Desarrollo Rural (SAGARPA: PPF/DGOPA-014/20).

JUSTIFICACIÓN

Los resultados de este estudio describen el análisis integral de un cuerpo de agua pequeño subtropical con dos estaciones climáticas marcadas, la gran mayoría de estudios similares se han hecho en latitudes templadas, por lo tanto, el presente estudio permite establecer protocolos para la evaluación de comunidades en diferentes lagos subtropicales, además identifica las variaciones en las estrategias de historias de vida de las especies, las cuales pueden reflejar las adaptaciones locales de las poblaciones, mostrando aquellas susceptibles a los impactos antrópicos y así con dicha información aportar datos útiles para su conservación.

RESULTADOS

Colecta de peces con red de tipo chinchorro. Fotografía aérea de la parte Norte del Lago de Zacapu, tomada por Luis Baltazar Cruz.

Capítulo I

Comparison of minnow trap efficiency for fish community evaluation in a small Sub-Tropical Lake

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Para someter a Fisheries Ecology and Management

Comparison of minnow trap efficiency for fish community evaluation in a small Sub-Tropical Lake

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Abstract

Exploring the effectiveness of collection methods with minimal impact on fish populations and their habitats is important for freshwater monitoring and conservation. The effectiveness of four low impact models of minnow traps (*rectangular minnow traps, folding minnow traps, metallic minnow traps, and circular minnow traps*) in a shallow Mexican subtropical lake was explored. The number of fish caught per hour was estimated for each minnow trap type, the species richness and fish relative abundance among traps were compared. A randomized block design was applied, with two blocks (baited and un-baited traps) and included three replicates of four minnow traps models set for two hours at three different depths: surface, mid-water, and bottom. The richness and relative abundance estimates were 40% and 80% higher, respectively, with metallic minnow traps than with other traps. Among 10 species captured, goodeids (as a group) were more abundant than other species in all four different minnow traps and achieved a higher relative abundance in baited traps. However, the relative abundance of individuals among traps was different among months. A general linear mixed model on presence-absence values of goodeids showed no effect from depth but confirmed a significant effect by month and trap type. The result from this study could help many ichthyologists and resource managers understand the methodological biases in fish sampling traps and lead to better monitoring and management of small endangered freshwater fishes in shallow lakes.

Keywords: monitoring, passive method, linear mixed model, shallow lake.

Introduction

Multiple collection methods are used for freshwater fish monitoring in standing waters depending on fish distribution and habitat diversity (Mercado-Silva and Bonar 2013). However, it is often not possible to have a complete sampling scheme in a system, using all recommended gears and methods (e.g., seining, electrofishing) due to various constraints. For instance, sampling methods could be banned by local or federal authorities (i.e., gillnetting, seining) given the sensitivity of some fishes to handling, especially in waterbodies subject to regulations and with threatened endemic species (Gonzáles-Pedrero 2006). Nevertheless, the conservation of these species requires that their populations be monitored (Lyons et al. 2019). It is thus important to explore the effectiveness of fish collection methods with minimal impact on fish populations, such as minnow traps (Mercado-Silva and Escandón-Sandoval 2008). Furthermore, it is important to evaluate differences in fish capture efficiency among the various types of minnow traps available on the market (Backiel and Welcomme 1980).

Standardization of sampling methods for freshwater fish is important to allow comparisons of data collected over the years and across large geographic areas (Bonar et al. 2009). When sampling processes are homogenized, they allow monitoring the abundance of rare or endangered species to aid in their conservation (Mercado-Silva and Bonar 2013). Freshwater fish collection methods have been compared to one another in different systems (Lapointe et al. 2006; Utrup and Fisher 2006; Mercado-Silva and Escandón-Sandoval 2008). The efficiency of some collection methods has also been evaluated (Parsley et al. 1989; Bailey and Herendeen 2000). A complex relationship between abundance and catch per unit effort data for a variety of sampling methods has been recognized. Catchability studies using different models of minnow traps have focused on commercially important species (Jorgensen et al. 2017), and other studies include the estimation of detection and abundance of endangered freshwater fish (Budria et al. 2015; Stewart et al. 2017). However, the effectiveness of various models of minnow traps is still little known, and information is needed to analyze how well they catch various fish species (depending on size or sex), and how well they estimate fish community abundance values.

In this sense, it is important to find sampling methods that may be implemented in subtropical shallow lakes to generate information for fish conservation and to understand their biases and effectiveness.

As a study model Lake Zacapu was used, located in Michoacán state, Mexico, this lake is small (approx. 20 ha.), shallow, volcanic, and maintained by the contribution of numerous spring tributaries (Ayala-Ramírez et al. 2007). This lake hosts native and endemic fish species (Moncayo-Estrada, 1996; Ramírez-García et al., 2021), and some are of conservation concern according to the International Union for Conservation of Nature (IUCN Red List 2019) and Mexican laws (NORMA-059-SEMARNAT-2010). Due to its high biodiversity, Lake Zacapu has declared a Protected Natural Area in 2003, and the management plan was published in 2005 (Zubieta-Rojas et al., 2005), however, it has not been updated to date. Therefore, a thorough evaluation using different fishing gear is necessary

This study aims to compare the effectiveness of four different models of minnow traps and evaluate the information they provide about the fish community, particularly for small, endemic fishes (Goodeidae). Establishing similarities and differences of fishing efficiency (the capture of different fish species and the number of individuals per species) among trap models should aid future efforts to define monitoring strategies and the interpretation of new and existing data based on low-impact fishing gears.

Materials and methods

Study site and sampling design: Lake Zacapu is located in central-western Mexico at 1980 meters above sea level and is part of the Lerma-Chapala River basin (19º 49´30” N and 101º 47´20” W). One sampling site located 1-2 m away from the shore was visited in daylight hours during September and December of 2018 and January and March of 2019 (Figure 1). This site was selected because of the presence of higher richness and abundance of fish species and the months were chosen because they represent the most common temporal differences in the ecosystem (dry, rainy, and between seasons; Moncayo-Estrada, 1996; Ramírez-García et al., 2022). Previous to the traps set we measured the physical and chemical characteristics of the water, such as water temperature (ºC), dissolved oxygen (O2 mg/l), salinity (ppt), reduction oxide potential (mv), total dissolved solids (TDS mg/L) and hydrogen potential (pH), were measured with a multiparameter probe (YSI EXO2; YSI Inc., Yellow Springs, OH, U.S.A).

The sampling in each month followed a randomized block design, divided into two subgroups or blocks (baited vs. un-baited traps). To get less variability within blocks than between blocks, the site was sampled one day with baited traps, we used corn dough as bait and the following day with unbaited traps in the same month. We used three replicates of four minnow traps models (12 traps in total; see below for description). Traps were set for two hours at three different depths: surface, mid-water, and bottom. Surface minnow traps were defined as those where the top of the trap was immersed in water, at the surface, with the bottom dangling in the water. Bottom minnow traps were defined as those in which the bottom of the trap was touching the substrate of the lake. Midwater traps were located at 0.5 total depth, floating.

We selected four kinds of minnow traps for comparison (Figure 2). They were selected because they are currently in use in fisheries and monitoring in nearby lakes (Paradis et al. 2012). *Rectangular minnow traps* (Cxp Boutiques) were made of reinforced steel wire (0.5 cm stretch mesh), 45 cm long, 20 cm wide, and 20 cm high, with two opening holes 7.5 cm in diameter. They were green and had a 15 cm zipper for baiting. *Folding minnow traps* (VGEBY) were made of an articulated structure of steel wire (color green, 0.5 cm stretched mesh) with six sides, 44 cm long and 30 cm high; each side had a hole of 22 cm long and 12 cm high. Each trap was one-meter-long on its base and 27 cm high. Traps had a large 30 cm zipper to take out captured fish and a 15 cm zipper in the center for baiting. *Metallic minnow traps* (Gees Feets G-40 Minnow Trap) were made of steel (stretch mesh 0.5 cm, silver color), cylindrical, 42 cm long, and 19 cm in diameter, with two 2.5 cm holes with inverted cone inlets. *Circular minnow traps* (artisan) were made with a steel bar structure covered with nylon (1 mm stretch mesh, green); they were 60 cm long, 42 cm diameter, of circular shape. They had a single 7 cm hole.

Data collection and description: For each trap, fishing effort (hours) and total catch were recorded. Captured fish were identified to species level (Miller, 2009). Sex was determined only for species with sexual dimorphism. All fishes were released back to the water at the site of capture, after processing. We describe and compare the species richness (composition) and relative fish abundance (proportion of the number of a species concerning the other species), and the catch per unit effort (CPUE, as the number of individuals caught per soak time: fish caught per hour), from the four trap types, depth, and month.

Statistical analyses: To test for differences in environmental variables among months, Kruskal–Wallis nonparametric analysis of variance and Dunn test (as a posteriori) were applied to identify significant differences per month. These statistics were chosen because the data were non-normal (Anderson–Darling, and Shapiro–Wilk tests). Some species or groups of species, in our case the Goodeidae, are important to be monitored, and we implemented models measuring the presence or absence of these fish within traps (binomial response variable). We fitted generalized linear mixed-effects models (GLMMs) to avoid bias because of the lack of temporal independence and the presence of zeros when the traps did not capture fish (Meintzer et al., 2018). Data were arranged by blocks, corresponding to the presence or absence of bait, and by three treatments (depth, month, and different types of traps). Design of block by treatment was with 16 replications in-depth and with 12 replications by season. Statistical analyses were performed using the package glmm in the R language (v. 3.6.1, R Core Team 2019).

Results

The physicochemical variables showed statistically difference among months in water temperature ($R^2 = 0.79$, $P = 0.0001$), pH ($R^2 = 0.70$, $P = 0.0001$), dissolved oxygen ($R^2 = 0.24$, $P = 0.0001$), total dissolved solids ($R^2 = 0.99$, $P = 0.0001$) and reduction oxide potential ($R^2 = 0.11$, $P = 0.0041$). The higest water temperature was in March (20.65 ± 0.12 ºC) followed by September (17.76 ± 0.80 ºC), similar months December (16.53 ± 1.62 ºC) and January (16.05 ± 0.27 ºC). The pH ranged from 6.62 ± 0.52 (in January) to 7.8 ± 0.37 (December) indicated slightly acid water. Total dissolved solids showed a range from

106.98 ± 1.22 mg/L in January to 250.10 ± 3.63 mg/L in December. Dissolved oxygen concentrations ranged between 6.83 ± 0.58 mg/L (September) to 18.25 ± 1.48 in March (Table 1).

Considering all traps tested, we caught a total of 10 of the 13 taxa reported in the lake (Table 2). A total of 823 organisms were captured, the highest relative abundance was of *Z. quitzeoensis* (27.21 %), followed by *Poeciliopsis infans* (25.27 %) and *S. lermae* (20.41 %). The least relative abundance was *Xenotoca variata* (2.06 %), *H. turneri* (0.60 %) and *Chirostoma humboldtianum* (0.24 %). Across all traps, higher species richness was obtained with metallic traps (10 species), followed by rectangular (5 species), folding fishing, and circular traps (four species each).

The CPUE estimates for *Z. quitzeoensis* in folding fishing trap (n =14) and metallic trap (n = 187) were higher than in other trap types. The count of *P. infans* individuals was highest in metallic traps (n = 193). *Goodea atripinnis* had the highest number of individuals in the metallic trap (n = 62). Average counts of the goodeid species were different among traps. In metallic traps the most common species were *Z. quitzeoensis* (n = 187), *S. lermae* (n = 157) and *G. atripinnis* (n = 62); the least common were *X. variata* (n = 17) and *H. turneri* (n = 5). A higher number of individuals per trap was obtained with the metallic trap (range = 4-312 individuals) than the other traps (rectangular trap = 2-9 individuals; folding fishing trap = 1-10; and circular trap = 2-32). A higher number of individuals of goodeid species were obtained in baited traps. Relative abundance of individuals among traps were not significantly different among depths ($\chi^2 = 4.1191$, d.f. = 2, P = 0.12; Fig. 3c). The relative abundance of goodeid species as a group was different when comparing the metallic trap against other traps and among months.

The general mixed linear model on the presence-absence values of goodeid fishes showed no effect for depth ($\chi^2 = 1.77$, d.f. = 2, $p = 0.41$; Fig. 3. 1a) but confirmed a significant effect for month ($\chi^2 = 17.38$, d.f. =3, $p = 0.0006$) and trap type ($\chi^2 = 23.05$, d.f. =3, p = 3.9e-05). Particularly for December and March, differences were significant, and the metallic trap had higher occupancy of fish (Fig. 3. 1b and 1c). We included the depth of the traps as the random variable in the analysis of interactions to reduce bias by the effect of the position of the traps. When we included the interactions of the remaining treatments (trap type and month) the folding trap and one month (January) and the metallic trap with two months (January and March) showed significant differences ($p = 0.01$, $p < 0.0001$, $p < 0.0001$, respectively).

Discussion

We have identified biases and captured efficiency differences among four common passive methods for sampling shallow lakes. We found that the metallic minnow trap outperformed the other minnow traps used in this study, with the highest number of organisms captured in all the months sampled and within the variables (baited vs. no baited; at different depths). These differences documented here will be of use to lake managers or other scientists charged with the monitoring of freshwater small fish species in shallow lakes.

The efficiency and selectivity of minnow traps are influenced by the probability that fish will encounter, enter, and be retained within the trap until it is retrieved (Portt et al. 2006). Metallic minnow traps were more effective than the others in assessing fish richness in Lake Zacapu. This type of trap captured 40% higher species richness than other minnow traps tested and can be used in many different types of habitats (rivers, streams, ponds). This minnow trap also produced ~ 80% higher relative abundance estimates versus other traps. Their simple trapping principle, based on inverted funnel-shaped cones, makes them efficient, easy to operate, and affordable, contributing to their wide use in aquatic ecology (MacRae and Jackson 2006; Paradis et al. 2012). However, the differences we have demonstrated here have implications when minnow traps are used for scientific or conservation purposes.

Similar to every other sampling methodology, certain biases must be considered when using minnow traps as sources of fish community information; minnow traps can attract predatory fish into the trap, be preferred as a refuge, or be highly dependent on randomness to capture individuals (Lyman and Smith 2001). Likewise, the previous capture of a species (e.g., *Poeciliopsis infans*), can attract its predator (e.g., *Alloophorus robustus*). A trap may serve as a refuge for small fish (mostly juveniles), which may show a stronger tendency to stay in the trap once caught (Jorgensen et al. 2017). Furthermore, the differences appeared to depend not only on the probability of fish entering the different traps but also on differences in the probability of escaping from them. Studies have shown that traps catch only a very low proportion of the fish that enter the near-field area of the gear (Cole et al. 2004).

The maximum size of fish that can enter the trap is determined by the size of the throat and, like mesh-based equipment, the minimum size of the fish retained is determined by the perimeter of the opening, which is typically very small (20- 30 mm) mesh (Portt et al. 2006). In consequence, fish size, trap color, and the trap attraction to the fish species as shelter or the presence of potential prey could generate differences in motivation or ease to escape from the metallic trap, which could explain their lower CPUE. The use of several traps with varying selectivity could produce better estimates for fish populations or communities, given that some species are more readily sampled with some gears than others; for this study, the metallic minnow traps were more efficient in all variables explored (depth, bait) given that the behavior of species (mostly goodeids) favored the catches. This may lead to assuming incorrectly that species have mutually exclusive distribution due to competition, predation, or other biotic and abiotic interactions (He and Lodge 1990).

Communities dominated by small-bodied species (cyprinids, goodeids, poeciliids, darters, sculpins) are effectively sampled with minnow traps, as we used in this study. In contrast, lakes with communities dominated by large-bodied species are better sampled by gill nets and coarse-mesh trap nets (Jackson and Harvey 1997; Portt et al. 2006). Gill nets can be used in most habitats where there is ample unobstructed depth to allow the mesh to be extended between the float and lead lines, except where there are strong currents (Portt et al. 2006). In many lakes, however, it is possible to combine minnow traps with other sampling methods to ensure a better representation of the entire community, especially in structurally complex habitats.

While our study focuses on comparing four sampling traps that are commonly used, it is important to note that some species can be more effectively captured with a particular trap, a fact that could alter estimates of species abundances. It is thus important to select the adequate minnow trap with the highest possibility to catch all different species in a waterbody (MacRae and Jackson 2006; Paradis et al. 2012), mainly related to their size and the position of the entrance in the trap. It is also important to consider a bias related to the bait used the type of diet of the species and the environmental characteristics (Portt et al. 2006). The abundance of the fish in minnow traps may be increased because the response of the fish may vary with bait quality, and appetite at the time of sampling (e.g., the species captured feed diurnally, Moncayo-Estrada 1996). Currents, turbidity, and consequently visibility also affect catch, resulting in higher abundances of individuals (Portt et al. 2006).

Most of the species captured in a baited minnow trap were also found in an unbaited minnow trap, suggesting that some species are attracted to the structure provided by minnow traps, not just by bait. It has been well-established that fishes use structurally complex habitats for various reasons (to reduce predator-prey encounter rates and reduce overall prey capture efficiency of predators) (Layman and Smith 2001). Water turbidity, habitat complexity, substrate, and water conductivity are some of the factors that may affect the efficiency of freshwater fish samplings traps (Lyons 1986; Bayley and Dowling 1990).

While there are advantages to the use of passive methodologies such as minnow traps in sites like Zacapu, their limitations should also be considered (Peterson et al. 2015). Minnow traps impose less stress on fish than electrofishing, though care must be taken when fish are held for several hours. Minnow traps offer an attractive alternative to passive capture methods for conducting estimates for susceptible species, especially when it is necessary to keep the fish alive and be able to release them back to the water (Peterson et al. 2015).

This is one of the first studies to be conducted in central Mexico water bodies comparing minnow traps efficiency, adding to the trend of increasing efforts to standardize fishing methodologies. The importance of this analysis relates to a large number of bodies of water with native and endemic small-size species (Lyons et al. 2019), difficult to evaluate with active sampling methodologies. There are different reasons for that: first, the collection of fish includes less labor (Meintzer et al. 2018). Second, susceptible fish are less harmed because they are freely swimming within the traps, an aspect that makes easy the identification and processing, and release of the individuals to the ecosystems. Third, traps have a low environmental impact compared to other extraction methods

Regarding the non-native species (*Cyprinus carpio* and *Ctenopharingodon idella*) reported for Lake Zacapu (Moncayo-Estrada 1996) were not caught with any of the sampling traps. This could be due to the large size of the species relative to species captured during the study and because it presents the lowest abundances in the lake (Ramírez-García et al., 2022).

Based on our results, we suggest minnow traps are efficient for monitoring small-sized species, especially for those listed by the IUCN or Mexican laws (NOM-059-SEMARNAT-2010). In lake Zacapu, Goodeids were the most abundant species group captured, regardless of the type of trap; the Goodeidae family is a small-bodied freshwater fish representative in lakes and rivers in the central plateau, however, the distribution and abundance of most species within the Goodeidae have declined during the last 20 years (Domínguez-Domínguez et al. 2008; Lyons et al. 2019). The poeciliid *P. infans* are also relatively abundant in the lake, this is related to vegetation cover, in part this habitat offers refuge to avoid predation (Ramírez-Herrejón et al. 2012b). Only two individuals of atherinopsid *C. humboldtianum* were captured during our sampling efforts (their sizes were between 50 to 60 mm of standard length), we believe these were accidental captures given that this species often occupies open waters in limnetic areas where they can feed on zooplankton (Moncayo-Estrada 1996: Ramírez-García et al., 2022).

Our results could help ichthyologists and resource managers understand the methodological biases in fish sampling traps; thus, they could contribute to better monitoring and management of endangered freshwater fishes, such as the Goodeidae family. Focusing on the numerous freshwater bodies with native and endemic species and most in some risk category, the use of passive methodologies does not cause harm to their habitats, we recommended the minnow traps for conservation strategies for a vulnerable group of fishes that lives in vulnerable environmental, as the goodeid family showed here.

With the minnow trap and methodologies used during this study, managers could quantitative survey abundance estimation of small-bodied fish, their higher catch efficiency will allow greater statistical power when comparing fish abundances among seasons, habitats, or ecosystems; evaluate fish communities in shallow lakes elsewhere and combine minnow traps with other sampling methods to ensure a better representation of the entire community, that could estimate the richness of species and their relative abundances, and catch fish to evaluate biology reproduction or trophic ecology.

Acknowledgments

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Tables and Figures

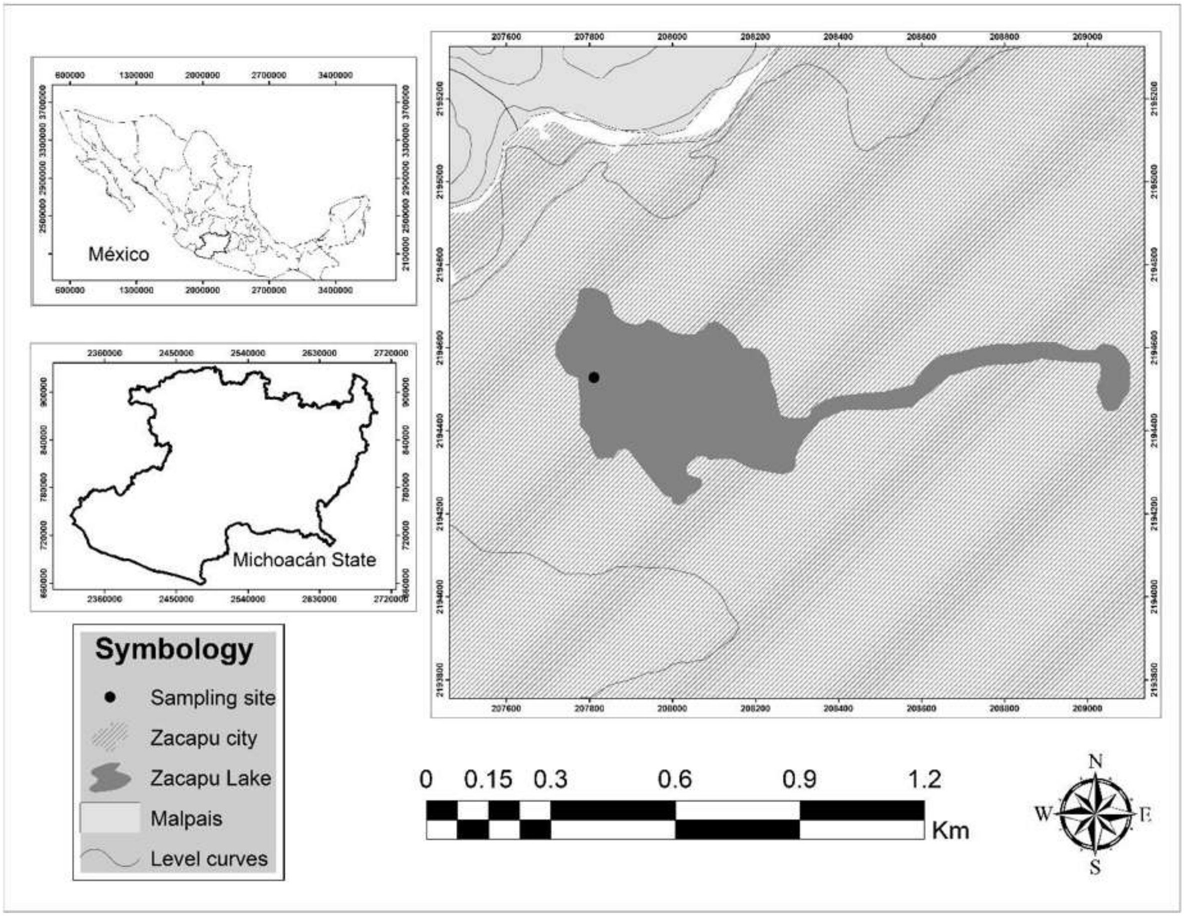
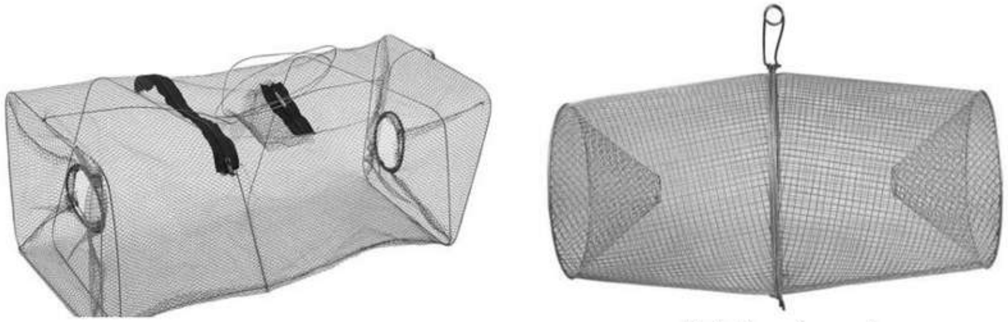
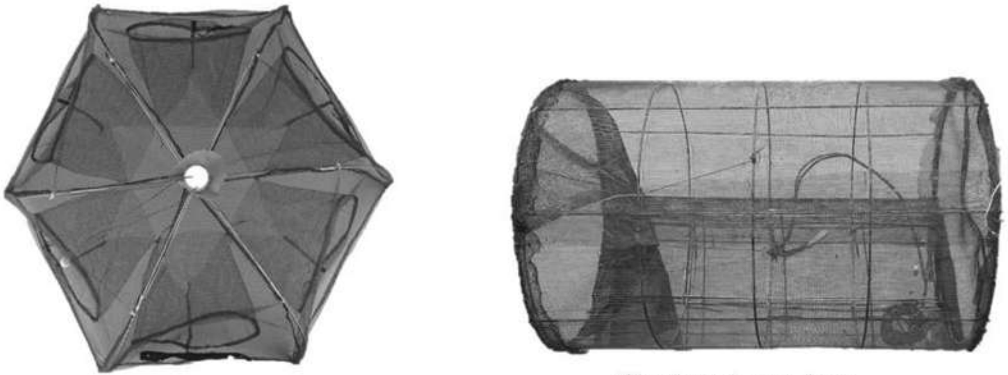


Figure 1. Location of sampling site in Zacapu Lake, Michoacán México



Rectangular minnow trap

Metallic minnow trap



Folding minnow trap

Circular minnow trap

Figure 2.- The different types of minnow traps used. *Rectangular minnow traps* (Cxp Boutiques), *Folding minnow traps* (VGEBY), *Metallic minnow traps* (Gees Feets G-40 Minnow Trap) and *Circular minnow traps* (artisan).

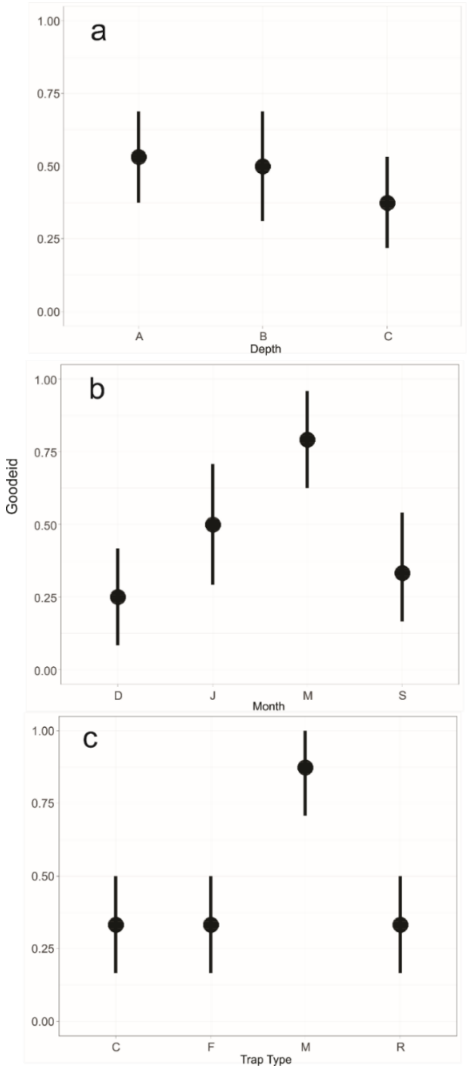


Figure 3.- Plots for presence-absence of goodeid fishes captured with four different trap models in four different sampling periods and at three depths of Lake Zacapu (see methods). Points represent mean values and lines 95% CI obtained by bootstrap. Depth includes A, B, and C related to the surface, mid-water, and bottom. Months include D=December, J=January, M=March, and S=September. Trap types include C = circular minnow traps, F = folding fishing minnow traps, M = metallic minnow traps, R = rectangular minnow traps.

Table 1. Physical and chemical water characteristics by months (September 2018, December 2018, January 2019 and March 2019) in the sampling study site in Zacapu Lake, Michoacán, Mexico. Tem = water temperature (°C), DO = dissolved oxygen (O2 mg/L), potential for hydrogen = pH, TDS = total dissolved solids (mg/L), reduction oxide potential (mV).

Month	**ODO mg/L**	**ORP mV**	**TDS mg/L**	**pH**	**Tem °C**
September 2018	6.83 ± 0.58	-110.36 ± 8.2	107.65 ± 1.96	7.07 ± 0.04	17.76 ± 0.80
December 2018	7.24 ± 0.72	-106.5 ± 6.42	250.10 ± 3.63	7.8 ± 0.37	16.53 ± 1.62
January 2019	7.04 ± 0.51	-118.28 ± 31.10	106.98 ± 1.22	6.62 ± 0.52	16.05 ± 0.27
March 2019	8.25 ± 1.48	-101.5 ± 1.74	111.13 ± 2.58	7.89 ± 0.27	20.65 ± 0.12

Table 2.- Species and total number of individuals collected in Lake Zacapu, values in the table were added for all sampling events. Information is presented for baited (Y) or unbaited (N) traps, and the type of trap: rectangular minnow traps (Trap 1), folding fishing minnow traps (Trap 2), metallic minnow traps (Trap 3) and circular minnow traps (Trap 4). Trap location represented by A = surface, B = mid-water, and C = bottom.

Species	Baited	Trap 1			Trap 2			Trap 3			Trap 4		
		A	B	C	A	B	C	A	B	C	A	B	C
Goodea atripinnis	Y				3		1	28	17	6		1	25
	N	3			1		2	7	4		3	2	1
Zoogoneticus quitzeoensis	Y	8	1		4	10		68	33	2		7	3
	N		1	1				77	7		1	1	
Skiffia lermae	Y		2	3	1			37	79	15	1	1	1
	N							5	20	1	1		1
Alloophorus robustus	Y							6	2				
	N		1					1	25				
Xenotoca variata	Y							3		1			
	N								13				
Hubbsina turneri	Y							2	1				
	N								2				
Poeciliopsis infans	Y		1	6				167	5		1	2	3
	N			1				1	17	3	1		
Chirostoma humboldtianum	Y												
	N						1	1					
Notropis grandis	Y								20	40			
	N												

Capítulo II

Temporal changes in the fish community structure of a small subtropical spring lake: decadal and seasonal analysis

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Sometido en Ecology Freshwater Fish

Temporal changes in the fish community structure of a small subtropical spring lake: decadal and seasonal analysis

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Running title: Decadal and seasonal changes in a small lake fish community

Abstract

In spring lakes, which have homogeneous environmental characteristics, it is expected that there will be no significant changes in the composition and structure of communities over time, and fluctuations will generally be related to the ecological attributes of the species. We studied the fish community in a small subtropical spring lake, Lake Zacapu, in two different decades to analyze its structural characteristics. Sampling was performed every three months at four sites from January to October 1995 and from May 2019 to May 2020. We determined the temporal variation (seasonal and decadal) in the fish community structure with respect to composition, abundance, diversity, and dominance. We evaluated the association between species and water quality. Our results showed spatial homogeneity in most physicochemical variables that remained in the same range across decades, although some nutrients (NO_3) recently increased. All species identified in the early samples were present in the recent surveys (eleven native and two nonnative species), indicating that the fish community composition had significant qualitative stability. However, the dominant littoral cyprinid in 1995 was replaced by the more limnetic atherinopsid in 2019-2020, and the diversity and abundance of sensitive fish decreased in recent samplings. Consequently, the current status of critically endangered species is supported for some restricted and microendemic fish. The changes in the community structure attributes, which show a tendency for reduction in native species, emphasize the need to implement efforts to conserve freshwater fish diversity in small spring lakes.

Keywords: spring lake, PERMANOVA, ISA, rarefaction and extrapolation, PSIRI, restricted species.

Introduction

Understanding what drives the structure of biological communities is one of the main goals in ecology (Begon et al., 2005). In general, fish communities are structured depending on abiotic factors, which limit the distribution of species at regional scales, and biotic factors, which determine the survival of species at a local scale (Martino & Able, 2003). Several studies have analyzed changes in fish communities in space and time based on system morphometry, water quality, productivity, and biotic interactions in temperate and subtropical lakes (Mehner et al., 2005; Murphy, 2012; Yu-Chun et al., 2020). To better understand these changes, the use of standardized protocols that allow long-term monitoring is required (Bonar et al., 2017). However, in some countries, including Mexico, the standardization of sampling data is being carried out on very small scales or is just beginning (Mercado-Silva & Bonar, 2013), and there is no official strategy for monitoring freshwater fish populations (Bonar et al., 2009a). Therefore, if there are historical data on the structure of fish communities, a comparison could be generated by obtaining new information from recent samples to determine which spatial and temporal patterns of the fish community have changed and which environmental dynamics could be responsible for these changes (Bahri et al., 2021). The sampling must follow the same procedures because the lack of standardized data limits the ability to compare the information between events (Bonar et al., 2009b) and to update management protocols (Grazia et al., 2016). Additionally, it is important to add more sampling methods not previously used that could give closer approximations of the structure of the fish community (Radinger et al., 2019).

It is important to monitor small water bodies because they are critical remnant ecosystems that act as refuges for endemic and restricted species, provide ecosystem services, and represent great cultural importance (Biggs et al., 2017). In small water bodies, seasonal environmental variations affect the fish community structure depending on the variability of the freshwater system (i.e., is it temporary or permanent; Escalera-Vázquez & Zambrano, 2010). Among small water bodies, spring lakes are one of the most common types, and they are typically the headwaters for creeks and rivers (Wisconsin Lakes, 2016). The primary water source of these lakes is groundwater flowing in from the bottom and closely adjacent sources of the system, and when they have high water inputs and a short water residence time, they exhibit water homogeneity (Downing, 2010). Consequently, it is expected that there will be no changes in the composition and structure of fish communities over time; therefore, the attributes of the species are more important for community structure, and important differences may arise that are mainly due to the life cycle strategies of the species (Beesley & Prince, 2010). Unfortunately, few studies are available on small subtropical lakes that incorporate temporal changes in different years separated by decades. In this context, as a model, we chose the small spring lake, Lake Zacapu (15 ha), which is a relic of a large wetland (15,000 ha) that was drained for agricultural purposes at the beginning of the 20th century (Zubieta-Rojas et al., 2005; Ayala-Ramírez et al., 2007). Lake Zacapu is a shallow water body (average ~ 2.7 m) fed by several springs (12), which promote high water turnover, and it is considered a monomictic subtropical ecosystem with low turbidity (Moncayo-Estrada, 1996; Valencia-Vargas & Escalera-Vázquez, 2021). The physical and chemical conditions of the water (i.e., water temperature, dissolved oxygen, hydrogen potential, total dissolved solids, and conductivity) are quite homogeneous throughout the lake ecosystem because of the high capacity for hydraulic renewal (Valencia-Vargas & Escalera-Vázquez, 2021; Ramírez-García et al., 2021). Consequently, it is expected that the lake has a high buffering capacity for pollutants (Domínguez-Domínguez et al., 2008). In 2004, the lake was declared a natural protected area, and in 2005, it was declared as a RAMSAR site (RAMSAR, 2005); however, no conservation actions were taken. At present, it has different perceptible impacts due to the influence of the city that borders the lake on more than 50% of its shore (on the south and southeast) with two types of use: residential and agricultural. Fishing pressures are also present in Lake Zacapu, and gillnets are used by a local fishing group (J. J. González-Cárdenas, personal communication, August 8, 2019).

Qualitative and quantitative data on the ichthyofauna of Lake Zacapu before the creation of the management plan in 2005 are available as well as recent samples following the same sampling protocol. Our aims were (1) to evaluate the temporal changes in community structure (composition, abundance of species, and diversity) over two decades and among seasons and (2) to identify patterns of association between fish community structure and physicochemical and biotic variables. We hypothesized that (1) the structure of the fish community does not change across decades because this small subtropical lake has homogeneous environmental characteristics, in part due to its higher renewal rate; and (2) seasonal rather than spatial differences will be present in the annual assembly process of the fish community.

Methods

Study area

Lake Zacapu is located in the state of Michoacán in central-western Mexico at 1980 meters above sea level; it is part of the Lerma-Chapala River Basin (Figure 1). The lake is also part of an important transitional biogeographical zone (the Trans-Mexican Volcanic Belt) where the Nearctic and Neotropical regions meet, which is characterized by high species endemism, including microendemism. This spring lake is where the Angulo River begins and subsequently flows (for 64 km) from south to north into the Lerma River (Ayala-Ramírez et al., 2007). Four sampling sites distributed in Lake Zacapu were chosen to represent the different shorelines (S1- S4 in Figure 1), including two major spring influence areas (sites 1 and 3; Ayala-Ramírez et al., 2007; Valencia-Vargas & Escalera-Vázquez, 2021; Ramírez-García et al., 2021).

Sampling Methods

Historical Samples. The fish assemblage was sampled seasonally in January, May, July, and October 1995 using a seine net (25 m length and 1.8 m height with a 5 mm mesh size). The fish samples were stored at the Ichthyology Collection of the Laboratory of Aquatic Biology of the Universidad Michoacana de San Nicolás de Hidalgo, Michoacán, Mexico. All specimens related to this collection were counted, weighed (g), and revisited to verify their identity based on identification keys and recent scientific literature (Miller et al., 2009).

Contemporary Samples. We replicated the sampling strategy previously used to allow comparison of the fish assemblage structure across decades by sampling in January, May, July, and October of 2019 and January, July, and October of 2020 with the same fishing gear. We used additional sampling methods to better describe the species composition. Five stainless steel cylindrical traps 42 cm long and 19 cm in diameter were set for one hour per site (0.5 cm stretch mesh with two 2.5 cm holes with inverted cone inlets), and we conducted electrofishing in the shallow areas close to the sites (DC-backpack electrofisher model ABP-3, ETS electrofishing systems, LLC, average power ~200 W, peak voltage ~250 V, peak current ~10 A). Before being released at the site of capture, each fish was identified to species, counted, and weighed. All field sampling techniques and fish handling protocols were reviewed and approved by the Mexican Ministry of Environmental and Natural Resources (SEMARNAT- SGPA/DGVS/00012/19), Ministry of the Environment, Climate Change and Natural Resources (SEMACCDET-OS. 0084/2019), and the Secretariat of Agriculture and Rural Development (SAGARPA: PPF/DGOPA-014/20).

Environmental variables. Simultaneously, we measured environmental variables at each site during the sampling. In 1995, the temperature was measured with a mercury thermometer (0 to 100 °C), depth was measured with a calibrated line attached to a weight, transparency was measured as the Secchi depth, pH was measured with a field potentiometer (Corning, Model 220), conductivity was measured with a field conductimeter (Hach, Model 44600), and dissolved oxygen was measured using the aside modification of the Winkler method. We collected water samples with a Van Dorn bottle (3 L) and determined the nitrogen nutrients with a spectrophotometer (Hach Model DRL 2000) according to the methods of the American Public Health Association (APHA, 1995). In the 2019-2020 sampling, we used a multiparameter probe (YSI EXO2). The variables measured were conductivity ($\mu s \cdot cm^{-1}$), temperature (°C), dissolved oxygen (O_2 $mg \cdot L^{-1}$), depth (m), reduction-oxidation potential (mv), total dissolved solids (TDS, $mg \cdot L^{-1}$), ammonia (NH_3, $mg \cdot L^{-1}$), nitrate (NO_3, $ml \cdot L^{-1}$), ammonium (NH_4, $mg \cdot L^{-1}$) and pH.

Data Analysis

A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used to compare the abundance values of the community among years and seasons with the Bray–Curtis dissimilarity, due to the high frequency of zeros. Because there was a lack of samples in May 2020, the data had an unbalanced annual design. Consequently, prior to the PERMANOVA, we tested the homogeneity of multivariate dispersions (PERMDISP) as heterogeneity could heavily influence the PERMANOVA results (Anderson, 2001). The PERMDISP showed no significant difference for years ($F = 1.28$ and $p = 0.28$) or seasons ($F = 2.26$ and $p = 0.11$). To quantify the pattern of redundancy that was responsible for changes in composition in different years, we implemented an indicator species analysis (ISA; Peck, 2016). This method calculates the importance value for each species based on the abundance and constancy among groups (Dufrêne & Legendre, 1997).

To identify general trends, the spatial and temporal characteristics of the fish community within the ordination of sites and months were represented using nonmetric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity. We calculated three-dimensional solutions from 250 random starts of real data with up to 1000 iterations to evaluate stability and obtained a final stress of 0.07. We incorporated the physicochemical water variables into the plot. However, these variables were not part of the NMDS analysis; they were incorporated as vectors and scaled according to their correlation with the axes, and their significance was assessed using permutations (Oksanen et al., 2020).

We evaluated the community diversity variables within years (seasons) and among years (1995, 2019, and 2020). Rarefaction was implemented to standardize the uneven number of samples, and extrapolation was used to predict the real diversity according to the expected number of species undetected by the sampling effort (Budka et al., 2018). We followed the proposal of Chao et al. (2014) and based both methods on the three Hill numbers: q = 0 (species richness), q = 1 (Shannon index), and q = 2 (inverse Simpson index). The confidence intervals for these numbers were obtained using the bootstrap method. The dominance was measured within sampling events with the prey-specific index of relative importance (PSIRI; Brown et al., 2012).

To test for differences in environmental variables among seasons and years, we applied a Kruskal–Wallis nonparametric analysis of variance and the Dunn test (as a posteriori test) to identify significant differences per pair of months and years. These statistics were chosen because the data were nonnormally distributed (Anderson–Darling and Shapiro–Wilk tests). The PERMANOVA, PERMDISP, and NMDS were computed using the vegan package (v. 2.5-7, Oksanen et al., 2020), rarefaction and extrapolation were measured using the iNEXT package (v. 2.0.20, Hsieh et al., 2016), and the Kruskal–Wallis test and the Dunn test were performed with the package Dunn.test (Dinno, 2017); all were performed in the R language (R Core Team, 2021). For the ISA method, we used the PC-ORD program (v. 6.0; McCune and Mefford, 2011).

Results

Fish species composition and community structure

We collected 11 species in four families with the seine net, most of which were native species and only one of which was a nonnative species (the grass carp, *Ctenopharyngodon idella*). Among the native species, Goodeidae was the family most represented in terms of the number of species (seven species), followed by Cyprinidae (two species) and Atherinopsidae and Poeciliidae (one species each; Table 1).

Insert Table 1 about here

In the PERMANOVA test, we observed a significant difference in species composition and abundance by year (*F* = 11.12, *p* = 0.0001) and season (*F* = 2.26, *p* = 0.007), but there was no interaction between the factors (*F* = 1.41, *p* = 0.09); no significant difference was found among sites (*F* = 1.32, *p* = 0.18). The 1995 sampling differed from the other years (2019, *F* = 15.07, *p* = 0.003 and 2020, *F* = 10.94, *p* = 0.003), and no significant difference was found between 2019 and 2020 (*F* = 0.48, *p* = 0.84). Seasonally, only January and October showed a temporally significant difference (*F* = 2.73, *p* = 0.02). The NMDS, as a free ordination method, showed an indirect gradient, and the first axis separated sites left to right, within months, from the previous (1995) to the recent samplings (2019-2020; Figure 2). This general trend was related to higher values of NO_3 and lower values of conductivity in recent years. On the second axis, we mainly found a clear separation of samples based on month in 1995 with January at the top of the plot and October at the bottom. This pattern was partially shown in the 2019 samples but not in the 2020 samples (Figure 2). As expected, the temperature was mainly related to the peak of the dry season and the summer months (May and July, respectively). In this context, the ISA indicated that between years, *Notropis grandis* (IV = 97.8, p = 0.0002), *Hubbsina turneri* (IV = 88.5, p = 0.0002), and *Skiffia lermae* (IV = 70.5, p = 0.02) were more frequent and abundant in 1995 than in recent years (on the left side of the NMDS plot). In contrast, *Chirostoma humboldtianum, Xenotoca variata,* and *Poeciliopsis infans* were more abundant in recent samplings (on the right side of the NMDS plot). The species *Zoogoneticus quitzeoensis* was closely related to the center of the plot and was consistent across years and seasons.

Diversity and dominance

We found the highest diversity in 1995, when more fish species were captured, including both native and nonnative species. All three diversity metrics decreased in recent samples, and the lowest values of the three metrics were found in 2019 (Table 2). Seasonally, all years generally showed higher values of diversity in October. In 1995, the lowest values were observed in May; the lowest values for the other years varied among months (Table 2).

Insert Table 2 about here

In 1995, *N. grandis* showed the highest abundance (47%), biomass (33%), and dominance (PSIRI = 42.9), followed by *Goodea atripinnis* (abundance 13%, biomass 53%, and PSIRI value 18.9; Figure 3). Additionally, *S. lermae* exhibited high abundance (24%), and *Chirostoma humboldtianum* had high dominance (PSIRI = 19.1). In 2019 and 2020, *C. humboldtianum* was the species with the highest abundance (38% in both years), biomass (49% in 2019 and 59% in 2020), and dominance (PSIRI = 24.6 in 2019 and 50.8 in 2020; Figure 3), followed by the goodeid *Xenotoca variata* (in 2019, abundance 19%, biomass 16%, and PSIRI 9.1; in 2020, abundance 17%, biomass 10%, and PSIRI 12.5). *Poeciliopsis infans* also showed high abundance (14% in 2019 and 12% in 2020), and *G. atripinnis* had high biomass (16% in 2019 and 10% in 2020).

Insert Figure 3 about here

Environmental conditions

The Kruskall–Wallis test showed that temperature (χ^2 = 11.3, p = 0.010 in 1995; χ^2 = 8.91, p = 0.030 in 2019; and χ^2 = 9.84, p = 0.007 in 2020) and pH (χ^2 = 10.2, p = 0.016 in 1995; χ^2 = 10.8, p = 0.012 in 2019; and χ^2 = 7.98, p = 0.018 in 2020) varied among months in the different years. In 1995, the water temperature (22.1±1.31) was significantly higher in July than in January (18.8± 0.25); in 2019, October had the maximum temperature (20.0±0.34) and January the minimum (17.2±0.28); and in 2020, July (22.2±0.46) had the highest temperature. We did not find significant differences among sites within years for any of the variables (Table 3). Among years, we did not find significant differences in temperature (χ^2 = 0.57, p = 0.748), DO (χ^2 = 0.66, p = 0.7165), depth (χ^2 = 3.0758, p = 0.2148), pH (χ^2 =

0.58, $p = 0.6511$), or NH_4 ($\chi^2 = 0.7268$, $p = 0.6953$). Conductivity was significantly different among years; 1995 showed the maximum values (ranging from 152 in January to 172 in May), and 2019 showed the minimum values (from 134 in January to 139 in July). Additionally, NO_3 exhibited significant differences between years ($\chi^2 = 8.9498$, $p = 0.01139$) with 1995 significantly lower than the other years. Transparency, which was only measured in 1995, did not show significant differences among months or sites ($\chi^2 = 7.06$, $p = 0.07$ and $\chi^2 = 2.63$, $p = 0.45$, respectively). However, temporally, May showed the lowest value, and spatially, site three had the highest value, which is related to the influence of La Angostura springs.

Insert Table 3 about here

Discussion

This is the first study of the fish community structure in a small subtropical spring lake using information from different decades. Over the years, we found a change in the dominant species, which have different habitat preferences. Additionally, there was a reduction in the abundance of sensitive native fish. Native species were dominant, and nonnative species had relatively low abundances. We captured only eleven species with the seine net in the 2019-2020 samples (Table 1); therefore, other capture methods were implemented (electrofishing and minnow traps), including fishermen's nets, and using all these methods, we confirmed that all previously reported species still remained in the lake. Although Lake Zacapu showed homogeneous environmental characteristics throughout the system (Table 3), and most environmental variables remained in the same range after decades, some other nutrients and ionic characteristics of the water had changed, which could affect and increase the trophic state of the ecosystem.

Information on the ichthyofauna in Lake Zacapu was scarce before 1995. Specifically, six species were found in 1969 (Barbour & Douglass, 1969), nine species in 1982 (Figueroa et al., 1982), and ten species were reported in 1991 (Medina-Nava, 1993; Moncayo-Estrada, 1993). This trend indicates that as a more complete sampling design was implemented in 1995, all species in the lake were captured. It is known that there have been changes in the system, and this is reflected in the changes in the community. However, the continued presence of all species that were detected in the early samples indicates that the fish community has significant qualitative stability or persistence (Matthews et al., 2013). This was mainly due to the characteristics of Lake Zacapu, including the small area with many springs, high exchange of water, and continuous environmental homogenization (Table 3). In other aquatic systems in central Mexico, there has been a decline in native species in recent decades (Mercado-Silva et al., 2006). In lentic systems, for example, Lake Pátzcuaro, which has had important alterations due to anthropic activities such as eutrophication, habitat degradation, and the introduction of nonnative species, there was a reduction in native species due to the loss of intolerant species and biological processes (species interactions) from 1900 to 2010 (Ramírez-Herrejón et al., 2014). Lake Cuitzeo and the lower portion of the Río Grande de Morelia have also experienced a drastic decline in native species; 26% of the 19 native fish species known from the basin have been extirpated, two endemic species have gone extinct, and 63% of species showed a restricted distribution due to the decrease in water quality and quantity (Soto-Galera et al., 1999). In lotic systems, the Teuchitlán River in Jalisco exhibited considerable environmental degradation, a decline in native fish species (including the extirpation of two microendemic species), and an increase in nonnative species (Mar-Silva et al., 2021).

In contrast to our first hypothesis, we identified changes in the community structure with regard to the diversity and dominance of species between years, which is probably related to the internal dynamics of the fish community. We found that native fish were still the most abundant and dominant species in Lake Zacapu over the years. The dominant species in 1995 was *N. grandis*; however, the average dominance of this species was low in 2019-2020. *Notropis* species typically feed on aquatic insects (Bean et al., 2010), and reproduction occurs on vegetated shallow shores in lakes (Bouvier et al., 2010). Both aspects are mainly related to submerged macrophytes and roots in Lake Zacapu. *Notropis* species are considered short-lived species; consequently, in the presence of disturbances to spawning or recruitment of juveniles over a period of several years, the populations could decline severely (Fossett, 2019). The most important species contributing to abundance, biomass, and dominance in 2019-2020 (Table 3) was *C. humboldtianum*, which was captured in all months. It has been documented that *C. humboldtianum*, which is one of the larger species in the genus (120 mm in length), is typically an open-water fish species that uses pelagic zones as feeding grounds (for zooplankton) (Elías-Fernández et al., 2008).

Additionally, this species uses a variety of reproductive habitats (Mercado-Silva et al., 2002) that can be located far from the littoral zone (Moncayo-Estrada et al., 2010). The change in dominance from *N. grandis* to *C. humboldtianum* across decades could be due to a combination of factors, such as the spatial distribution of the species (littoral vs. limnetic zones, respectively), feeding habitat (periphytophagous vs. planktivorous, respectively), and reproduction (littoral vs. littoral and limnetic, respectively). Spatial habitat heterogeneity in the lake was documented, and the areas with dense vegetation (*Potamogeton pectinatus*, *Myriophyllum spp*, *Ceratophyllum demersum*, and *Sagittaria sp*.) are more restricted to the spring zones, whereas the rest of the lake has less vegetation (Valencia-Vargas & Escalera-Vazquez, 2021), reducing spawning spaces for *N. grandis*.

In the 1995 samples, one of the nonnative species (*C. idella*) and the endemic *Allotoca zacapuensis* were captured only in October and had low relative abundances (0.04). Currently, in addition to *C. idella*, *Cyprinus carpio* was also present in the lake, as we observed during fieldwork with the fishermen and in the official fishing reports (fishers use gillnets with a 4 cm mesh to capture large individuals). However, the populations of these three species appear to remain relatively low because *C. idella* and *C. carpio* are the most important species for commercial fishing (J. J. González-Cárdenas, personal communication, August 8, 2019); apparently, fishermen regulate their populations in a manner that does not allow an increase in their abundances. Regarding *A. zacapuensis*, this species is well established in Lake Zacapu but has a restricted distribution, and its population reproduces effectively in one of the springs (Site 3; Ramírez-García et al., 2021). Nevertheless, *A. zacapuensis* is a microendemic in this lake and was absent from almost 95% of the total ecosystem, according to the results obtained with traps and electrofishing, both of which support its current status as critically endangered (Lyons et al., 2019; Koeck, 2019a).

Although we could expect that commercial fishing has an important effect on the fish community and species diversity indices (Blanchard et al., 2004), there is no evidence that proves this. According to statistics from the Regional Center for Fisheries Research (CRIAP Pátzcuaro) in 2019, the total fish catch was 574 specimens totaling 143.293 kg, and the main species caught were *C. humboldtianum, C. carpio*, *G. atripinnis,* and *C.*

idella. Compared with our results, *C. humboldtianum* and *G. atripinnis* were among the species with the highest abundances in the recent samplings, which could be related to good fishing practices. Although the management plan was not carried out with strict rigor, the fishermen managed the closures at the corresponding times to avoid a decrease in the populations of the different species that are important in the market.

Another aspect of the structure of the fish community related to native fish are the species of the Goodeidae subfamily. This is the best represented taxon in Lake Zacapu, with seven species. The PSIRI values were lower in recent samplings than in 1995 for all species of goodeids; however, the results obtained with the other sampling methods (electrofishing and minnow traps) showed the presence of all species at relatively higher abundances for all sites and months sampled. Some goodeids are sensitive to water quality and are vulnerable to predation, and they possess different habitat requirements such as vegetation and stones, which they use as refuges (Soto-Galera et al. 1998; Lyons et al., 2000; Domínguez-Domínguez et al., 2008). In Lake Zacapu, goodeid species are well established and exhibit effective reproduction, having the highest fertility rates compared with other populations of the same species in other aquatic systems and compared with other species of goodeids (Ramírez-García et al., 2021). However, the decrease in the abundance of *H. turneri* between decades (1995 vs. 2019-2020) was notable. The critical aspect of this decrease was that *H. turneri* has been considered a sensitive species (Lyons et al., 2019), and unfortunately, it has disappeared from other systems (Cuitzeo basin and Coinzio dam) that it used to inhabit (Ramírez-Herrejón et al., 2010). Currently, it is restricted to the Lake Zacapu Basin and cataloged as critically endangered (Lyons et al., 2019; Koeck, 2019b).

Regarding our second hypothesis, we found more seasonal than spatial differences in the structure of the fish community (Figure 2) because the water parameters were homogeneous and showed no significant spatial differences, even across different decades. The water has continuous circulation with little zonation based on the shallowness of the system, high capacity for hydraulic renewal, and small spatial dimensions (Ayala-Ramírez et al., 2007). This allowed us to conclude that the structure of the fish community is affected by the behavioral characteristics of the species related to reproduction, recruitment, and organism size. However, our results revealed that nitrate and conductivity differed significantly between decades (Table 3). An indirect estimation of the trophic state of lakes is the Secchi depth, and according to the average value measured in 1995 in Lake Zacapu (1.26±0.4 m), the system is eutrophic (Carlson and Simpson, 1996). This result is similar to the findings from another study that used transparency and other limnological variables (Díaz-Argüero, 1997). The eutrophication process of Lake Zacapu could be related to human activities from at least two sources: chronic effluent discharges from industrial and domestic wastewater and nutrients to the lake from recreation areas and cultivation that could damage natural habitats and increase nutrient output to the lake.

Small freshwater ecosystems represent habitats that serve as refuges for some species that have disappeared from other aquatic systems (Biggs et al., 2017). However, small water bodies are exposed to anthropic threats; for this reason, it is important to create monitoring programs to protect the biodiversity that they host and to make good use of the ecosystem services that they provide to ensure that decision-makers consider them in conservation actions (Clarke, 2015). Habitat structure plays an essential role in maintaining fish communities in aquatic systems, and the ecological guilds of species can change when habitat loss occurs (Bond & Lake, 2005). Although the species have persisted over time, the change in dominant species across decades is notable, and the abundance of sensitive species has decreased. Consequently, it is essential to implement conservation efforts for the lake. For example, the management plan has not been updated for Lake Zacapu (Zubieta-Rojas et al., 2005); therefore, based on our results, we recommend two management actions for fish conservation in this ecosystem. The presence of several springs promotes the spatial stability of the lake by hydraulic renewal, so it is recommended to avoid changes in land use in the upper parts of the basin that can affect the load of the aquifers. Additionally, it is necessary to prevent new permissions for direct water extraction from springs to irrigate cultivars. Because of the increased nutrient concentration found recently (mainly NO_3), it is recommended to avoid input from discharges of domestic water and fertilizers from agriculture to reduce the potential effect of severe eutrophication.

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Author contribution

All authors contributed to the integration of the manuscript: R.M.E., J.D.C.A., and E.L.L. collected and interpreted information in 1995, and A.R.G. and O.D.D. collected and interpreted information in recent samples; A.R.G., R.M.E., and O.D.D. conceptualized the study, J.D.C.A., E.L.L., and R.M.E. helped with the methodology and the software, A.R.G. and R.M.E. structured the first draft of the manuscript, all authors contributed to the writing, reviewing, and editing of the final manuscript, and J.D.L.C.A. and O.D.D. obtained the resources to support the project.

Data Availability Statement

The datasets generated for this study are available on request to the corresponding author.

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Tables

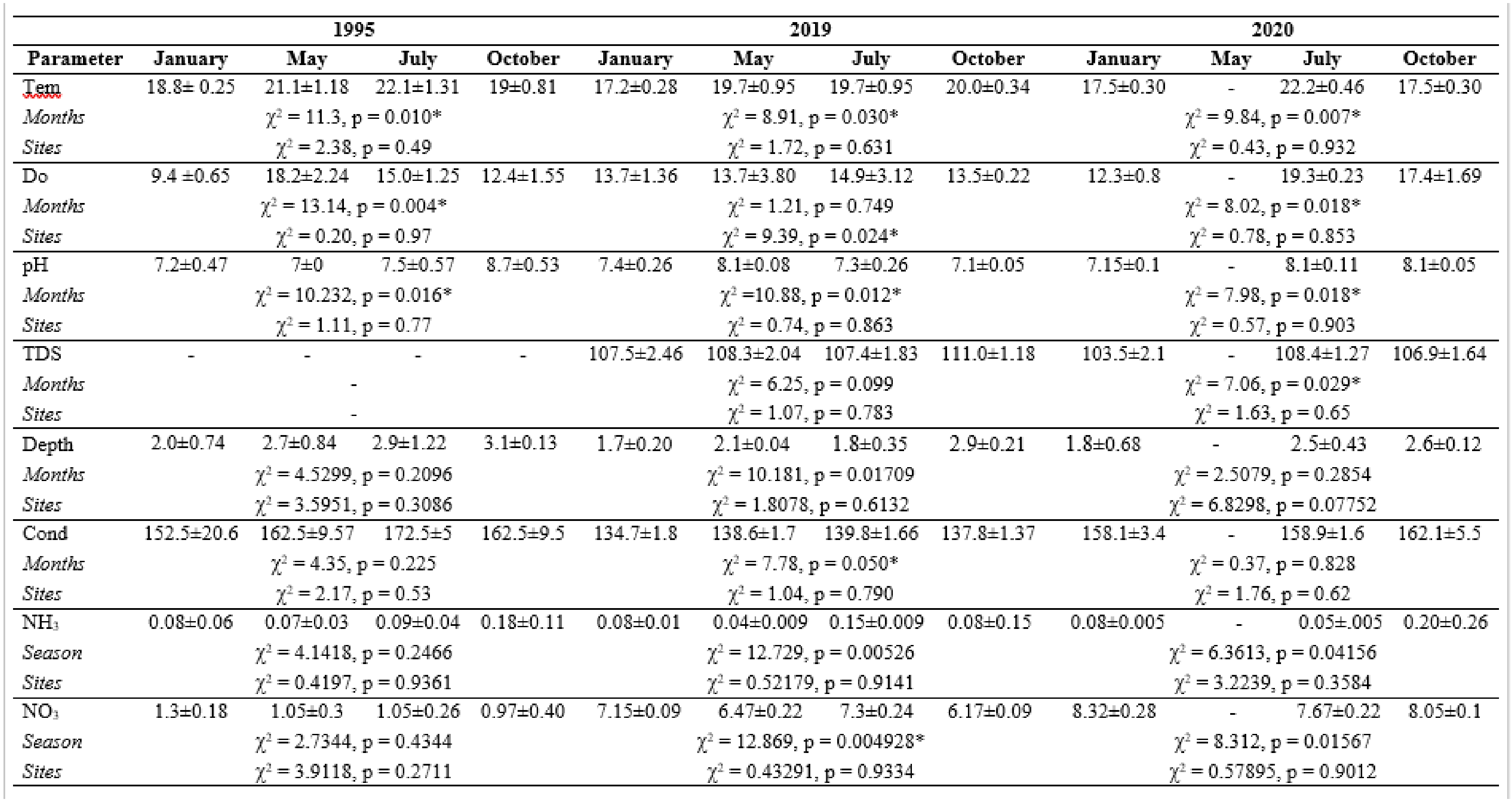
Table 1.- Fish community composition in different years in Lake Zacapu.

	Years		
Species	**1995**	**2019**	**2020**
Cyprinidae			
Notropis grandis	X	X	X
Ctenopharyngodon idella	X	0	0
Goodeidae			
Alloophorus robustus	X	0	X
Allotoca zacapuensis	X	0	0
Goodea atripinnis	X	X	X
Hubbsina turneri	X	X	X
Skiffia lermae	X	X	X
Xenotoca variata	X	X	X
Zoogoneticus quitzeoensis	X	X	X
Poeciliidae			
Poeciliopsis infans	X	X	X
Atherinopsidae			
Chirostoma humboldtianum	X	X	X

Table 2.- Temporal variation in species diversity according to Hill's numbers in Lake Zacapu including the different periods (years) and seasons (months). *q* = 0 is species richness; *q* = 1 is Shannon index; and *q* = 2 is inverse Simpson index.

	1995	2019	2020	
Seasons	4	4	3	
q = 0	11	8	9	
q = 1	8.34	7.3	8.09	
q = 2	7.67	6.96	7.61	
	January	May	July	October
		1995		
q = 0	7	6	7	11
q = 1	6.66	4.79	6.28	9.39
q = 2	6.33	4.05	5.83	8.4
		2019		
q = 0	7	8	7	7
q = 1	6.7	7	6.67	6.76
q = 2	6.39	6.31	6.37	6.53
		2020		
q = 0	8	-	8	9
q = 1	7.06	-	7.67	7.96
q = 2	6.21	-	7.35	7.22

Table 3.- Physical and chemical water characteristics in Lake Zacapu, Michoacán, Mexico. Tem = water temperature (°C), DO = dissolved oxygen (O_2 mg·L^{-1}), pH = potential for hydrogen, TDS = total dissolved solids (mg·L^{-1}), Depth = Depth (m), Cond = conductivity (μs·cm^{-1}), NH_3 = ammonia (mg·L^{-1}), NO_3 = nitrate (mg·L^{-1}). $\bar{X}$ ± DS. Kruskal-Wallis differences among months and sites. * Significant differences.



	1995				**2019**				**2020**			
Parameter	**January**	**May**	**July**	**October**	**January**	**May**	**July**	**October**	**January**	**May**	**July**	**October**
Tem	18.8± 0.25	21.1±1.18	22.1±1.31	19±0.81	17.2±0.28	19.7±0.95	19.7±0.95	20.0±0.34	17.5±0.30	-	22.2±0.46	17.5±0.30
Months	χ^2 = 11.3, p = 0.010*				χ^2 = 8.91, p = 0.030*				χ^2 = 9.84, p = 0.007*			
Sites	χ^2 = 2.38, p = 0.49				χ^2 = 1.72, p = 0.631				χ^2 = 0.43, p = 0.932			
Do	9.4 ±0.65	18.2±2.24	15.0±1.25	12.4±1.55	13.7±1.36	13.7±3.80	14.9±3.12	13.5±0.22	12.3±0.8	-	19.3±0.23	17.4±1.69
Months	χ^2 = 13.14, p = 0.004*				χ^2 = 1.21, p = 0.749				χ^2 = 8.02, p = 0.018*			
Sites	χ^2 = 0.20, p = 0.97				χ^2 = 9.39, p = 0.024*				χ^2 = 0.78, p = 0.853			
pH	7.2±0.47	7±0	7.5±0.57	8.7±0.53	7.4±0.26	8.1±0.08	7.3±0.26	7.1±0.05	7.15±0.1	-	8.1±0.11	8.1±0.05
Months	χ^2 = 10.232, p = 0.016*				χ^2 =10.88, p = 0.012*				χ^2 = 7.98, p = 0.018*			
Sites	χ^2 = 1.11, p = 0.77				χ^2 = 0.74, p = 0.863				χ^2 = 0.57, p = 0.903			
TDS	-	-	-	-	107.5±2.46	108.3±2.04	107.4±1.83	111.0±1.18	103.5±2.1	-	108.4±1.27	106.9±1.64
Months	-				χ^2 = 6.25, p = 0.099				χ^2 = 7.06, p = 0.029*			
Sites	-				χ^2 = 1.07, p = 0.783				χ^2 = 1.63, p = 0.65			
Depth	2.0±0.74	2.7±0.84	2.9±1.22	3.1±0.13	1.7±0.20	2.1±0.04	1.8±0.35	2.9±0.21	1.8±0.68	-	2.5±0.43	2.6±0.12
Months	χ^2 = 4.5299, p = 0.2096				χ^2 = 10.181, p = 0.01709				χ^2 = 2.5079, p = 0.2854			
Sites	χ^2 = 3.5951, p = 0.3086				χ^2 = 1.8078, p = 0.6132				χ^2 = 6.8298, p = 0.07752			
Cond	152.5±20.6	162.5±9.57	172.5±5	162.5±9.5	134.7±1.8	138.6±1.7	139.8±1.66	137.8±1.37	158.1±3.4	-	158.9±1.6	162.1±5.5
Months	χ^2 = 4.35, p = 0.225				χ^2 = 7.78, p = 0.050*				χ^2 = 0.37, p = 0.828			
Sites	χ^2 = 2.17, p = 0.53				χ^2 = 1.04, p = 0.790				χ^2 = 1.76, p = 0.62			
NH_3	0.08±0.06	0.07±0.03	0.09±0.04	0.18±0.11	0.08±0.01	0.04±0.009	0.15±0.009	0.08±0.15	0.08±0.005	-	0.05±.005	0.20±0.26
Season	χ^2 = 4.1418, p = 0.2466				χ^2 = 12.729, p = 0.00526				χ^2 = 6.3613, p = 0.04156			
Sites	χ^2 = 0.4197, p = 0.9361				χ^2 = 0.52179, p = 0.9141				χ^2 = 3.2239, p = 0.3584			
NO_3	1.3±0.18	1.05±0.3	1.05±0.26	0.97±0.40	7.15±0.09	6.47±0.22	7.3±0.24	6.17±0.09	8.32±0.28	-	7.67±0.22	8.05±0.1
Season	χ^2 = 2.7344, p = 0.4344				χ^2 = 12.869, p = 0.004928*				χ^2 = 8.312, p = 0.01567			
Sites	χ^2 = 3.9118, p = 0.2711				χ^2 = 0.43291, p = 0.9334				χ^2 = 0.57895, p = 0.9012			

Figures

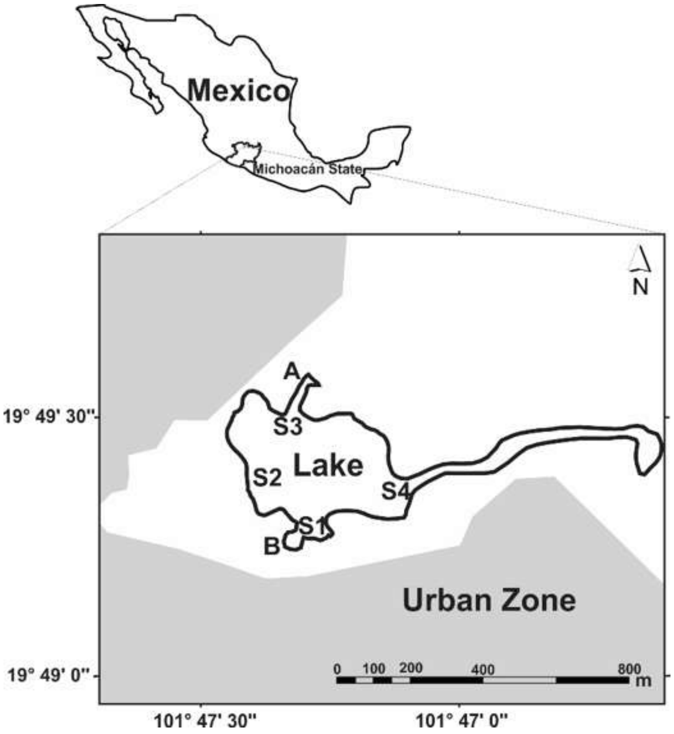


Figure 1.- Location of Lake Zacapu showing the four sampling sites. Letters represent the mainsprings: A is the spring zona La Angostura and B is the spring Ojo de Agua.

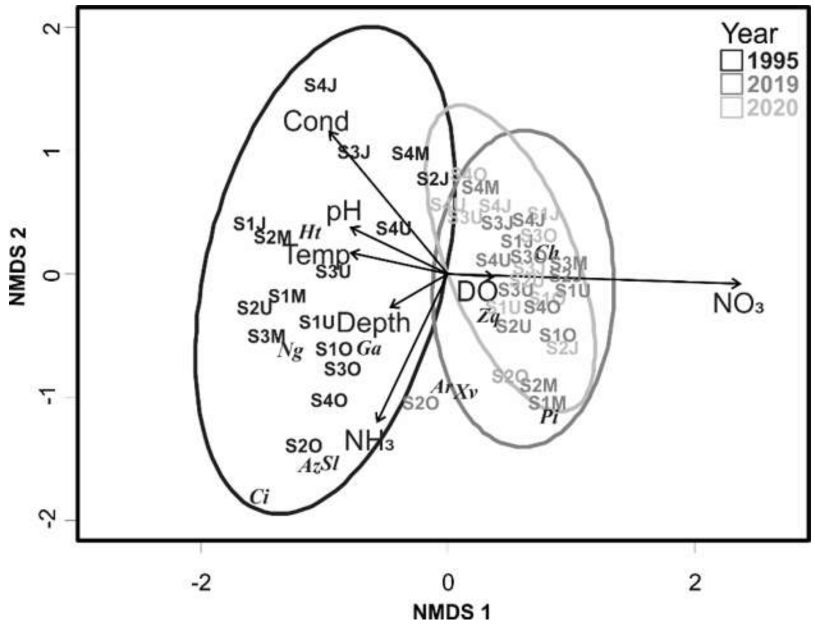


Figure 2.- NMDS ordination axes 1 and 2 of Zacapu Lake, including sampling sites within months, fish species, and environmental variables (stress = 0.07). Italics represent the species (Ar = *Alloophorus robustus*, Az = *Allotoca zacapuensis*, Ht = *Hubbsina turneri*, Sl = *Skiffia lermae*, Xv = *Xenotoca variata*, Zq = *Zoogoneticus quitzoensis*, Ch = *Chirostoma humboldtianum*, Pi = *Poeciliopsis infans*, Ci = *Ctenopharingodon idella* Ng = *Notropis grandis*, Ga = *Goodea atripinnis*). Cond = conductivity, Depth = depth, DO = dissolved oxygen, and Temp = temperature.

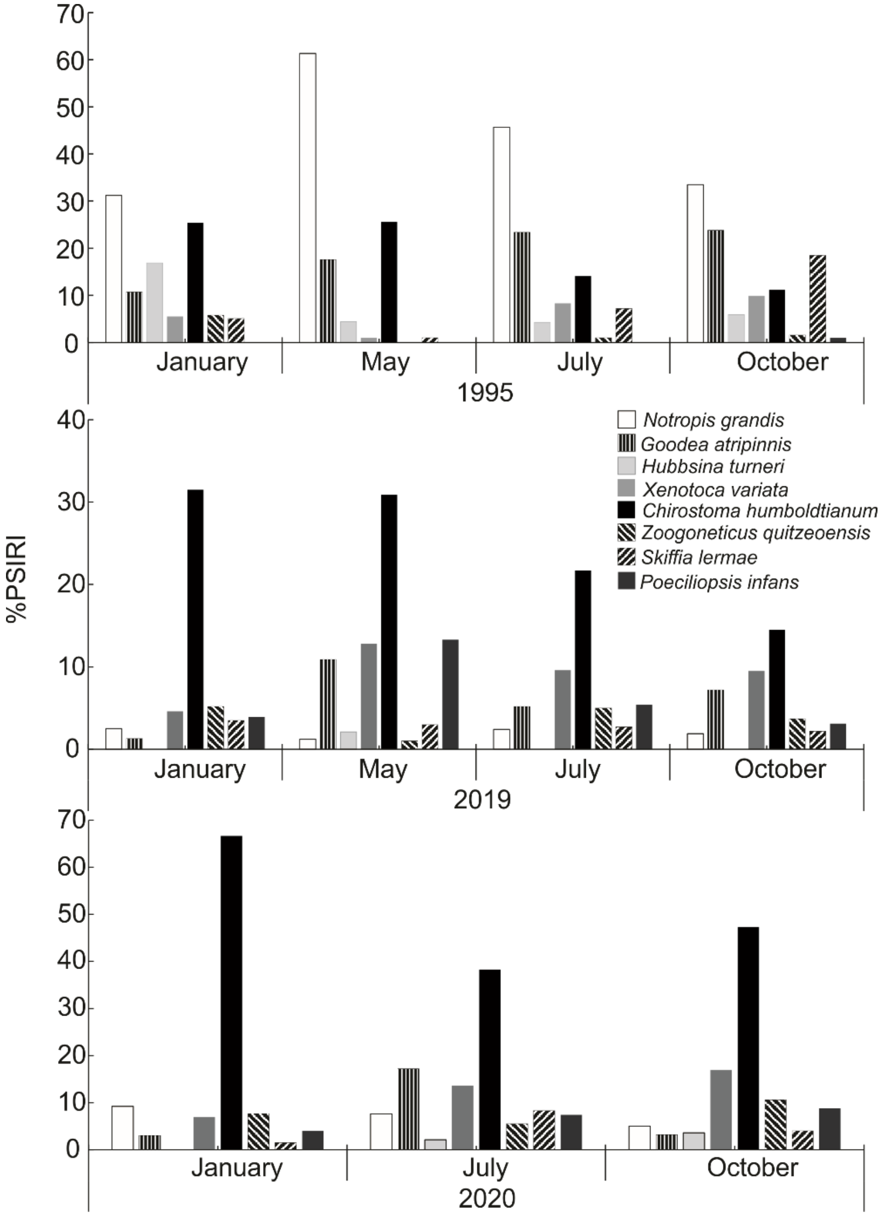


Figure 3.- Variation in Prey-Specific Index of Relative Importance (PSIRI) values of the species across sampling months in the different years

Capítulo III

Reproductive cycle of native viviparous fish species (Actinopterygii: Cyprinodontifomes: Goodeidae) in a subtropical Mexican lake

Arely Ramírez-García, Rodrigo Moncayo-Estrada, Juan José González-Cárdenas y Omar Domínguez-Domínguez

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Reproductive cycle of native viviparous fish species (Actinopterygii: Cyprinodontiformes: Goodeidae) in a subtropical Mexican lake

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Reproductive tactics and strategies contribute to the persistence and maintenance of long-term populations in fish species. Members of the subfamily Goodeinae are a group of small-bodied freshwater fish with specialized reproduction (viviparity-matrotrophy). They are found in the highlands of central Mexico, most of them endemic. The aim of this study was to conduct a comprehensive investigation to evaluate the annual reproductive cycle of seven species of goodeines (splitfins). We carried out our study in the subtropical Lake Zacapu, Mexico, with bi-monthly sampling from May 2019 to March 2020. We obtain the fertility, size at first maturity (L50), sex ratio, and gonadosomatic index. Our result shows that populations of goodeines have high fertility compared to other populations of the same species in other aquatic systems and also to other species of goodein. We found that males mature at smaller sizes than females, the observed proportion of females was greater than males in all the goodeines. Lake Zacapu goodeines have two reproductive peaks, one in spring (April to June) and another in fall (September to November). These tactics (fertility rates, sex ratio, reproductive period) and strategies (viviparity-matrotrophy) favor reproductive success in this environmentally stable subtropical lake in the highlands of Mexico.

Keywords: Fertility, First sexual maturity, Goodeines, Lake Zacapu, Reproduction.

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Las tácticas y estrategias reproductivas contribuyen a la persistencia y el mantenimiento de las poblaciones a largo plazo en especies de peces. Miembros de la subfamilia Goodeinae son un grupo de peces de agua dulce con reproducción especializada (viviparidad-matrotrofia). Se encuentran en el centro de México, la mayoría de ellos endémicos. El objetivo de este estudio fue realizar una investigación integral para evaluar el ciclo reproductivo anual de siete especies de goodeines o mexclapiques. Realizamos nuestro estudio en el lago subtropical de Zacapu, México, con muestreo bimestral de mayo de 2019 a marzo de 2020. Nuestros resultados muestran que las poblaciones de goodeines tienen una alta fertilidad en comparación con otras poblaciones de la misma especie en otros sistemas acuáticos y también con otras especies de goodeines. Encontramos que los machos maduran en tamaños más pequeños que las hembras, la proporción observada de hembras fue mayor que los machos en todas las goodeines. Los goodeines del lago Zacapu tienen dos picos reproductivos, uno en primavera (abril a junio) y otro en otoño (septiembre a noviembre). Estas tácticas (fertilidad, proporción de sexos, período reproductivo) y estrategias (viviparidad-matrotrofia) favorecen el éxito reproductivo en este lago subtropical ambientalmente estable en el altiplano de México.

Palabras clave: Fertilidad, Goodeines, Lago Zacapu, Primera madurez sexual, Reproducción.

INTRODUCTION

Reproductive strategies and tactics are important components in the life history of a species (Nikolsky, 1963; Balon, 1984; Snelson, 1989; Stearns, 1992). Reproductive strategies are specific adaptations such as distinct breeding systems (oviparity, viviparity, and ovoviviparity), sex-specific reproductive behaviors, and number of partners. Alternatively, reproductive tactics are linked life history traits that develop as adaptations towards environmental conditions and ecological niches (Murua, Saborido-Rey, 2003). Fishes exhibit a wide range of reproductive tactics such as variations in age of sexual maturity, fertility, and reproductive period (Wootton, Smith, 2014). The variety in reproductive characteristics that fishes exhibit has been argued as an evolutionary advantage in allowing exploitation of a huge range of niches, leading to fish being the most diverse group of vertebrates in the world (Wootton, Smith, 2014; Pérez-Rodríguez *et al*., 2015; Nelson *et al*., 2016).

The reproductive success is mainly related to age of sexual maturity, fertility, and sex ratio, and influence the population's growth and dynamics. A population with successful reproductive tactics exhibits features such as a clear size structure (organisms of different sizes, from juveniles to mature adults), reproductive seasonality for best offspring survival, and individuals with a healthy body condition factor (Caddy, Agnew, 2004; Wootton, Smith, 2014). Reproductive tactics can help us understand when, where, and how the reproductive cycle of a species functions and determines how spatial and temporal environmental factors affect recruitment success and, consequently, population persistence (Balon, 1984; Pecquerie *et al*., 2009).

Among the most reproductively specialized groups of fishes, it is the subfamily Goodeinae (*i.e.*, teleost fish endemic to Mexico known as splitfins) (Uribe *et al*., 2018). Specializations in this group include: modification of the anal fin (the gonopodium) in males, permitting internal fertilization (Turner *et al*., 1962); strong sexual selection, female choice related to male color patterns, fin size, courtship display, and body shape (Macías-García *et al*., 1994; Macías-García, Ramírez, 2005) and male choice influenced by female belly area, hue, and size (Méndez-Janovitz, Macías-García, 2017); and specialized embryonic development in the ovary whereby embryos develop a complex ribbon-like tissue, known as atrophotaenia, through which the interchange of nutrients and gases between the female and embryo takes place (Uribe *et al*., 2014; 2018). The Goodeinae includes around 40 species of small-bodied freshwater fishes found in the central Mexican highlands, most of them endemic or microendemic to a specific water body or spring (Domínguez-Domínguez *et al*., 2008; Lyons *et al*., 2019).

Within the freshwater ecosystems of central Mexico, Lake Zacapu is considered a hotspot of biodiversity, hosting two introduced and 11 native species of fish in its small area (15 ha) (Moncayo-Estrada, 1996; personal obs.). The introduced species (*Ctenopharyngodon idella* (Valenciennes, 1844) and *Cyprinus carpio* Linnaeus, 1758)) have been largely identified as a threat to native fish in other aquatic systems (Lowe *et al*., 2000; Cudmore *et al*., 2017; Gibson-Reinemer *et al*., 2017). Among the native species, there are seven goodeines: Catarina Allotoca (*Allotoca zacapuensis* Meyer, Radda & Domínguez-Domínguez, 2001), Bulldog Goodeid (*Alloophorus robustus* (Bean, 1892)), Blackfin Goodea (*Goodea atripinnis* Jordan, 1880), Olive Skiffia (*Skiffia lermae* Meek, 1902), Jeweled Splitfin (*Xenotoca variata* (Bean, 1887)), Picotee Splitfin (*Zoogoneticus quitzeoensis* (Bean, 1898)), and Highland Splitfin (*Hubbsina turneri* (de Buen, 1940)). Both *A. zacapuensis* and *G. turneri* are microendemic to the lake (Domínguez-Domínguez *et al*., 2008). According to the International Union for Conservation of Nature and Mexican Federal laws, *A. zacapuensis* and *G. turneri* are Critically Endangered (CR), whilst the remaining five species are of conservation concern (NOM-059-SEMARNAT-2019; Lyons *et al*., 2019; IUCN, 2020). Despite the status the fishes have been poorly studied. Only the general biology of single species (Moncayo-Estrada, 2012), taxonomic studies of fish parasites (Martínez-Aquino *et al*., 2012), and biological integrity at a sub-basin level (Ramírez-Herrejón *et al*., 2012).

In addition, although Lake Zacapu is considered an environmentally stable water body because several springs feed the system, water is extracted for urban use, and most of its shoreline is occupied by the town of Zacapu. As such, the ecosystems of the lake are under threat due to pollution and a drop in water level. This is of particular concern as the lake acts as a refuge for several species that have disappeared from other water bodies (Domínguez-Domínguez *et al*., 2008).

This study aims to evaluate the reproductive cycle and to describe the annual variation of the sex ratio, size at first maturity, gonadosomatic index, fertility and condition factor in seven species of goodeines or splitfins inhabiting Lake Zacapu. According to the limnological characteristics prevailing at Lake Zacapu, we hypothesize that the native species present a combination of life-history traits (early maturity, high fertility rates, good condition) producing high reproductive success. The results of this study have important conservation implications and can be used to support specific conservation actions and management to maintain biological diversity in the lake and other small sub-tropical lake ecosystems in Mexico.

MATERIAL AND METHODS

Study area. Lake Zacapu is a small sub-tropical lake (*ca.* 15 ha) located in the State of Michoacán, central-western Mexico, at 1980 m above sea level and is part of the Lerma-Chapala River basin. It is considered a monomictic ecosystem with low turbidity. The lake is maintained by the contribution of 12 large springs, presenting a high hydraulic renewal (approx. five days) and high buffering capacity (Ayala-Ramírez *et al*., 2007; Domínguez-Domínguez *et al*., 2008; Valencia-Vargas, Escalera-Vázquez, 2021). The lake is one of the most important areas in central Mexico for aquatic fauna conservation, it is also considered homogeneous, with good water quality, and low variations in physical and chemical conditions spatially and temporarily (Moncayo-Estrada, 1996; Ramírez-Herrejón, 2008; Ramírez-Herrejón *et al*., 2012; Ramírez-García, Domínguez-Domínguez, 2019; Valencia-Vargas, Escalera-Vázquez, 2021).

Field samples. We conducted sampling across an annual cycle with bimonthly sampling from May 2019 to March 2020 in four locations. Sampling locations covered different habitat characteristics that have been argued to affect the distribution of fish species in Lake Zacapu (Moncayo-Estrada, 1996), such as difference in the type of substrate, depth, location of tributaries and effluents, presence of vegetation, and human influence (Fig. 1).

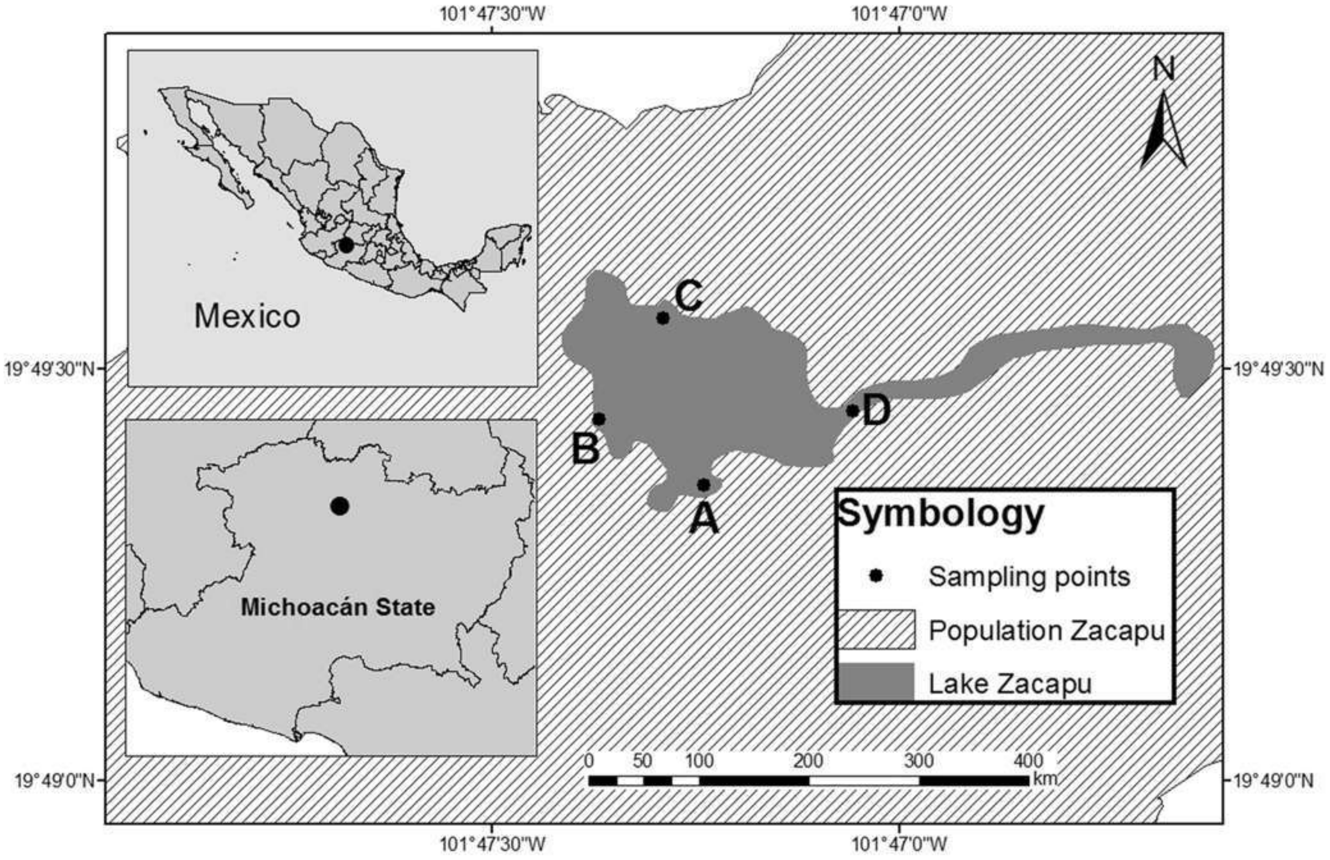

FIGURE 1 | Location of the Lake Zacapu (Michoacán, Mexico) and study sites (A, B, C and D).

We used a seine net (25 m length, 1.8 m height, and 5 mm mesh size) and five minnow traps set for one hour per site (stainless steel, stretch mesh 0.5 cm, cylindrical, 42 cm long, and 19 cm in diameter, with two 2.5 cm holes with inverted cone inlets). The fish captured were preserved in 4% formaldehyde, then they were identified, quantified, measured (SL, 0.01 mm), and weighed (WW, 0.001 g). Voucher specimens were incorporated to the fish collection at the Universidad Michoacana de San Nicolas de Hidalgo in Mexico (CPUM, registration key: MICH.-PEC-227-07-09). Catalogue numbers: *A. zacapuensis* (14887); *A. robustus* (14888), *G. atripinnis* (14889), *S. lermae* (14890), *X. variata* (14891), *Z. quitzeoensis* (14892), and *G. turneri* (14893).

Data analysis. Size structure was monthly analyzed, grouping the data into length ranges (Sturges, 1926). We applied Kruskal Wallis non-parametric analysis of variance, and Dunn (as a posteriori) tests to identify significant differences in size between months and species. Additionally, we used Mann-Whitney U tests (α = 0.05) to identify size differences between sexes for each species. These statistics were chosen because in all cases data were no-normal (Anderson-Darling and Shapiro-Wilk tests). We used the libraries MVN (Korkmaz *et al*., 2014) and Dunn.test (Dinno, 2017) in the program R (R Development Core Team, 2021, version 1.4.1106).

Gonad maturity. Estimated per month with the modification of the criteria proposed by Ramírez-Herrejón *et al.* (2007) (Tab.1).

Sex ratio. was described per site and season following the criteria of Sparre, Venema (1997). We established the statistical significance by fitting to a Chi-squared test (χ^2, α = 0.05).

TABLE 1 | Gonadal maturity stages of viviparous fishes from Lake Zacapu, Mexico, modified from Ramírez-Herrejón *et al.* (2007)

Females		Males	
Phase	Description	Phase	Description
I	Small ovaries, very thin, reaching less than 20% of the visceral cavity.	I	Small testes, very thin, reaching less than 10% of the visceral cavity.
II	Ovaries longer than in the previous stage, reaching less than 30% of the visceral cavity.	II	White testes longer than in the previous stage, reaching less than 20% of the visceral cavity. More turgid than the last stage.
III	Ovaries with free and very small eggs and embryos; enclosed within a common membrane	III	Turgid and yellow testes occupying 30% of the visceral cavity.
IV	Ovary with embryos no completely formed, eyes of the embryos are not completely developed, occupying 50% of the visceral cavity.	IV	Yellow turgid testes, occupying 40% of the visceral cavity.
V	Ovary with embryos completely develops, the membrane of the gonad shows visibly the embryos.	V	Complete turgid and yellow opaque testes
VI	Long ovary with no embryos, recovery after spawning.	VI	Long flaccid and transparent testes, corresponding to semen ejaculation phase.

Size at first maturity (L_{50}). Related to the standard length using the logistic regression model to fit sigmoid curves, according to the following equation $M(L) = 1/(1 + e^{(-aL + b)})$, where *M(L)* is the probability of an individual of being mature at a determinate *L* length, *b* is the intercept, and *a* is the slope. We used the sizeMat package in R to estimate the size and confidence limits derived by Bayesian inference based on stochastic simulation (Torrejon-Magallanes, 2020).

Gonadosomatic index (GSI). Calculated per sampling season and sex by dividing the gonad mass by total body mass (values in grams) × 100 (Zeyl *et al*., 2014). We analyzed the differences between months and sites with Kruskal Wallis and Dunn tests.

Fertility. We dissected the ovaries of each female and quantified embryonated eggs and embryos. We derived a fertility (F) model and adjusted it to the potential model (Holden, Raitt 1975; Schoenherr, 1977): $F = a L^{b}$, where *a* and *b* are constants in the potential model. We applied a correlation analysis (Pearson's coefficient) to determine the relationship between size (standard length) and fertility (number of embryos).

Condition factor. Assessed with Fulton's condition factor (K) (Froese, 2006): $K = 100 (W/L^{3})$, where *W* is the body wet weight (g), and *L* is the length (cm), and the value of 100 is used to bring *K* close to unity. As in the case of the gonadosomatic index, we analyzed the differences among months and sites with Kruskal Wallis and Dunn tests.

Physicochemical parameter. We measure conductivity (μs/cm), water temperature (^{o}C), dissolved oxygen (O_2 mg/l), reduction oxide potential (mv), total dissolved solids (TDS mg/L), and hydrogen potential (pH), per month and sampling sites with a multiparameter probe (YSI EXO2; YSI Inc., Yellow Springs, OH, U.S.A). We applied Kruskal Wallis tests to describe differences among sites and months. We measured the relationship between the environment and reproductive features (GSI and K) with correlation tests (Spearman correlation, 0.05). We built Linear Models to identify which environmental measures (predictor variables) best explained the fish reproduction (response variables). We used the library Hmisc (Harrell, 2021) and the function lm in the R program to obtain the correlation and multiple regression, respectively.

RESULTS

In this study, we examined 112 specimens of *Hubbsina turneri* (72 females and 40 males), 113 of *Allotoca zacapuensis* (75 females and 38 males), 188 of *Alloophorus robustus* (138 females and 50 males), 278 of *Xenotoca variata* (303 females and 76 males), 283 of *Skiffia lermae* (159 females and 124 males), 531 of *Goodea atripinnis* (415 females and 116 males), and 972 of *Zoogoneticus quitzeoensis* (553 females and 419 males).

Size structure. *Goodea atripinnis* presented the largest range of size structure, 15.1 to 173.0 mm in SL for females and 15.0 to 121.2 mm in males. The smallest range of size structure was found in *G. turneri*: 12.6 mm to 45.9 mm of SL in females and 17.7 mm to 40.1 mm in males (Tab. 2). There were not significant differences in sizes among sexes in all species. *Alloophorus robustus* (w = 328, p = 0.403), *A. zacapuensis* (w = 288, p = 1), *G. turneri* (w = 337, p = 0.296), *S. lermae* (w = 350, p = 0.204), *Z. quitzeoensis* (w = 301, p = 0.798), *G. atripinnis* (w = 280, p = 0.877), and *X. variata* (w = 330, p = 0.391).

There were significant differences in sizes by months and sites in *Z. quitzeoensis* (χ^2 = 18.2 months, p = 0.002; χ^2 = 9.2 sites, p = 0.025) and *A. robustus* (χ^2 = 13.4 months, p = 0.019; χ^2 = 18.3 sites, p = 0.0003). There were significant differences by sites in *A. zacapuensis* (χ^2 = 45.7, p = 6.447e–10) and *G. turneri* (χ^2 = 0.6, p = 0.001) and by months in *S. lermae* (χ^2 = 11.5, p = 0.04), *X. variata* (χ^2 = 13.3, p = 0.020) and *G. atripinnis* (χ^2 = 35.7, p=1.071e–06). There were not significant differences in sizes by sites in *S. lermae* (χ^2 = 4.2, p = 0.23), *X. variata* (χ^2 = 1.7, p = 0.63) and *G. atripinnis* (χ^2 = 0.3, p = 0.941) and by moths in *A. zacapuensis* (χ^2 = 0.2, p = 0.99), and *G. turneri* (χ^2 = 9.1, p = 0.102).

Gonad maturity stage. March and May showed the highest percentage of mature individuals (stages IV and V) for all species. In general, July, November, and January showed the highest percentage of juveniles (stages I, II, and III) (Fig. 2).

Sex ratio. Overall female:male ratio was significantly different from expected 1:1 ratio in all species*:* *A. robustus* (3:1, χ^2 = 41.19, p = 1.38e–10), *A. zacapuensis* (2:1, χ^2 = 11.11, p = 0.0005), *X. variata* (4:1, χ^2 = 135.12, p < 2.2e–16), *G. turneri* (2:1, χ^2 = 9.14, p = 0.002), *G. atripinnis* (4:1, χ^2 = 168.36, p < 2.2e–16), *S. lermae* (1:1, χ^2 = 4.328, p = 0.037) and *Z. quitzeoensis* (1:1, χ^2 = 17.74, p = 2.524e–05).

Size at first maturity. Males mature at smaller sizes than females in all the species. In *S. lermae* reproduction was found to begin at the smallest size for both sexes (29.5 ± 5.7 mm SL in females and 25.2 ± 5.4 mm SL in males). In *A. robustus* reproduction was found to begin at the largest size for both sexes (87.4 ± 24.0 mm SL for females and 69.0 ± 17.5 mm SL for males) (Tab. 2).

TABLE 2 | Reproductive biology information for species of goodeines or splitfins from Lake Zacapu, Mexico. *Significative Pearson coefficient. SD = Standard deviation.

Characteristics	***A. robustus***		***A. zacapuensis***		***G. atripinnis***		***G. turneri***		***S. lermae***		***X. variata***		***Z. quitzeoensis***	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Range of size (SL) mm	22.3-152.0 ± 35.9	21.36-132.0 ± 31.3	18.3-58.2 ± 11.4	18.2-47.8 ±10.1	15.1-173.0 ±27.7	15.0-121.23 ± 27.9	12.6-45.9 ± 9.2	17.7-40.1 ± 6.5	15.8-45.8 ± 7.0	15.4-42.3 ± 6.1	17.6-59.9 ± 10.4	14-93.3 ± 16.2	13.3-50.6 ± 9.5	12.4-57.3 ± 7.1
Sex ratio	3.1:1		2:1		3.6:1		1.7:1		1.3:1		4:1		1.3:1	
Size at sexual maturity mm	87.4 ± 24.0	69.0 ± 17.5	40.7 ± 3.6	39.8 ± 4.9	65.8 ± 17.6	65.6 ± 20. 7	34.9 ± 5.0	30.3 ± 4.3	29.5 ± 5.7	25.2 ± 5.4	68.8 ± 13.7	36.7 ± 6.8	35.5 ± 10.2	26.2 ± 6.7
Reproductive peak (GSI Index)	May to Jul, and Mar	May to Nov and Mar	Mar to Jul and Nov	May to Jul and Nov	May to Jul and Jan	Sep and Jan	May to Jul	Sep and Mar	May and Sep	May and Jan	May to Jul and Nov	Mar	May to Jul	Nov
Range of fertility (Mean ± SD)	19-152 (62 ± 37.1)		81-38 (25 ± 5.3)		35-198 (88 ± 40.9)		12-32 (21 ± 5.2)		6-23 (12 ± 4.5)		12-111 (38 ± 21.8)		5-30 (16 ± 6.7)	
SL *vs.* Number of embryos Pearson coef. (r)	0.68*		-0.13		0.43*		0.23		0.25		0.77*		0.78*	

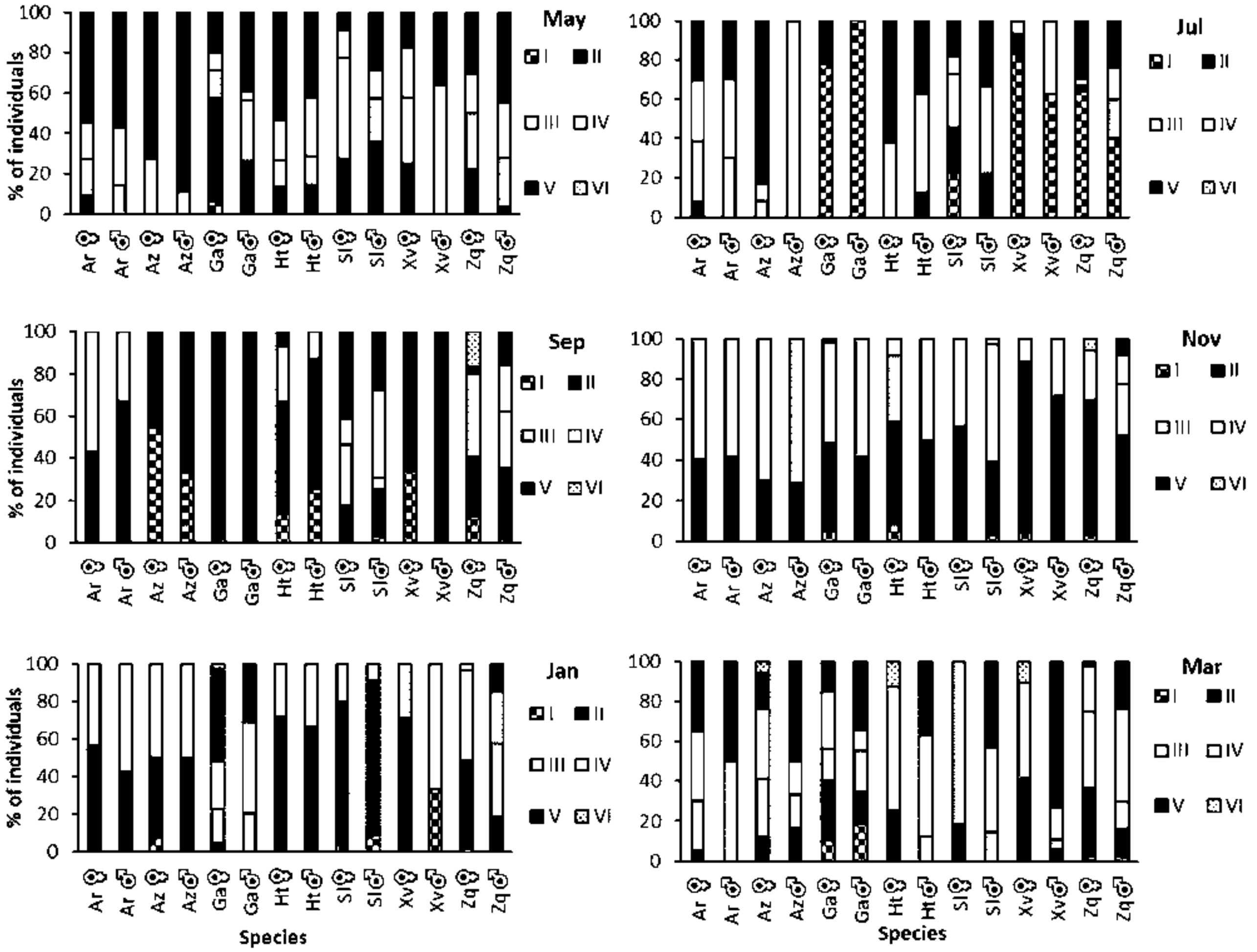

FIGURE 2 | Gonadic maturity stages of species of goodeines in percentage (Ar = *Alloophorus robustus*, Az = *Allotoca zacapuensis*, Ga = *Goodea atripinnis*, Ht = *Hubbsina turneri*, Sl = *Skiffia lermae*, Xv = *Xenotoca variata* and Zq = *Zoogoneticus quitzeoensis*) for each month in Lake Zacapu, Mexico.

Gonadosomatic index (GSI). The values of the GSI show a reproductive peak from May to July for all the species and both sexes. *Skiffia lermae* and *G. turneri* extend their reproductive peak until September. *Xenotoca variata* shows a second reproductive peak in November for females and March for males. *Goodea atripinnis* shows a second reproductive peak in November for males and in January for females. *Allotoca zacapuensis* and *A. robustus* show a second reproductive peak in March for females and January for males (Fig. 3). There were no significant differences between GSI values by months (Tab. 3), only in *G. atripinnis* did Dunn tests shows that September is different from other months (alpha = 0.05, $p < 0.02$). There were significant differences by sites in *G. turneri* and *A. zacapuensis* (Tab. 3).

Fertility. *Skiffia lermae* possess the lowest fertility value (range 6 to 23, average of 12 ± 4.5 embryos per female). The highest fertility was found in *G. atripinnis* (range 35 to 198, average 88 ± 40.9 embryos per female). We found a significant influence of

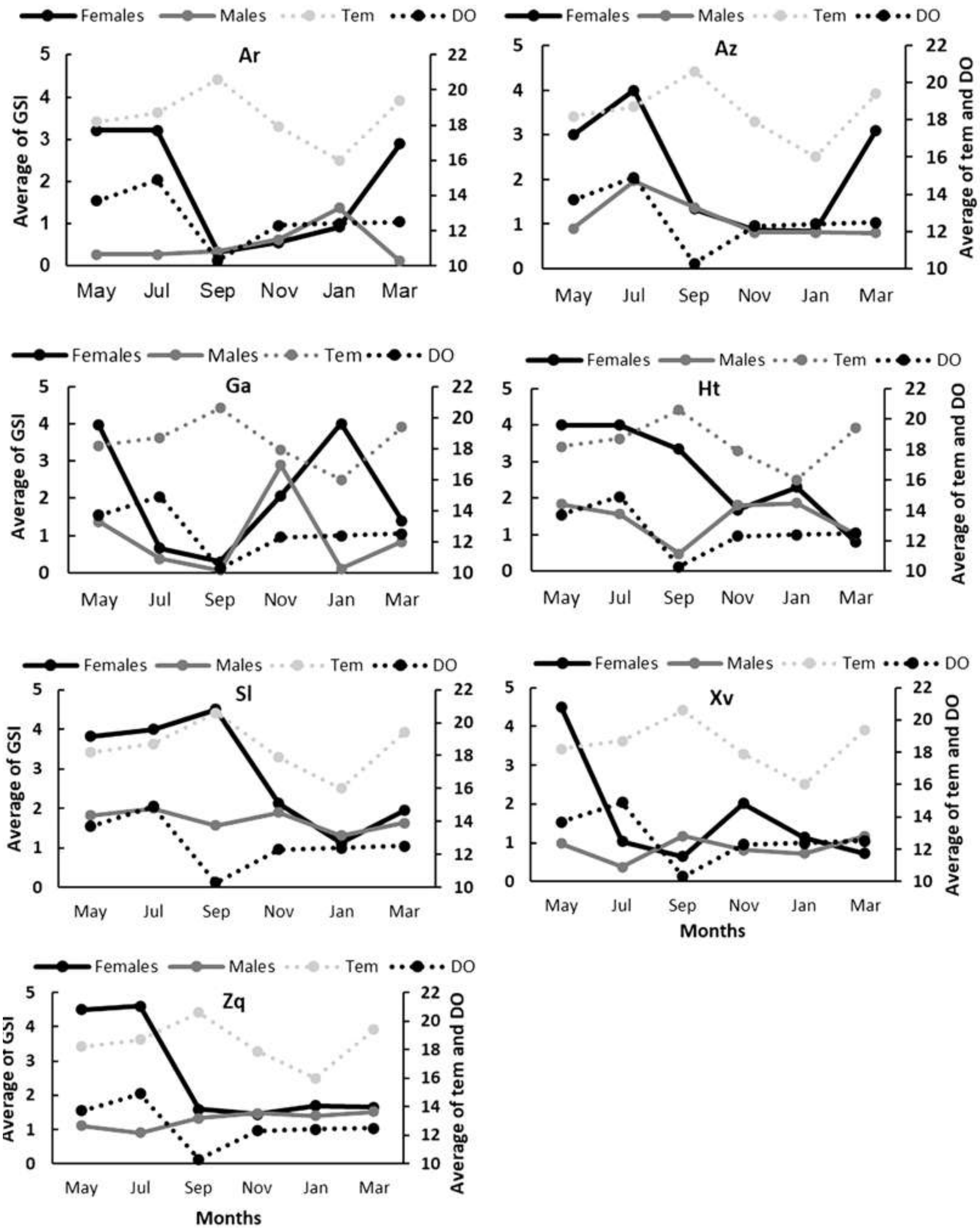

FIGURE 3 | Bimonthly variation in the average of the GSI values and temperature (tem, C°) and dissolved oxygen (DO, O_2 mg/L), the average for each sampling month for females (black line) and males (gray lines) of all goodein species (Ar = *Alloophorus robustus*, Az = *Allotoca zacapuensis*, Ga = *Goodea atripinnis*, Ht = *Hubbsina turneri*, Sl = *Skiffia lermae*, Xv = *Xenotoca variata* and Zq = *Zoogoneticus quitzeoensis*) in Lake Zacapu, Mexico.

standard length of females on the number of embryos in the species *X. variata* (r = 0.77; P = 0.0001), *Z. quitzeoensis* (r = 0.78; P = 0.0001) and *A. robustus* (r = 0.68; P = 0.0001) (Tab. 2). Correlation was marginally significant in the species *G. atripinnis* (r = 0.43; P = 0.0001), *G. turneri* (r = 0.23; P = 0.31), and *S. lermae* (r = 0.25; P = 0.15). Whereas *A. zacapuensis* showed a marginally inverse correlation (r = -0.13; P = 0.5).

TABLE 3 | Kruskal Wallis Test for GSI (gonadosomatic index) and K (Fulton's condition factor) for each goodein species from Lake Zacapu, Mexico. χ^2 = Chi-square value, *= significant differences.

Species	Indexes	Temporal		Spatial	
		χ2	P-value	χ2	P-value
Alloophorus robustus	GSI	7	0.22	4.4	0.22
	K	3.7	0.59	14.8	0.0019
Allotoca zacapuensis	GSI	0.1	0.99	45.7	6.447e-10*
	K	0.1	0.99	45.7	6.447e-10*
Goodea atripinnis	GSI	20.3	0.001*	1.0	0.78
	K	21.4	0.0001*	0.1	0.98
Hubbsina turneri	GSI	5.2	0.39	17.3	0.0005*
	K	4.0	0.54	17.6	0.0005*
Skiffia lermae	GSI	1.1	0.95	8.1	0.043
	K	8.0	0.16	0.8	0.83
Xenotoca variata	GSI	6.2	0.28	1.8	0.60
	K	8.8	0.12	0.8	0.84
Zoogoneticus quitzeoensis	GSI	3.2	0.67	2.4	0.49
	K	9.7	0.08	3.9	0.27

Condition factor (K). Condition factors showed a similar tendency as the reproductive peaks of GSI values in both sexes for all the species. All the species showed the highest average of K during May (Fig. 4). There were no significant differences between the Fulton factor values by months (Tab. 3), only in *G. atripinnis* did Dunn tests shows significant differences by months ($p < 0.0001$). There were significant differences (Dunn test: alpha = 0.005, $p < 0.001$) by sites in *G. turneri*, and *A. zacapuensis* (Tab. 3).

Physicochemical water conditions. The temperature ranged from 16.0 ± 0.2 °C (in January) to 20.6 ± 1.6 °C (in September). The pH (8–9) indicated slightly basic water, with moderate electrical conductivity in a range from 135.9 ± 1.7 µs/cm in January to 155.2 ± 9.8 µs/cm in September. Total dissolved solids showed a range from 105.8 ± 1.9 mg/L in May to 109.9 ± 3.5 mg/L in September. Dissolved oxygen concentrations ranged between 10.3 ± 2.0 mg/L in September to 14.9 ± 3.1 mg/L in July (Tab. 4).

There were not significant differences between sampling sites in water temperature ($\chi^2 = 0.3$, $p = 0.28$), dissolved oxygen ($\chi^2 = 4.5$, $p = 0.206$), total dissolved solids ($\chi^2 = 4.9$, $p = 0.1788$), and pH ($\chi^2 = 0.2$, $p = 0.96$). The Spearman correlation showed a significant relationship in females between GSI and the total dissolved solids in *S. lermae, Z. quitzeoensis*, and *A. robustus* ($R^2 = -0.5$, $p = 0.011$; $R^2 = -0.4$, $p = 0.02$; $R^2 = -0.5$, $p = 0.004$, respectively) and a significant relationship between the GSI and temperature in *G. atripinnis* ($R^2 = -0.4$, $p = 0.02$). For the males only *A. robustus* showed a significant relationship between the GSI and temperature ($R^2 = -0.5$, $p = 0.012$).

The linear models between the environmental variables and the GSI recovered significant relationships in *G. atripinnis*:(temperature t-value= –2.7, $p = 0.013$; dissolved oxygen t-value= 2.3, $p = 0.029$; total dissolved solids t-value= 3.1, $p = 0.005$; conductivity t-value= -2.9, p = 0.008). In *S. lermae* GSI was recovered with a significant relationship with pH (t-value= -2.1, p = 0.045). In the case of the males no relationship was found in all species in the linear models.

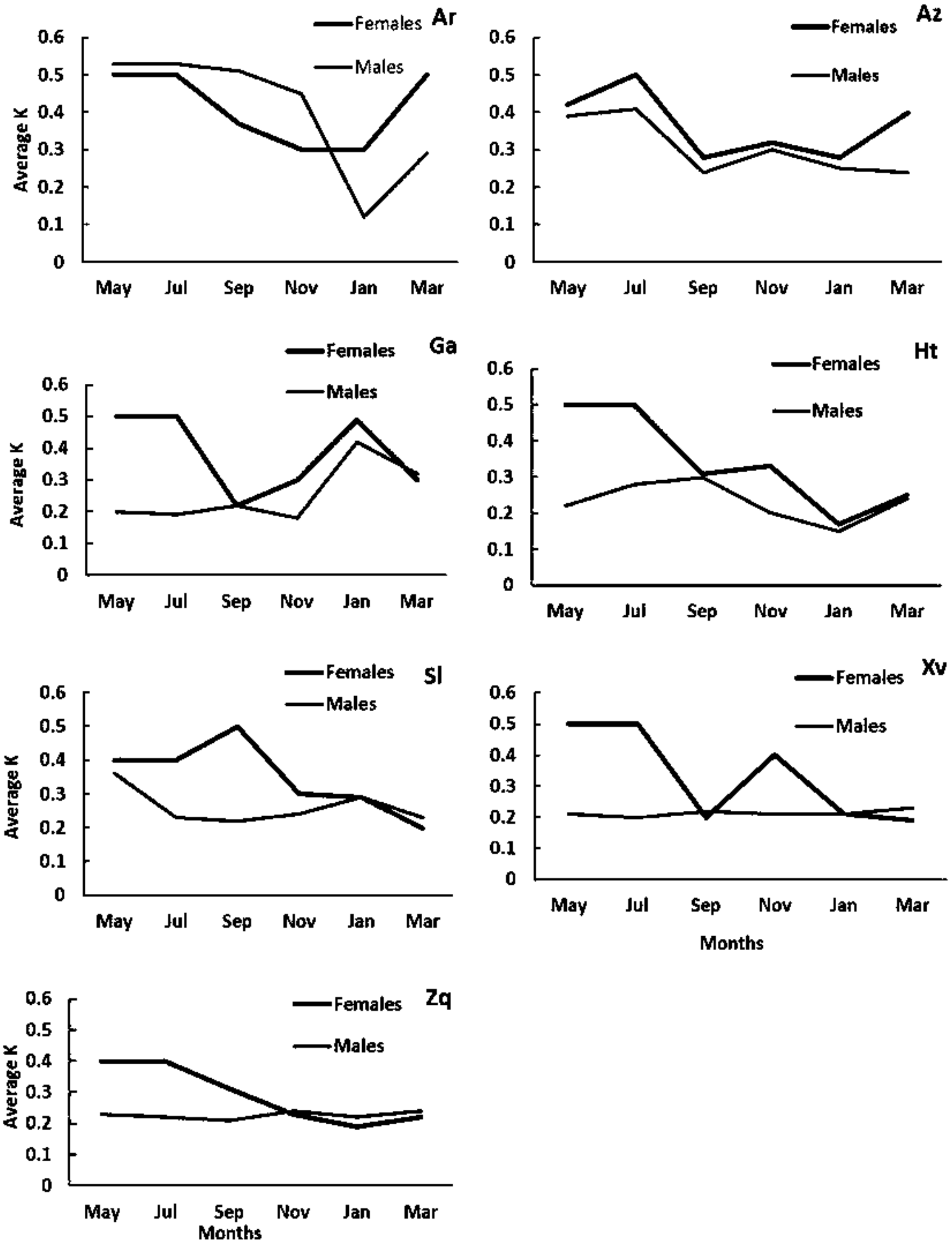

FIGURE 4 | Bimonthly variation in the average of K values for each sampling month for females (black line) and males (gray lines) of all goodein species (Ar = *Alloophorus robustus*, Az = *Allotoca zacapuensis*, Ga = *Goodea atripinnis*, Ht = *Hubbsina turneri*, Sl = *Skiffia lermae*, Xv = *Xenotoca variata* and Zq = *Zoogoneticus quitzeoensis*) in Lake Zacapu, Mexico.

TABLE 4 | Physical and chemical water characteristics in Lake Zacapu, Michoacán, Mexico. Tem = water temperature (°C), DO = dissolved oxygen (O_2 mg/L), pH = potential for hydrogen, TDS = total dissolved solids (mg/L), Cond = conductivity (µs/cm). SD = Standard deviation.

Parameter	May Mean ± SD	Jul Mean ± SD	Sep Mean ± SD	Nov Mean ± SD	Jan Mean ± SD	Mar Mean ± SD
Tem	18.2±0.6	18.7±0.8	20.6±1.6	17.9±0.8	16.0±0.3	19.4±0.9
Min-max	17.3-18.8	17.9-19.8	18.6-22.1	17.1-18.9	15.5-16.1	18.3–20.5
DO	13.7±3.8	14.9±3.1	10.3±2.0	12.3±1.7	12.4±1.9	12.5±2.1
Min-max	9.4–18.6	10.7–17.5	8.6–13.1	11.1–14.9	9.9–14.5	9.9–14.6
pH	9.2±0.5	8.0±0.2	8.3±0.3	8.4±0.2	8.3±0.2	8.9±0.1
Min-max	8.8-10	7.8–8.2	8.2–8.5	8.2–8.6	8.2–8.5	8.7–9.0
TDS	105.8±1.9	106.4±2.3	109.9±3.5	107.7±1.4	107.0±1.4	106.0±2.6
Min-max	104.8–108.3	104.2–108.9	107.6–115.3	105.8–109.2	105.9–109.0	103.4–109.8
Cond	141.7±3.9	143.9 5.7	155.2±9.8	143.5±4.2	135.9±1.7	146.1±6.2
Min-max	136.7–145.7	138.9–151.0	145.4–167.8	138.8–148.8	134.21–138.2	141.1–154.6

DISCUSSION

The present study documents the reproductive cycle of seven native splitfin species of the Goodeinae subfamily in a sub-tropical lake in Central Mexico. The favorable and stable environmental condition that Lake Zacapu provides to the species of splitfins (shallow, monomythic, fed by springs, subtropical ecosystem, high food availability; Moncayo-Estrada, 1996; Ayala-Ramírez *et al*., 2007; Domínguez-Domínguez *et al*., 2008; Valencia-Vargas, Escalera-Vázquez, 2021) could be related to high reproductive success. These environmental features, contrast to those experienced by the same species or other species of the same subfamily in other water bodies in Central Mexico (Tab. 2) (Mendoza, 1962; Ramírez-Herrejón *et al*., 2007; Cruz-Gómez *et al*., 2013; Ramírez-García *et al*., 2020).

Xenotoca variata and *G. atripinnis* show size dimorphism, with *X. variata* the most dimorphic (males are smaller than females) and the species with the brightest coloration. This sexual dimorphism in size has been shown in other species of goodeines (*i.e*., splitfins) (Ritchie *et al*., 2007). Several hypotheses have tried to explain these differences: Firstly, relating to the energetics, a greater investment in testes and sperm production leading to smaller males (Wootton, Smith, 2014). Secondly, the loss of feeding opportunities and extra-spend energy in species with active courtship in males leading to smaller males, as demonstrated in Darkedged Splitfin (*Girardinichthys multiradiatus* (Meek, 1904)) (Macías-García, Valero, 2010). Thirdly, ontogeny considerations (developmental constraints hypothesis), selection should favor prolonged development, but if juvenile mortality exceeds adults, selection for survival should favor rapid development and maturation at a smaller size. If reproductive success is not positively correlated with body size in males, this selection for early maturation will dominate among males, leading to protandry and female-biased size dimorphism (Fairbairn, 1990). Fourth, an indirect consequence of the mating systems (Magurran, Macías-García, 2000), for example, males maneuver better at the smaller size when trying to copulate (Clutton-Brock, Parker, 1995). Fifth, predation has also been related to size dimorphism. Laboratory experiments in *X. variata* demonstrate that specimens with more marked secondary sexual traits, such as a conspicuous distal edge yellow band in males, may increase predation risk (Moyaho *et al*., 2004). Species with the bright yellow band suffer more damage in this area, and consequently, as more tissues must be regenerated, they gain mass more slowly (Macías-García, Ramírez, 2005).

The observed proportion of females was greater for most studied species from Lake Zacapu. Sex ratio generally favors females in wild populations to ensure the offspring (Wootton, Smith, 2014). These sexual differences have frequently been attributed to foraging behavior and male-biased high predation mortality (Rodd, Reznick, 1997). In goodeines, which show strong sexual dimorphism in appearance (males more colorful or/and ornamented than females) and behaviour (with the males undertaking an elaborate courtship to persuade the female to copulate), males are more prone to predation (Macías-García *et al*., 1994; Macías-García, Valero, 2010), all these features are similar to poeciliids (Magalhães, Jacobi, 2017). It has been demonstrated that individuals with more secondary sexual traits may be at an increased risk of predation, especially in clear waters where prey fish can be easily identified by predatory fish, reptiles, and wading birds (Macías-García *et al*., 1994; Moyaho *et al*., 2004). The sexual dimorphism and courtship behavior of goodeines in combination with the high-water transparency of Lake Zacapu (> 120 cm), could promote male-biased predation and consequently observed sex ratio biased to females in the seven studied species, as have been previously explained for *Girardinichthys multiradiatus* (Macías-García *et al*., 1998), and poeciliid species, such as the guppy *Poecilia reticulata*, black molly *Poecilia sphenops*, Yucatan molly *Poecilia velifera*, green swordtail *Xiphophorus hellerii*, southern platyfish *Xiphophorus maculatus*, variable platyfish *Xiphophorus variatus* (Rodd, Reznick, 1997; Magalhães, Jacobi, 2017) and *Gambusia holbrooki* (Kahn *et al*., 2013).

An important factor that could be related to reproductive success is food availability. If food availability is limited or environmental conditions are unfavorable for reproduction, females animals have lower fertility rates than predicted and/or reproduce at smaller sizes (Lombardi, Wourms, 1988; Hollenberg, Wourms, 1994; Wootton, Smith, 2014; Magalhães, Jacobi, 2017). Food availability is especially important in viviparous fishes (Trexler, DeAngelis, 2003; Tobler, Culumber, 2018). Goodeines are matrotrophic, with the embryos growing up to 38,700% after yolk absorption (Hollenberg, Wourms, 1995), nourished through a placenta-like structure connecting the embryo lower gut to the mother's ovarian cavity (Macías-García, Valero, 2010). Therefore, the nutrition condition of the female (related to food availability; Reznick *et al*., 1996; Wourms, 2005; Trexler, DeAngelis, 2003), is closely linked to the quality and quantity of embryos (Blackburn, 2005; Uribe *et al*., 2018). An indicator of the nutrition condition of a species is the Fulton factor (Hutchings, Gerber, 2002). We found that developing embryos increased more in mass and volume in the most robust individuals (highest Fulton factor), leading to an increase in the female reproductive allocation (Fig. 4). In Lake Zacapu, fishes reach sexual maturity at larger sizes and have higher fertility rates compared to fish in other aquatic systems (Mendoza, 1962; Navarrete-Salgado *et al*., 2007; Ramírez-Herrejón *et al*., 2007; Cruz-Gómez *et al*., 2011; Gómez-Márquez *et al*., 2013; Ramírez-García *et al*., 2020). The higher food availability and stable habitat conditions in Lake Zacapu (Valencia-Vargas, Escalera-Vázquez, 2021) may lead to an increased rate of development of individuals, compared to the members of the same species in other habitats. For example, Lake Patzcuaro is a eutrophic lake with low transparency, high wastewater discharges, and low food availability (Mendoza, 1962; Ramírez-Herrejón *et al*., 2014), and Teuchitlán river, is a system with high dominance of exotic species, completely modified by human settlements, highly polluted and with low availability of food (Ramírez-García *et al*., 2020; Hernández-Morales *et al*., 2020; Mar-Silva *et al*., 2021). In Lake Zacapu relative to in other habitats, goodeines could use more energy for growth and offspring nutrition (Wootton, 1998), resulting in higher fertility rates. Previous studies in the Teuchitlan River, a system with high anthropic pressures (*e.g*., pollution, introduction of non-native species and habitat modification), and low food availability, (Herrerías-Diego *et al*., 2018; Hernández-Morales *et al*., 2020; Mar-Silva *et al*., 2021) show that species of goodeines, including *G. atripinnis* and *Z. purhepechus*, mature at lower size and present lower fertility rate relative to Lake Zacapu (Ramírez-García *et al*., 2018, 2020). Consequently, the unfavorable conditions of Teuchitlan River could be causing the species to produce offspring early in life but in low numbers (Ramírez-García *et al*., 2020).

It has been frequently found that hydrologic variability and environmental variables affect reproduction in fish in different aquatic ecosystems (Mims, Olden, 2012). Temperature, pH, and dissolved oxygen are closely linked to reproductive periods in different species of viviparous fishes, such as poeciliids (Gómez-Márquez *et al*., 1999, 200, 2016; Ramírez-García *et al*., 2018) and goodeines (Mendoza, 1962; Moncayo-Estrada, 1996, 2012; Ramírez-García *et al*., 2020). Although in the species studied, we found the same two reproductive peaks, one in spring (April to June) and other in fall (September to November) as have been found for other goodein species (Ramírez-Herrejón *et al*., 2007; Cruz-Gómez *et al*., 2013; Silva-Santos *et al*., 2016; Ramírez-García *et al*., 2020), in general, our results did not find a relationship between the reproductive peaks and environmental variables, except for *G. atripinnis* and *A. robustus* (Fig. 3). The lack of correlation between environmental variables and reproduction could be explained to a variety of factors: In the past, the wider Zacapu region (Fig. 1) was a swamp area of 15,000 ha fed by several springs. At the beginning of the 20th century Zacapu was dried out for agricultural purposes, and currently the remaining wetland constitutes 15 ha of lake (Lake Zacapu) fed by 12 springs, which promote high water turnover (Zubieta-Rojas *et al*., 2005) which give to the waterbody more stable and homogenous physicochemical conditions in space and time than other aquatic ecosystems (Tab. 4) (Moncayo-Estrada, 1996; Ayala-Ramírez *et al*., 2007; Domínguez-Domínguez *et al*., 2008; Valencia-Vargas, Escalera-Vázquez, 2021). In this case, there is the possibility of reproductive resilience of the fish species (Lowerre-Barbieri *et al*., 2015), to adapt to changing conditions to maintain the level of reproductive success needed to result in long-term population stability in abundance but not changing its key traits, such as reproductive periods, despite the desiccation of the wider Zacapu wetland and the expected homogenization of the physicochemical parameters given the high water exchange resulting from the contribution of the 12 springs that feed the lake. Another possibility to explain the lack of correlation between environmental variables and reproduction may be linked to viviparity, a common reproductive strategy of the studied species. Since eggs and embryos develop inside the female's body, they are less influenced by several external environmental conditions. Also, the physiological and energetic cost associated with the gestation period (Wourms, 1981; Lombardi, Wourms, 1988) could force females to undertake a period of rest or recovery before becoming pregnant again, leading to the appearance of two reproductive peaks. This hypothesis is supported by controlled experiments, whereby two reproductive periods with a consistent time between them have been found in matrotrophic species in captivity (Mendoza, 1962; Silva-Santos *et al*., 2016). One final possibility is that we simply have not included in our study the environmental variables that may be related to the reproductive periods of the studied species.

Goodeines or splitfins from Lake Zacapu show high reproductive effort, and favorable reproductive tactics: Female biased sex ratios, early maturity at small sizes, and females reach larger sizes than males, thus increasing their fertility with a large number of embryos. Additionally, the reproductive strategy (viviparity-matrotrophy) of the goodein species helps to promote this reproductive success together with the favorable conditions that Lake Zacapu offers to the species. Although Zacapu Lake is a protected area (Zubieta-Rojas *et al*., 2005), the conservation strategies included in the management plan must be implemented. We recommend some conservation management strategies to protect aquatic biota in Lake Zacapu: regulate the water extraction from the lake and recharge basin; urban development plan on the shore of the lake that prioritizes the conservation of the lake system, lakeshore restoration program, cessation of water pollution in Lake Zacapu, and through environmental restoration, increase the wetland areas in Lake Zacapu, cessation of the reintroduction of non-native species, including translocation from neighbor areas.

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AUTHORS’ CONTRIBUTION

Arely Ramírez-García: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Rodrigo Moncayo-Estrada: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

All field sampling techniques performed and laboratory fish handling protocols followed in this study were reviewed and approved by the Mexican Ministry of Environmental and Natural Resources (SEMARNAT-SGPA/DGVS/00012/19), Ministry of the Environment, Climate Change and Natural Resources (SEMACCDET-OS. 0084/2019) and the Secretariat of Agriculture and Rural Development (SAGARPA: PPF/DGOPA-014/20).

COMPETING INTERESTS

The authors declare no competing interests.

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Capítulo IV

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Diet and trophic structure of the fish community in a small sub-tropical lake in central Mexico

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Abstract

Analyses of the trophic structure and the feeding habits of the fish community can provide information about the complex biotic and abiotic interactions in lake ecosystems. Based on stomach content and $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses, we conducted a comprehensive study of the diet of the fish community and its trophic structure in subtropical Lake Zacapu in central Mexico. Fish diets consisted mainly of aquatic macroinvertebrates, which are abundant in the lake. Most species were secondary consumers and trophic generalists across four sites and two seasons, reflecting homogeneous physicochemical conditions resulting from short water residence in the system. The food web structure did not differ significantly between the four sampling sites or seasons. Our results suggest a higher position of native species in terms of spatial trophic niche and niche width conservation of Lake Zacapu. Although there was a relatively good agreement between the results based on the diet and isotope analysis, the stomach content did not fully capture the trophic position, likely because it only provides a snapshot of the consumer, while stable isotopes integrate diet information over longer periods. Our study is the first one to describe trophic interactions in Lake Zacapu which is rich in endemic species and an important resource for human communities

Keywords

Native species, Stable isotopes, $\delta^{13}C$, $\delta^{15}N$, diet analysis, SIBER analysis.

Introduction

Small lakes are often immersed in areas of urban development, and subject to productive or agricultural activities (Brown et al., 2006) and thus vulnerable to eutrophication (Rawcliffe et al., 2010). Small lakes are especially sensitive to climate change, introduction of non-native species, overexploitation of natural resources, and habitat degradation (Cantonati et al., 2012). Moreover, being closely connected with the terrestrial environment, allochthonous energy sources and nutrient input may be higher than in large lakes, which has implications for the trophic structure (Stouffer, 2005).

Fish are important drivers of food webs in lakes; they occupy a great variety of trophic niches and circulate matter and energy from basal resources to the highest levels of the web (Delong et al., 2011). Fish trophic structure studies are essential for the conservation of aquatic ecosystems and the integrated assessment of their resources (Fauvelle et al., 2017). Evaluation of the feeding habits of fishes in different parts of their life cycle is useful to determine the status of the species within the food web and thus contribute to the understanding of the community structure (Garrison and Link, 2000).

Analyzing diets of different fishes in a community can provide information about inter- or intraspecific interactions and the mechanisms that determine the distribution of resources (Dantas et al., 2013). Competition occurs when species share the same prey (Pianka, 1981), and the resources available are limited (Sánchez-Hernández et al., 2011). Competitive interactions are usually much stronger within than between different species of a community and when competition is for the consumption of the same resource, it can affect habitat selection patterns and niche overlaps (David et al., 2007).

Elucidating the trophic position of different fish species in a community may help to understand the complexity and functioning of a food web (Hussey et al., 2014). Changes in the trophic position of species are often associated with abiotic and biotic factors, such as the availability of prey, diet composition, hydrological stability, ecosystem area and the body size of organisms (Hayward and Hutchings, 2011; Eloranta et al., 2015).

Identification of the trophic position also helps reveal the functional role of a species within the trophic web and its specific contribution in energy flow pathways (Hussey et al., 2014).

Stomach content analysis constitutes a classical method to elucidate the diet of aquatic organisms (Davis et al., 2012). However, data obtained by stomach content techniques may not fully capture all food items of a species, as it only provides a snapshot of the diet of the consumer (Svanbäck et al. 2015). Stable isotope analysis techniques have been incorporated to integrate energetic information over longer periods. In stable isotope studies, carbon signatures identify energy sources, while nitrogen signatures are related to the trophic position of a consumer within food web (Fry, 2006; Layman et al., 2012). Joint use of both methods allows a more comprehensive method to study food web relationships in an ecosystem (Hill et al., 2015). When used together, diet analysis and stable isotope approaches are effective tools to understand the trophic position of species, and how species (for example native versus non-native species) interact (Pilger et al., 2010).

The combined use of stomach content analysis and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) has been successful in the modeling of food webs in freshwater and marine systems (Thomas et al., 2016; Sánchez-Hernández et al., 2017; Laske et al., 2018; Mwijage et al., 2018). Using both analytical approaches it is possible to model the trophic structure (Bearhop et al., 2004; Vander Zanden et al. 2006a) of an ecosystem, and to get information of the position of each species in the web, as well as on the trophic interactions and energy flow (Layman et al., 2012). However, there are few investigations comparing the results of the two methods in lakes (Jones and Waldron 2003; Franssen and Gido, 2006).

We analyzed stomach content and stable isotope data of fishes from Lake Zacapu, in central Mexico. The lake is small (~ 20 hectares), shallow (average ~ 2.7 m) and maintained by the contribution of numerous springs. The lake is a monomictic subtropical ecosystem with low turbidity (Moncayo-Estrada, 1996; Valencia-Vargas and Escalera-Vazquez, 2021; Ramírez-García et al., 2021). The hydraulic renewal is fast (5.076 days), due to the continuous flow of water, leading to good water quality, with a high buffering capacity for pollutants, and it is considered an area with little human disturbance (Ayala-

Ramírez et al., 2007; Domínguez-Domínguez et al., 2008). Moreover, the lake has many native and endemic species (Ramírez-García et al., 2021; 2022).

Here we describe the diet of fishes in the lake, and temporally (two seasons) and spatially (4 sampling stations) document their trophic position in the food web. Our hypotheses were that 1) the homogeneous environmental characteristics of the lake led to high availability and diversity of food resources for the fish species, 2) the trophic position of fishes evaluated from stable isotope data will be mimicked in by diet data.

Materials and methods

Study area

Lake Zacapu is a sub-tropical lake (*ca.* 15 ha) located in central-western Mexico at 1980 m. a.s.l. and is part of the Lerma-Chapala River basin (Figure 1). The seasonal variation in air temperature in the region is between 7 °C and 27 °C, with an annual average of 16.7 °C (Moncayo-Estrada, 1996). In 2003 the lake was declared a Natural Protected Area; its management plan was published in 2005 (Zubieta-Rojas et al., 2005). The lake is fed by 12 springs. It has a high hydraulic renewal rate of approx. five days and high buffering capacity (Ayala-Ramírez et al., 2007; Domínguez-Domínguez et al., 2008). The lake is also considered homogeneous, with good water quality, and low spatial variations in physical and chemical variables (Moncayo-Estrada, 1996; Ramírez-Herrejón, 2008; Ramírez-Herrejón et al., 2012; Valencia-Vargas, Escalera-Vázquez, 2021; Ramírez-García et al., 2021; Ramírez-García et al., 2022).

Environmental variables

For physical-chemical characteristics, we used a multiparameter probe (YSI EXO2; YSI Inc., Yellow Springs, OH, U.S.A) and measured conductivity (µs/cm), temperature (ºC), dissolved oxygen (O2 mg/l), reduction oxide potential (mv), total dissolved solids (TDS mg/L), ammonia (mg/L), nitrate (mg/L), ammonium (mg/L) and pH.

Fish collection

We conducted fish sampling over an annual cycle from May 2019 to May 2020, at four locations in the lake. For diet analysis every three months, and for stable isotopes two season (dry and wet). Multiple fishing methods were used in fish collections. We used a seine (25 m length, 1.8 m height, and 5 mm mesh size) to sample fishes in areas with maximum depth of 1.5 m. We also used minnow traps (stainless steel, square mesh 0.5 m, cylindrical, 42 cm long, and 19 cm in diameter, with two 2.5 cm holes with inverted cone inlets) set for one hour per site. Shallow (< 1m) areas near shores within a site were also sampled with electrofishing for half an hour (DC-backpack electrofisher model ABP-3, ETS electrofishing systems, LLC, average power ~200 W, peak voltage ~250 V, peak current ~10 A). In addition, specimens were also obtained from local fishermen. We identified fish species using published keys (Miller et al., 2009). Fishes were preserved in ice water and transported to the Aquatic Biology Laboratory from the Universidad Michoacana de San Nicolás de Hidalgo. All field collections were carried out under permits (SEMARNAT- SGPA/DGVS/00012/19) (SEMACCDET-OS. 0084/2019) and (SAGARPA: PPF/DGOPA-014/20).

Invertebrate collection

In addition to fish, we obtained samples of other food web components. We sampled benthic aquatic macroinvertebrates using a 500 µm D-shape net. The collected specimens were separated in situ of the abiotic material and subsequent transport to the laboratory. Macroinvertebrates were processed per individual when the organism’s size was sufficient to obtain at least 2 mg (dry weight); if individuals were not large enough (i.e., *Hyallela*), we pooled all available individuals from each site per season. Also, the spatial-temporal analysis of the macroinvertebrate community was evaluated in terms of dominance, diversity, and spatial organization just to have a better description of the food items of the fish species. Plankton were collected by filtering 300 liters of water covering the entire water column using two nets of different mesh size (64 µm and 200 µm). These bulk samples contained a mix of phytoplankton (larger sizes) and zooplankton. All the samples were frozen at -20˚C until laboratory processing.

Laboratory analysis

Individual fish were measured for standard length and weight. Fish was dissected to get the stomach to preserved in 5% formaldehyde. Diet analysis was carried according to the quadrant method proposed by Hynes (1950) and prey items were identified to the lowest possible taxonomic level. Prey items were identified using keys for invertebrates (for insects: Merritt et al., 2019; and non-insects: Thorp and Covich, 2010).

From the same fish muscle tissue samples (2 cm^3) from the lateral back region of three specimens of all species of fish were taken, labeled, stored in plastic bags, and frozen at −20 °C and stored until processing.

Fish muscle tissue, plankton samples and macroinvertebrates individuals were dried, pulverized and ~1 mg was weighed into tin capsules analyzed for $\delta^{15}N$ and $\delta^{15}C$ stable isotopes. Stable isotope analysis was performed at the University of New Mexico Department of Earth and Planetary Sciences. Two percent of all samples were processed in duplicate (mean standard error was 0.5‰ for C and 1.5‰ for N). Stable isotope analyses were carried out based on 112 fish, 4 phytoplankton, 4 zooplankton and 29 invertebrates from the wet season and 118 fish, 4 phytoplankton, 4 zooplankton and 26 invertebrates from dry season.

Data analysis

Environmental variables: We tested for differences in environmental variables among seasons and sites, using Kruskal Wallis non-parametric analyses of variance (Dunn test, as a posteriori).

Diet analysis: To determine whether the number of analyzed stomachs accurately described the diet of the species, a prey accumulation curve was created for the species, following the criteria of Ferry and Cailliet (1996). A modified version of the Index of Relative Importance (IRI) proposed by Yañez-Arancibia et al. (1976) was used to determine the trophic diet: IIR = (F x A)/100, where, F is the frequency of occurrence, and A is the area of collection. The frequency of occurrence was expressed as percentages of their frequency of appearance (F) as follows: F = (n*100)/n. where "n" is the number of times a certain prey appears in the stomach and is expressed as the percentage with respect to the total number of stomachs analyzed (N). Further we calculated the percent of prey-specific index of relative importance (%PSIRI) to get the dominance of prey, using the following equation: $\%PSIRI = \%FO_i \times (\%PN_i + \%PW_i)/2$ (Brown et al., 2012). The %PSIRI includes the percent frequency of occurrence ($\%FO_i$ = number of stomachs with prey *i* divided by the total number of stomachs). The trophic niche width was calculated using the standardized Levin´s index (Bi), where: Bi= 1/∑pj 2. Pj: is the proportion of individuals found or used in the resource j, ranging between 0 and 1. In this index, a Bi close to 0, indicates a specialist predator that uses few prey resources and prefers certain prey, while values close to 1 indicate a generalist predator that uses all resources without preference (Krebs, 1989). The trophic level of each taxa allows us to gain information of the position that organisms occupy in the food web (Paul et al., 2000); it was estimated using the TrophLab software. The results were expressed as a trophic level between 1 and 5, where 0-1 corresponds to decomposers, 1-2 to primary producers, 2-3 to primary consumers, 3-4 to secondary consumers and >4 are considered tertiary consumers. The omnivory level was estimated by the omnivory index (IO) proposed by Pauly et al. (1993). The index is dimensionless and describes the distribution of interactions at each trophic level and the vales are in the range between 0 and 1. When IO is close to 0, the consumer is considered a specialist. If the value of IO is close to 1, the consumer feeds on several trophic levels. Diet overlaps between different fish taxa was assessed via Horn´s index (Krebs, 1989) using the following equation: Ro= ∑(Pij+Pik) log (Pij+Pik)-∑pij log Pij - ∑pik logPik /2log 2. Where: Ro = is Horn´s niche overlap index between the species; Pij is the proportion of resource i that is used by species j; Pik is the proportion of the resource i that is used by the species k; and N: total number of resources. The values in this index vary from 0 to 1. The trophic superposition is classified according to the scale proposed by Langton (1982), where values between 0 and 0.29 indicate a low superposition, values between 0.30 and

0.65 indicate medium superposition and values > 0.66 indicate high overlap. Fish species diets according with the PSIRI index were compared using a cluster analysis, following the Bray–Curtis ordination method and Euclidian distance as an index of dissimilitude. To complement the cluster analysis, the data was visualized in a principal component analysis (PCA). To test for significant differences in the diet composition between the groups that emerged from the cluster analysis, a non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA; Bray Curtis index) was performed.

Stable Isotopes: differences in carbon and nitrogen isotopic signatures between species from different sites were analyzed with ANOVA with a post-hot hoc Tukey test to identify significant differences, for differences between season a student´s test was applied. A bivariate plot of the mean (±1SE) isotopic values (δ^{15} N on the y-axis; δ^{13} C on the x-axis) was made for all fishes (per species), including grouped benthic invertebrates, zooplankton, and phytoplankton.

The niche breadth and isotopic overlap degree were estimated between the species, computerizing the standard Bayesian ellipses area in R (SIBER) in the bidimensional isotopic space of δ^{15} N and δ^{13} C values. These metrics reflect assemblage trophic niche space as the area occupied within a d^{13}C–d^{15}N biplot as: range in δ ^{13}C (CR), range in δ ^{15}N (NNR), mean distance to the centroid (CD), and total area (TA). CR is a measure of basal δ ^{13}C variation, NNR provides information on the food chain length, CD indexes trophic diversity within the assemblage and TA represents the total trophic niche space occupied by the assemblage. The extent of trophic redundancy within the assemblage was measured by two additional metrics: mean nearest neighbor distance (MNND) and standard deviation of the nearest neighbor distance (SDNND). Theoretically, smaller MNND and SDNND indicate greater trophic redundancy (groups have more similar trophic niches; Abrantes et al., 2014). Therefore, Bayesian standard ellipse area corrected (SEAc) was used to quantify the trophic niche space of fish community and the overlap niche was obtained between season and sites (Jackson et al., 2011). To determine trophic position of the fish species, we used a Bayesian model using the package tRophicPosition in R, for the calculation of consumer trophic position using stable isotopes of C and N.

Results

Environmental variables

Kruskal-Wallis test showed no significant differences between the dry and wet season for temperature ($x^2 = 3.6$, $p = 0.056$), dissolved oxygen ($x^2 = 0.2$, $p = 0.599$), TDS ($x^2 = 0.8$, $p = 0.369$), conductivity ($x^2 = 1.8$, $p = 0.170$), NO_3 ($x^2 = 2.6$, $p = 0.102$) and NH_4 ($x^2 = 2.2$, $p = 0.134$) (Table 1). Significant differences were, however, found for pH ($x^2 = 6.4$, $p = 0.01129$) and NH_3 ($x^2 = 6.1$, $p = 0.012$). Dunn tests shows that pH in dry season was higher than in the wet season (alpha = 0.05, $p < 0.01$), and vice versa for $NH_{3.}$ (alpha = 0.05, $p < 0.01$). We did not find significant differences among sites for any of the variables (Table 1).

Diet analysis

Thirteen species were recorded in the lake, belonging to four families, the Goodeidae being the most common (68% of all the species) (Table 2). Apart from two species (*Ctenopharingodon idella* and *Cyprinus carpio*) all species are native to Mexico. From a total of 3403 stomachs analyzed, 3229 (94%) were analyzed and used in establishing feeding groups. The remaining stomachs were empty or with indeterminate dietary content.

The food items represented were classified as follows: Chordata (including whole fish, scales, fins and fish remains); Arthropoda (including insect remains and the family Chironomidae); Crustacea (including Malacostraca [genera *Hyallea* and *Cambarellus*], Ostracoda, Branchiopoda [genus *Bosmina*], and Maxillopoda [copepods]); Mollusca (including Gastropoda and Bivalvia); Rotifera (comprising the Monogononta, genus *Keratella*); Diatomista (including the Diatomea [genus *Fragilaria, Synedra, Cymbela*]; Magnoliophyta (including vegetal remains and the Liliopsida with the genus *Potamogeton*), and Bryozoa (genus *Plumatella*) (Table 2).

Based on the PSIRI index the *Alloophorus robustus* was found feeding mainly on *Cambarellus* (13.0) followed of remains of fish (7.1). *A. zacapuensis, H. turner, X. variata* and *C. humboldtianum* were feeding mainly of *Hyallea*. The species *C. idella* was the only consuming *Potamogeton* (Table 2).

C. idella had the most specialized niche breath and *G. atripinnis* was the most generalist species (Table 3). All the species belonged to two positions in the trophic web: primary consumers and secondary consumers (Table 3). The omnivory index indicate that most of the species were generalist (Table 3). *G. atripinnis, S. lermae* and *A. robustus* had high omnivory index values, indicating that these species were feeding on more trophic levels than other species. Horn's niche overlap index indicated high food overlap between the species *A. robustus* vs *C. carpio*; *A. zacapuensis* vs *H. turneri*, *X. variata*, *Z. quitzeoensis*; *S. lermae* vs *C. idella*, *G. atripinnis*; *X. variata* vs *Z. quitzoensis*, *C. humboldtianum*, *N. grandis*; *C. humboldtinum* vs *N. grandis*; and *G. atripinni*s vs *S. lermae* (Table 4).

The combination of the PSIRI values for each dietary item (Table 2) used in the cluster analysis revealed a classification into three trophic groups: Carnivore (3 species, mostly feeding on insects, and mollusks), omnivore-carnivore (6 species mostly feeding on copepods, ostracods, *Hyalella* and remains of fish), and omnivore-herbivore (4 species being omnivores mostly feeding on rotifers, cladoceran, aquatic plants, diatoms, and detritus) (Figure 2, 3). The principal component analysis (PCA) separated out the same three trophic groups (Figure 3), with the first two axis explaining 66% of the variation (PC1 = 47% and PC2 = 19%). The PERMANOVA test shows strong statistical support for this classification, with significant differences in the PSIRI index value for the dietary items between the groups ($F = 6.35$, $p < 0.001$).

Stable isotopes

We found significant differences between seasons in $\delta^{13}C$ for *A. tincella* ($t= 0.506$, $p = 0.016$) and *C. carpio* ($t = 0.947$, $p = 0.002$); post-hoc test showed the most enriched values in the wet season. Significant differences between season in $\delta^{15}N$ were found for *H. turneri* ($t = 0.320$, $p = 0.021$) and *P. infans* ($t = 0.238$, $p = 0.005$), the post- hoc test showed the values to be the most enriched in the dry season. Significant differences among sites in $\delta^{13}C$ ($F = 8.047$, $p = 0.001$) and $\delta^{15}N$ ($F=4.149$, $p = 0.021$) was only found for *G. atripinnis*; the Tukey test showed that site 3 had the highest values of $\delta^{13}C$ and the lowest values of $\delta^{15}N$ (alpha 0.05). *Poeciliopsis infans* showed significant differences in $\delta^{15}N$ ($F= 3.4811$ $p =$

0.033) and *Z. quitzeoensis* differences in δ^{13}C (F= 3.436, p = 0.037) among sites; Tukey test showed that site 1 had the lowest values for both species. *Alloophorus robustus* occupied the highest fish trophic position in food web, based on relative δ^{15} N values and food components (Figure 4), while *G. atripinnis*, and *C. idella* had the lowest position. *Algansea tincella* had the most enriched δ^{13} C values of all the food web components. Except *C. humboldtianum* and *A. tincella*, the fish species had average δ^{13} C values between -28 and -18‰.

No clear seasonal pattern was found in the community-wide trophic structure (Figure 5, Table 5). However, the degree of trophic diversity, measured as CD, was greatest in the dry season. Site 3 had the lowest value of CD (Table 5), while sites 1 and 4 had the same and higher value (2.77). The metric MNND, which declines in webs with overlap, indicated a divergent trophic niche or low overlap in both seasons and at all sites. The metric SDNND, which measures the evenness of species isotopic distributions, was highest in the dry season and at site two (Figure 5, Table 5).

The δ^{13} C isotopes values of the baseline (macroinvertebrates) for the site 1 was mean -21.9 ± 1.4, site 2 -22.8 ±1.1, site 3 -22.8 ±1.3 and site 4 -22.8 ± 1.9, for δ^{15} N values mean 7.1 ± 1.5 for site 1; 7.3 ± 1.4 for site 2; 7.6 ± 1.4 for site 3 and 7.8 ±1.9 for site 4 (Figure 6). The δ^{13} C values for the consumers (fish) was 23.0 ± 2.2 for site 1; -22.8 ± 2.0 for site 2; -21.9 ± 1.8 for site 3 and -22.7 ± 2.1 for site 4, while the δ^{15} N values were 10.6 ± 1.4 for site 1; 10.5 ±1.6 for site 2; 10.6 ±1.3 for site 3 and 10.8 ± 1.4 for site 4 (Figure 6).

There were not significant differences between sites in δ^{13} C (F = 1.6057, p = 0.1881) and δ^{15} N (F = 0.6551, p = 0.5803). In the wet season the values of the consumers are δ^{15} N 10.6 ± 1.4 and δ^{13} C -22.5 ± 2.0. For dry season the consumer in δ^{13} C -22.7 ± 2.1 and δ^{15} N 10.7 ±1.4; the baseline (macroinvertebrates) in dry season is δ^{13} C -22.5 ±1.8 and δ^{15} N 7.5 ±1.6; in wet season δ^{13} C -22.5 ±1.0 and δ^{15} N 7.3 ±1.6. The baseline of Zoo in the wet season is δ^{13} C -24.6 ± 2.1 and δ^{15} N 4.4 ±1.1 and in dry season is δ^{13} C -22.9 ±5.2 and δ^{15} N 6.1 ±1.1 (Figure 6). There were not significant differences between dry and wet season in δ^{13} C (F = 0.5600, p = 0.4548) and δ^{15} N (F = 1.4406, p = 0.2310).

Discussion

This study reveals the diet and the trophic structure of fish species from Lake Zacapu and demonstrates the usefulness of combining analysis of stomach content and analysis of $\delta^{13}C$ and $\delta^{15}N$, the trophic relationship of the native and non-native species, the great availability and diversity of food resources for the fish species in the lake and the trophic structure of a group of related species (the family goodeidae) exhibiting similar feeding habits.

In accordance with our first hypothesis, we found the lake has many internal food resources, so the contributions of terrestrial organisms were of minor importance as food sources for the fish. The aquatic macroinvertebrates data revealed 79 genera, distributed in 43 families and 21 orders, the grouping analysis of the macroinvertebrate samples showed no differences among sites in community structure and organization. The most abundant genera were *Hyallela* (40%), *Cambarellus* (4.5%), *Belostoma* (3.2%) and the group of gastropods (*Physella*: 12.5%, *Pomatiopsis*: 6.3% and *Valvata*: 8.0%), indicating a good distribution of resources for the fish in Lake Zacapu, that may reduce competition between the species. Accordingly, we found no spatial variation in the water variables, suggesting spatial homogeneity (Table 1), which concur with other investigations of various environmental variable from this lake (Moncayo-Estrada, 1996; Valencia-Vargas and Escalera-Vázquez, 2021; Ramírez-García et al., 2021; 2022), however significant differences found in only pH and NH_3, may be due to human activities that near to the lake, these play a fundamental role in the eutrophication process (Díaz-Argüero, 1997), caused by industrial discharges or agriculture, and the recreation areas present in the lake.

Most fish species in the lake consumed macroinvertebrates to some degree, for example, the endemic species *Notropis grandis*, is considered an omnivorous species with a tendency to carnivory (Figure 2) and feeds mainly on the genus *Hyalella* (Table 2), concurring with an earlier study by Moncayo-Estrada (1996) in this lake, and with other species of the genus (Bean et al., 2010). The relict species *H. turneri* also bases its feeding habits mainly on *Hyalellas* and some microcustraceans (copepod and cladoceran), similar to what has been reported in other studies (Moncayo-Estrada, 1996; Moncayo-Estrada, 2012), regarding the microindemic species, *A. zacapuensis*, its feeding habits are similar to what was found in this project (Moncayo-Estrada, 1996), mainly ingesting *Hyalellas* and remains of aquatic insects (Table 2).

These three species are restricted to this small lake *N. grandis* (Domínguez-Domínguez et al., 2009), *H. turneri* (Moncayo-Estrada et al., 2022) and *A. zacapuensis* (Meyer et al., 2001), showing similar feeding habits by ingesting similar prey (*Hyalella*, and aquatic insects), however, although the availability of food is sufficient to avoid competition, the two species of goodeids present low abundances and are restricted to some areas of the lake (Ramírez-García et al., 2022) nowadays are cataloged as critical endanger (Lyons et al., 2019; Koeck, 2019), this could be more related to the fact that goodeid species are usually sensitive species to water quality, and need different habitat requirements such as vegetation which they use as refuge (Domínguez-Domínguez et al., 2008; Lyons et al., 2019), similar than *N. grandis*, which is also considered a species sensitive to environmental changes (Domínguez-Domínguez et al., 2009), these could be related to environmental conditions rather than necessary to find resources to feed.

The stomach content data and isotopic signatures provided similar results for trophic position for most species, except for *C. carpio* and *A. tincella* (Figure 4), confirming our second hypothesis. *Cyprinus carpio* occupied a lower position, based on $d^{15}N$ than revealed from the diet (Figure 3), positioning this species as omnivorous, as reported in other aquatic systems where it is non-native species, for example, Lake Pátzcuaro (Ramírez-Herrejón et al., 2014) and Lake Xochimilco (Zambrano et al., 2010) as well as in other parts of the world (Gallardo et al., 2016). *A. tincella* showed the most enriched values of carbon and low values of $d^{15}N$, positioning the species as omnivorous, different from our diet analysis results (positioned as carnivorous; Figure 3), the genus Algansea, in other aquatic systems, is considered an omnivorous and feeds mainly on filamentous algae, algae, benthic invertebrates and zooplankton (Orbe-Mendoza et al., 2002; Miller, 2009), concurring with the observed niche overlap in our isotopic results (Figure 4), this species together with *C. carpio* are the least abundant in the lake (Ramírez-García et al., 2022).

Species from the same family, such as *Z. quitzeoensis, A. zacapuensis*, *H. turneri* and *X. variata* were grouped into the same guild due to the similarity of the resources they consumed (Figure 2, 3), which may be related to the taxonomic proximity between the species (German and Horn, 2006). We found the presence of taxonomically related species, with similar feeding habits. In principle, closer species should be strongly competitive, limiting their coexistence (Canvender-Bares et al., 2009), as we found high diet overlap between some species of Goodeid family (Table 4), indicating that the species share similar resources and occupy similar niches, however it has been documented that a high value does not necessarily mean that the species are competing, the resource may be abundant enough not to be limiting for any of the species and not unleash competition (Mérona and Rankin-de-Mérona, 2004).

Regarding the non-native species of the lake, we found a diet overlap of *C. carpio* with *A. robustus* and of *C. idella* with *S. lermae*, respect to the other species they presented relatively low values (Table 4), indicating that they do not show overlap of diet. It has earlier been documented that the behavior of *C. carpio* during its feeding activity is the one that could cause changes in ecosystems (Zambrano et al., 2001; 2006), since it resuspends the sediment and increases the turbidity of the water, which is harmful in terms of productivity and physical alteration of the habitat for other species (Scheffer et al., 2003; Özbay, 2008), however, in Lake Zacapu the short residence time may have prevented an increase in turbidity of the water as we found low concentrations of total suspended solids (Table 1).

Common carp has been described as one of the worst vertebrate pests worldwide (Gallardo et al., 2016; Stuart et al., 2021), in our study the presence of carp is not considered as an important driver of ecology trophic of fish in Lake Zacapu, due to its relatively low trophic position (Figure 4), also, low abundances of the species has been reported in the lake (Ramírez-García et al., 2022), indicating that the species not present high success in this system or is being controlled under the fisheries in the lake, this species it is highly valued for aquaculture (Vilizzi, 2012; CRIAP, 2019).

The SIBER analysis indicated the dry and wet season gave similar values in the isotopic niche space (SEAc) and similar trophic diversity based on the values of NNR, CR, and CD (Table 5, Figure 5), which was supported by the similar values of MNND and SDNND (trophic redundancy). This suggests the fish in this lake exploit similar resources in both seasons. There was, however, a tendency to obtain lower CD and SEAc values at site 3, and lower values of MNND and SDNND at site 1 (Table 5; Figure 5), indicating less trophic diversity although the species exploited similar resources within the same habitat. These sites were spring fed and positioned where most of water entered the lake. The fish had aquatic macroinvertebrates as their main source of energy. However, the stable isotope data suggest that they may also be consuming foods with enriched δ^{13}C values, such as zooplankton (Figure 6). In the subtropical regions, the gradients of seasonal variation of temperatures are low compared to the temperate regions (Yu-Chun et al., 2020), in our study no significant environmental changes were observed that could influence on the trophic ecology of the lake species.

Lake Zacapu had environmental conditions that favor fish that are trophic generalists. Our findings reveal that local food web structure did not differ significantly between the four sampling sites (Figure 6). The results of this study are supported by the great abundance of aquatic macroinvertebrates found in Lake Zacapu, also by the characteristics of the system, such as environmental homogeneity of the water (Table 1) and the unique characteristics of each species (generalists or specialists; Table 3). Our results suggest a higher position of native species in terms of spatial trophic niche and niche width conservation of Lake Zacapu as center adaptative for fished and other groups, as a system with water regulation thought the lake, and as important resource for human communities. Although there was a relatively good agreement between the results based on the diet and isotope analysis, the stomach content did not fully capture the trophic position likely because the diet technique only provides a snapshot of the consumer, while the stable isotopes integrate over a longer time.

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Tables and figures

Table 1.- Physical and chemical water characteristics from Lake Zacapu, Michoacán, Mexico. Tem = water temperature (°C), DO = dissolved oxygen (O_2 mg/L), pH = potential for hydrogen, TDS = total dissolved solids (mg/L), Cond = conductivity (µs/cm), NH_3 = ammonia (mg/L), NO_3 = nitrate (mg/L), NH_4 = ammonium (mg/L). Average and deviation standard ($\bar{X}$ ± DS). Kruskal Wallis differences among season and sites. * Significant differences.

Parameter	**Dry season**	**Wet season**
Tem	18.5±1.5	19.9±0.7
Season	$x^2 = 3.6486$, $p = 0.056$	
Sites	$x^2 = 1.723$, $p = 0.631$	
Do	13.7±2.7	14.3±0.2
Season	$x^2 = 0.2757$, $p = 0.599$	
Sites	$x^2 = 9.3971$, $p = 0.064$	
pH	7.7±0.4	7.3±0.2
Season	$x^2 = 6.419$, $p = 0.011$	
Sites	$x^2 = 0.74108$, $p = 0.86$	
TDS	107.9±2.1	109.2±2.4
Season	$x^2 = 0.80397$, $p = 0.37$	
Sites	$x^2 = 1.0738$, $p = 0.78$	
Cond	136.7±2.6	138.8±1.8
Season	$x^2 = 1.875$, $p = 0.17$	
Sites	$x^2 = 1.0429$, $p = 0.79$	
NH_3	0.07±0.02	0.11±0.03
Season	$x^2 = 6.1799$, $p = 0.012$	
Sites	$x^2 = 0.18107$, $p = 0.98$	
NO_3	7.4±1.0	6.7±0.6
Season	$x^2 = 2.6694$, $p = 0.10$	
Sites	$x^2 = 0.13889$, $p = 0.98$	
NH_4	0.06±0.02	0.09±0.05
Season	$x^2 = 2.2443$, $p = 0.13$	
Sites	$x^2 = 0.0171$, $p = 0.99$	

Table 2.- Diet and trophic classification of fish species sampled in Lake Zacapu. The values for each item type and fish species represent the Variation in Prey-Specific Index of Relative Importance (PSIRI). Minor taxon identified abbreviation are the followed: Fish/R = fish and fish remains; AcIn/R = Aquatic insects remains; Chi= Chironomidae; Hya = Hyalella; Cam = Cambarellus; Ost= Ostracods; Bos = Bosmina, Cop = copepods; Gas = gastropods, Biv = Bivalvia, Ker= Keratella, Frag= Fragilaria; Dia =diatoms; Veg/R = remains vegetal; Pot= Potamogetom; Plu = Plumatelidae.

	Phylum	**Chordata**	**Arthropoda**		**Crustacea**					
	Class	**Actinopterygii**	**Insecta**		**Malacostraca**		**Ostracoda**	**Branchiopoda**	**Maxillopoda**	
	Minor taxon identified	**Fish/R**	**AcIn/R**	**Chi**	**Hya**	**Cam**	**Ost**	**Bos**	**Cop**	**Detritus**
Fish species										
A. robustus		7.1	1.2		1.9	13.0			0.3	0
A. zacapuensis			13.8	4.8	22.9		0.6		0.8	0
G. atripinnis		4.5		1.5			6.9	7.5	2.5	9.7
H. turneri			3.9	2.7	31.2		2.3	4.5	3.9	0
S. lermae		0.7	4.6		0.9		0.4	6.0	1.6	5.1
X. variata		8.1		8.2	27.4		9.3		4.9	0.3
Z. quitzeoensis		7.6	2.2	3.9	13.7			0.4	10.9	3.6
C. humboldtianum		1.5	0.5	0.5	27.1	0.4	2.2	31.0	5.2	0
P. infans		3.1	0.2	0.2	0.6		0.9	24.6		6.1
C. idella										21.3
C. carpio				1.8		5.4				0
N. grandis					20.3		13.3	9.6	1.9	0
A. tincella			28.6	1.0		4.5				0

	Phylum/division	Mollusca		Rotifera	Diatomista		Magnoliophyta		Bryozoa
	Class	**Gastropoda**	**Bivalvia**	**Monogononta**	**Diatomea**			**Liliopsida**	**Phylactolaemata**
	Minor taxon identified	**Gast**	**Biv**	**Ker**	**Frag**	**Dia**	**Veg/R**	**Pot**	**Plu**
Fish species									
A. robustus		5.7	1.2						
A. zacapuensis						0.4			
G. atripinnis		1.0	0.4	3.0	4.4	13.9			
H. turneri			3.6			0.3			0.9
S. lermae				0.2	14.8	1.1	0.6		
X. variata			0.6	0.1	0.1	0.1	0.1		0.2
Z. quitzeoensis						0.4			
C. humboldtianum		0.9	0.9	2.6			0.2		
P. infans						1.8			
C. idella								48.2	13.2
C. carpio		8.9	1.5						
N. grandis		6.8			0.6	0.1			
A. tincella		2.3	18.0						

Table 3.- Levin´s index (Bi), trophic level and omnivory index for all the fish species caught in Lake Zacapu.

Fish species	**Levin´s index (Bi)**	**Trophic level**	**Omnivory index**
A. robustus	0.31	3.5 ± 0.52	0.20
A. zacapuensis	0.12	3.3 ± 0.45	0.10
G. atripinnis	0.47	2.8 ± 0.37	0.29
H. turneri	0.17	3.1 ± 0.40	0.12
S. lermae	0.31	2.8 ± 0.35	0.22
X. variata	0.21	2.8 ± 0.37	0.10
Z. quitzeoensis	0.31	3.0 ± 0.39	0.12
C. humboldtianum	0.21	3.3 ± 0.44	0.25
P. infans	0.08	3.1 ± 0.46	0.05
C. idella	0.05	2.6 ± 0.14	0.01
C. carpio	0.17	3.3 ± 0.0	0.09
N. grandis	0.28	2.9 ± 0.38	0.15
A. tincella	0.14	3.3 ± 0.48	0.12

Table 4. Values of Horn's niche overlap index for all fish species in Lake Zacapu. Ar = *Alloophorus robustus*, Az = *Allotoca zacapuensis*, Ht = *Hubbsina turneri*, Sl = *Skiffia lermae*, Xv = *Xenotoca variata*, Zq = *Zoogoneticus quitzeoensis*, Ch = *Chirostoma humboldtianum*, Pi = *Poeciliopsis infans*, Ci = *Ctenopharingodon idella*, Cc = *Cyprinus carpio*, Ng = *Notropis grandis*, Al = *Algansea tincella*, Ga = *Goodea atripinnis*. White color = low superposition, light gray color = medium superposition, dark gray color = high overlap between the species.

	Ar	***Az***	***Ht***	***Sl***	***Xv***	***Zq***	***Ch***	***Pi***	***Ci***	***Cc***	***Ng***	***Al***	***Ga***
Ar	1	0.33	0.35	0.16	0.40	0.38	0.30	0.19	0.00	0.79	0.29	0.56	0.15
Az		1	0.87	0.37	0.83	0.72	0.54	0.13	0.00	0.19	0.52	0.48	0.20
Ht			1	0.47	0.88	0.79	0.79	0.33	0.00	0.20	0.72	0.41	0.38
Sl				1	0.45	0.52	0.49	0.51	0.66	0.12	0.50	0.24	0.76
Xv					1	0.93	0.67	0.24	0.03	0.15	0.72	0.30	0.36
Zq						1	0.63	0.33	0.07	0.12	0.66	0.25	0.45
Ch							1	0.68	0.01	0.12	0.80	0.13	0.50
Pi								1	0.10	0.03	0.45	0.04	0.57
Ci									1	0.00	0.04	0.00	0.38
Cc										1	0.23	0.61	0.13
Ng											1	0.07	0.52
Al												1	0.13
Ga													1

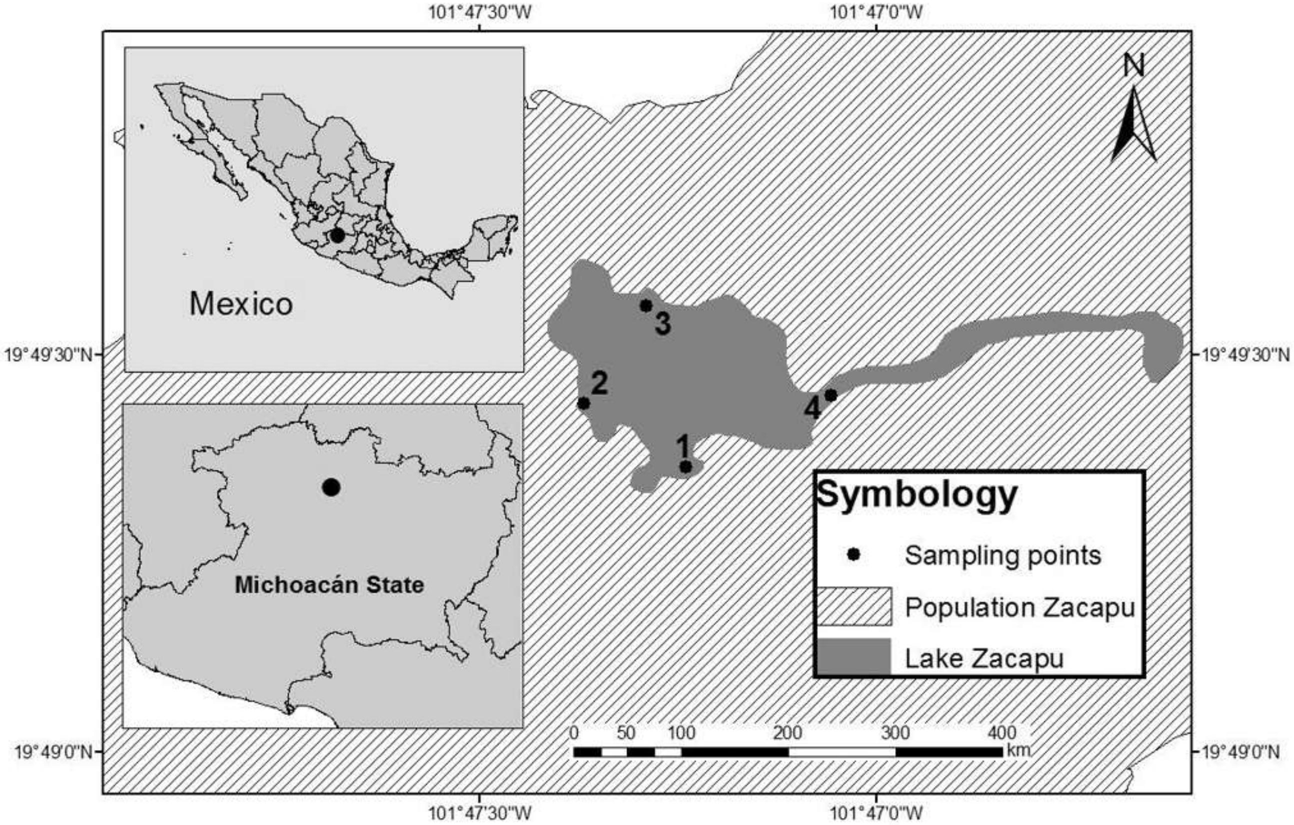

Figure 1.- Geographic location of the study area and sampling sites (S1-S4) located in Lake Zacapu, Michoacán, México

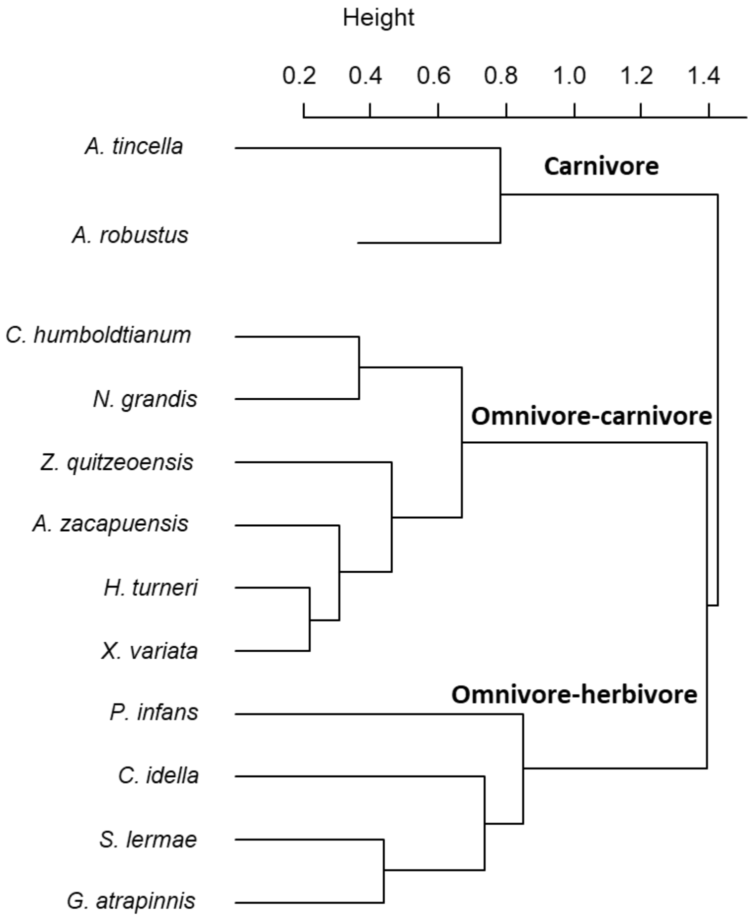

Figure 2.- Cluster analysis on the trophic classification of all fish species from Lake Zacapu

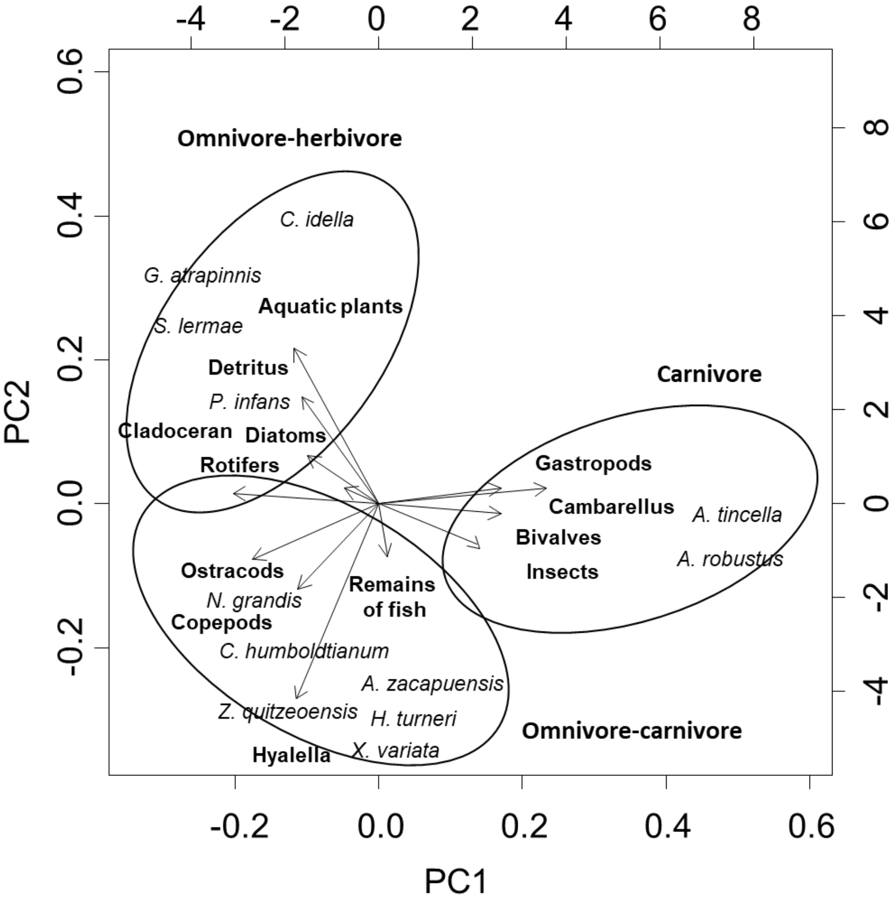

Figure 3.- Principal component analysis showing position of the trophic groups of fish species in Lake Zacapu

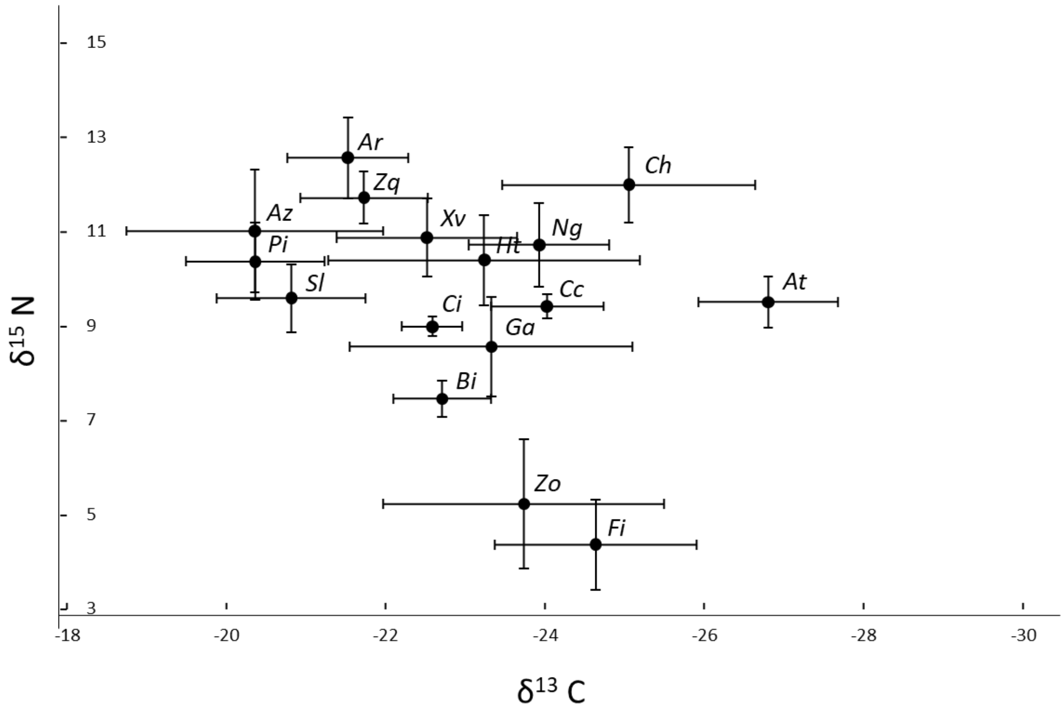

Figure 4.- Lake Zacapu food web plot based on analysis of δ^{13} C and δ^{15} N stable isotope values, mean δ^{13} C and δ^{15} N (±1SE). Acronyms: Ar = *Alloophorus robustus*, Az = *Allotoca zacapuensis*, Ht = *Hubbsina turneri,* Sl = *Skiffia lermae,* Xv = *Xenotoca variata,* Zq = *Zoogoneticus quitzeoensis,* Ch = *Chirostoma humboldtianum*, Pi = *Poeciliopsis infans*, Ci = *Ctenopharingodon idella*, Cc = *Cyprinus carpio*, Ng = *Notropis grandis*, At = *Algansea tincella*, Ga = *Goodea atripinnis,* Bi= benthic invertebrates, Zo = zooplankton, Fi =phytoplankton.

Table 5.- Metrics of the niche breadth and isotopic overlap between the species per site and season. Abbreviations: CR= range in δ ^{13}C, NNR = range in δ ^{15}N, TA = total area, SEA = Bayesian standard ellipse area, SEAc = Bayesian standard ellipse area corrected.

	NNR	**CR**	**TA**	**SEA**	**SEAc**
Wet season	11.3	10.7	82.4		
Fish			49.5	9.1	9.2
Phyto			1.7	2.3	3.5
BMI			21.5	4.8	4.9
Zoo			4.3	5.3	7.9
Dry Season	10.8	12.7	88.3		
Fish			49.5	9.1	9.2
Phyto			1.7	2.3	3.5
BMI			21.5	4.8	4.9
Zoo			4.3	5.3	7.9
Site 1	10.7	8.9	64.0		
Fish			38.2	9.7	9.8
BMI			15.1	5.7	6.1
Phyto-Zoo			3.0	3.6	5.4
Site 2	9.1	12.6	74.8		
Fish			39.2	9.6	9.7
BMI			10.7	4.8	5.2
Phyto-Zoo			8.6	10.5	15.7
Site 3	10.6	9.8	63.6		
Fish			34.2	7.5	7.5
BMI			10.6	5.2	5.8
Phyto-Zoo			5.1	6.3	9.5
Site 4	10.3	9	68.19		
Fish			32.7	9.0	9.2
BMI			22.8	9.6	10.5
Phyto-Zoo			1.8	2.2	3.3

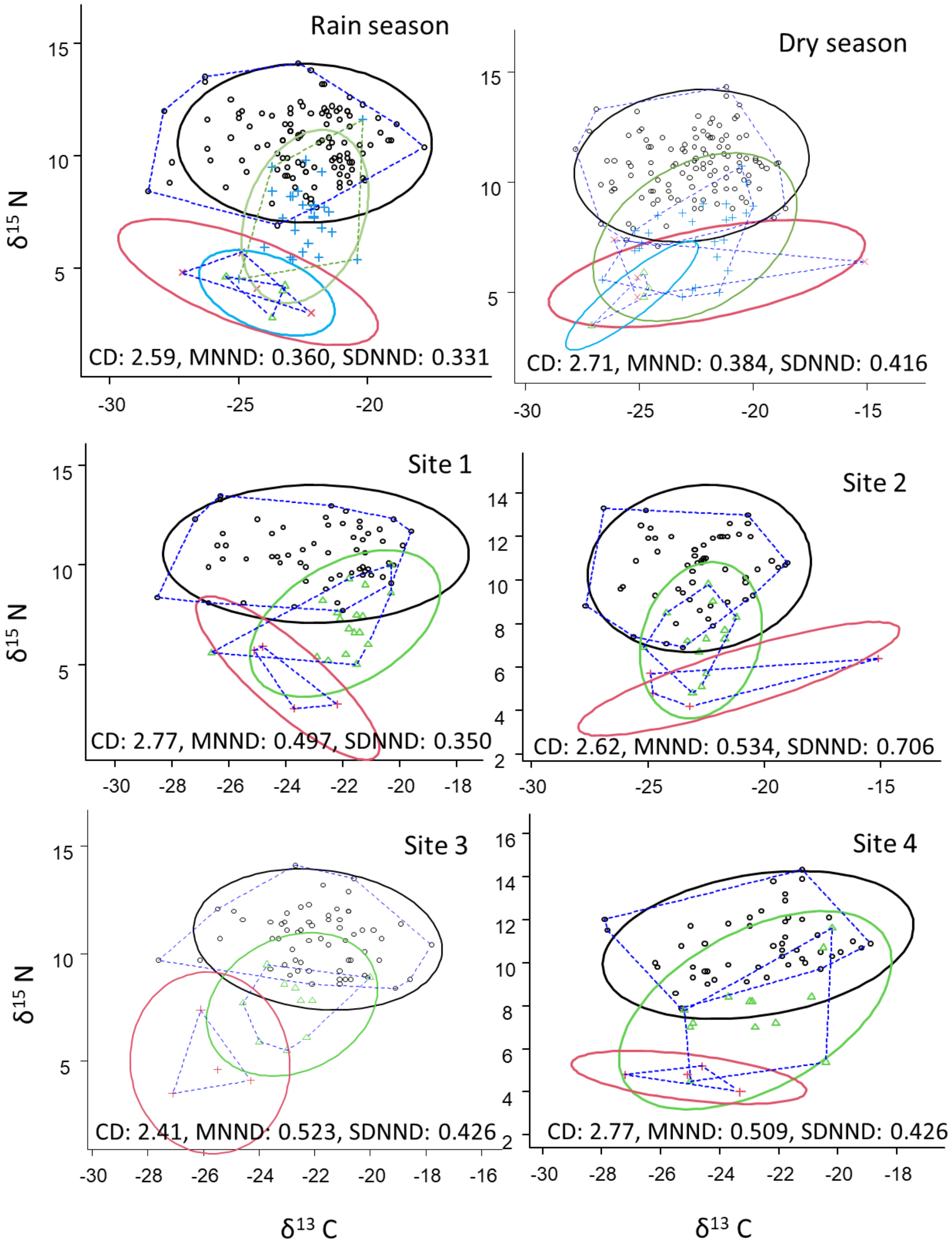

Figure 5.- Stable isotope ellipses encircling one standard deviation of the bivariate data for fish species (black line), macroinvertebrates (green line), phytoplankton (blue line) and zooplankton (red line) collected in Lake Zacapu. Layman metrics for each season and sites are shown in the plots; per sites phytoplankton and zooplankton communities are show together (red line). CD mean distance to centroid; MNND mean nearest neighbor distance; SDNND standard deviation of nearest neighbor distance.

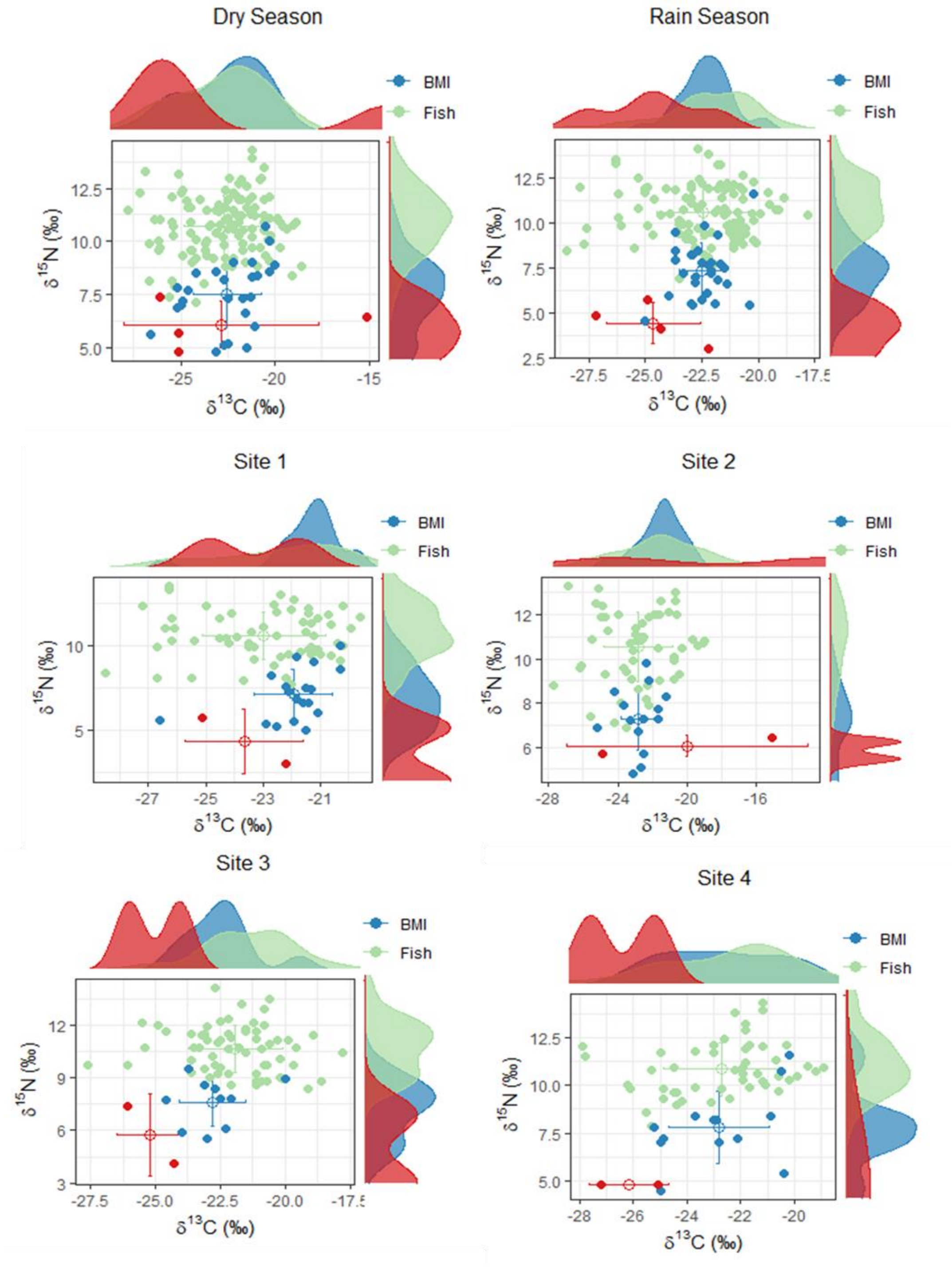

Figure 6.- Bayesian model for the calculation of consumer (fish species) trophic position using stable isotopes of C and N with BMI (macroinvertebrates) and Zooplankton (red color) as baseline from the different sites and seasons in Lake Zacapu.

DISCUSIÓN GENERAL

El presente estudio evaluó la comunidad íctica de un lago subtropical pequeño del centro de México, y aborda diversos temas relacionados con su ecología, su monitoreo y su manejo. El documento inicia con una discusión y análisis de uno de los métodos de captura para la obtención de organismos. Sigue con una descripción de cómo la comunidad de peces presenta los mismos valores en términos de riqueza y composición, pero con cambios en la estructura (densidad y dominancia) de 1995 a 2019-2020. Después, se analiza la biología reproductiva de los goodeidos en el sistema, encontrando que éstos muestran un adecuado desarrollo, con valores más altos de fertilidad que en poblaciones de otros sistemas acuáticos del centro de México. Finalmente se analiza la dieta y estructura trófica de los peces en el lago, incluyendo algunos componentes de la red alimentaria (macroinvertebrados, fitoplancton y zooplancton). Se encuentra que la comunidad de peces depende de una alimentación principalmente basada en macroinvertebrados acuáticos, que la mayoría de las especies son consumidores secundarios y generalistas, y que la estructura de su dieta no varía entre los sitios o a través del tiempo, debido a la gran abundancia de macroinvertebrados en el lago y la homogeneidad ambiental del agua.

En la evaluación de la comunidad íctica de 1995 por Moncayo-Estrada, solo se utilizó un arte de pesca (red de tipo chinchorro). Actualmente, el uso de varios métodos de colecta con selectividad variable podría producir mejores estimaciones, en términos de riqueza y abundancias para las comunidades de peces, dado que algunas especies se capturan más fácilmente con algunos artes que con otras (Radinger et al., 2019). En la construcción del primer capítulo se utilizaron artes de pesca pasivos, incorporando cuatro modelos distintos de trampas, y observando cual era la más eficaz para la obtención de organismos en el lago Zacapu. Los resultados del capítulo I demuestran que la trampa metálica tipo nasa fue la más eficiente en todas las variables exploradas (profundidad de la trampa, con carnada o sin) para obtener la mayor riqueza, y abundancia de las especies del lago Zacapu.

Las comunidades de peces en sistemas dulceacuícolas, principalmente en cuerpos de agua pequeños, albergan niveles altos de diversidad y presentan diferentes funciones ecosistémicas importantes (Biggs et al., 2017). Esto concuerda con el presente estudio, donde se encontró que el lago Zacapu alberga 13 especies de peces, una alta riqueza dada su pequeña área (20 ha.), y en comparación con otros lagos mucho más grandes también del centro de México (Lago de Pátzcuaro, Ramírez-Herrejón et al., 2014; Lago de Cuitzeo, Soto-Galera et al., 1999). De estas trece especies del lago Zacapu, once son nativas y dos no nativas, cinco son de interés para la conservación de acuerdo con la Unión Internacional para la Conservación de la Naturaleza (Lista Roja de la UICN 2020) y la Norma Oficial Mexicana (NORMA-059-SEMARNAT-2019). Esto además de una salamandra endémica (Valencia-Vargas y Escalera-Vázquez, 2021). La familia Goodeidae es la más representativa con siete especies. Respecto a los datos históricos que se tienen (que datan de 1995), se detectó que el mismo número de riqueza de especies permanece en el lago (capítulo II), lo que indica que la composición de la comunidad de peces tiene una estabilidad y persistencia a lo largo del tiempo, con la dominancia de las especies nativas. En la actualidad, la mayoría de los cuerpos de agua en México se encuentran dominados por especies no nativas (Zambrano et al., 2001; Zambrano et al., 2010; Ramírez-Herrejón et al., 2014; Mar-Silva et al., 2021). La persistencia de las especies nativas en este lago se aborda desde tres enfoques, que a su vez están interconectados.

1) El lago de Zacapu se considera un sistema pequeño, pero con presencia de muchos manantiales, lo que permite un alto recambio de agua y homogeneización ambiental continua (Ayala-Ramírez et al., 2007). Por ello, no acumula solidos disueltos en el agua y se evita la acumulación de desechos. Esto coincide con lo reportado donde se menciona que el lago Zacapu es una de las pocas zonas del Centro de México que puede ser considerada como con baja

alteración antrópica, poco contaminada (Domínguez-Domínguez et al., 2008), y que además se ha mantenido buena la integridad biótica del sistema (Ramírez-Herrejón et al., 2012). En consecuencia, solo para algunas variables ambientales se mostraron diferencias significativas estacionales, pero no se encontró variación espacial significativa, debido a que los parámetros del agua fueron homogéneos, incluso considerando las dos décadas (1995 y 2019-2020) para los que se cuenta con datos. Esto corrobora lo ya mencionado por Valencia-Vargas y Escalera-Vázquez, (2021) en torno a la homogeneidad ambiental del Lago de Zacapu.

Además de lo anterior, es importante mencionar que el nitrato y la conductividad cambiaron significativamente entre 1995 a 2019-2020, y que el pH y el amoniaco tuvieron variación estacional. Esto está posiblemente asociado a actividades humanas, que cerca del lago juegan un papel fundamental en el proceso de eutrofización (Díaz-Argüero, 1997) y que podrían aumentar la entrada de nutrientes al lago y son principalmente los desagües domésticos, industriales, agrícolas, y las áreas de recreación. Al igual que otros sistemas dulceacuícolas, la calidad del agua es importante y, en particular, la eutrofización sigue siendo un proceso abiótico que ejerce gran presión para los organismos que viven en las aguas continentales (Brönmark y Hansson, 2002).

2) El lago tiene alta disponibilidad de recursos alimentarios. Esto se concluye con, base en las colectas de macroinvertebrados acuáticos realizadas en el sistema (resultados mostrados en el capítulo IV) y que, en conjunto con las variables hídricas, influyen directamente en la estructura trófica de las especies de peces, promoviendo su persistencia en el tiempo (Wootton y Smith, 2014). La mayoría de los peces del lago de Zacapu se alimentan en cierto grado de macroinvertebrados acuáticos (capítulo IV), sin embargo, es muy probable que la gran abundancia de estos organismos evite la competencia entre especies de peces. En otros estudios se ha documentado que algunas especies muestran algún grado de traslape de dieta, sin embargo, la disponibilidad de alimento es suficiente para evitar la competencia entre especies (Mérona and Rankin-de-Mérona, 2004).

En este sentido, los macroinvertebrados juegan un papel clave en la estructura y función de los ecosistemas de agua dulce (Tomanova et al., 2006) y son fundamentales para la dinámica de los nutrientes, la descomposición, el flujo de energía (Vadeboncoeur et al. 2002) en las cadenas tróficas y podrían ser indicadores de perturbaciones antropogénicas y del éxito de la restauración y la calidad del agua por sus características ecológicas (largos ciclos de vida y su limitado movimiento; Fleituch et al., 2002). En el último aspecto, los resultados obtenidos para los macroinvertebrados del lago de Zacapu señalan la presencia de una gran cantidad de grupos taxonómicos intolerantes a la eutroficación (capítulo IV), lo que representa una buena condición del hábitat. Por lo tanto, se ha documentado que el aumento de los niveles de eutrofización provoca una disminución de la diversidad de macroinvertebrados (Donohue et al., 2009).

Aunado a lo anterior y como se documentó en el artículo de revisión de este trabajo (introducción general), la biomasa y composición de otros grupos de la red alimentaria (ej., fitoplancton y zooplancton) son importantes para la persistencia de las especies en el tiempo (Vesterinen et al., 2016; Beaver et al., 2019). Estos grupos también son consumidos por los peces del lago de Zacapu, pero en menor cantidad (capítulo IV), además de ser importantes de la función del ecosistema acuático (Kovalenko et al., 2019).

Los peces son importantes elementos estructurales de las redes alimentarias en los lagos, ocupan una gran variedad de nichos tróficos, hacen circular materia y energía desde los recursos basales hasta los niveles más altos de la red (Delong et al., 2019). Los resultados obtenidos muestran que las especies de peces pertenecen a los consumidores primarios y secundarios (capítulo IV), indicando un flujo de energía entre los peces, los macroinvertebrados (capítulo IV), el zooplancton y el fitoplancton (anexo I). Además, la abundancia y riqueza de macroinvertebrados (capítulo IV), zooplancton y fitoplancton (anexo I), sugiere disponibilidad de recursos para todas las especies de peces en el lago.

3) El éxito reproductivo de las especies, y los rasgos de historia de vida de los organismos permite que maximicen su capacidad de sobrevivencia en el lago de Zacapu, teniendo en cuenta las tácticas y estrategias reproductivas de las especies. En el lago Zacapu se encuentran especies con tres estrategias reproductivas, siete especies vivíparas (familia Goodeidae), una especie ovovivípara (*Poeciliopsis infans*; Ponce de León-González, 2022) y cuatro especies ovíparas (nativas: *Chirostoma humboldtianum, Notropis grandis*, y *Algansea tincella*; no nativas: *Ctenopharyngodon idella* y *Cyprinus carpio*).

Se ha documentado que uno de los factores importantes para la sobrevivencia de las crías es la disponibilidad de alimento, el bajo riesgo de depredación y el evitar las condiciones físicas adversas (Wootton y Smith, 2014). Al igual que para los organismos adultos, la disponibilidad de alimento en el momento de la reproducción es importante para la procreación de crías, y el lago de Zacapu presenta buena disponibilidad de alimento (capítulo IV). Adicionalmente, para el caso de las especies vivíparas (también matrotróficas), se presentan varias tácticas reproductivas como tasas de fertilidad altas, proporción de sexos favorecido hacia las hembras, periodos reproductivos establecidos, condiciones robustas de los juveniles y adultos en todo el lago (capítulo III), lo que indica distribución de los recursos destinado a la reproducción de las especies y condiciones físicas favorables.

Respecto a la especie ovovivípara, Ponce de León-González (2022) documenta actividad reproductiva durante un ciclo anual para ambos sexos, proporción sesgada hacia las hembras y condición robusta de los organismos, con estadios gonadales desde juveniles hasta adultos, por lo que se puede inferir que esta especie presenta una población reproductiva estable en el Lago de Zacapu. La actividad reproductiva continua a lo largo de un ciclo anual ha sido documentada en otros estudios de pecílidos (Gómez-Márquez et al., 1999; 2016; Ramírez-García et al., 2018). Las otras tácticas (ej. altas tazas de fertilidad, madurez temprana en machos) que presenta *P. infans* son similares a las de las especies vivíparas del lago, y todas en conjunto son consideradas como tácticas reproductivas favorables y se complementan con su estrategia reproductiva ovovivípara lecitotrófica (Nelson, 2016) con superfetación moderada (Wourms, 1981). Dichas características se ven favorecidas en condiciones ambientales estables (Snelson, 1984), como son las que prevalecen en el lago Zacapu.

En cuanto a las especies ovíparas del lago, fue posible evaluar algunos aspectos reproductivos de *N. grandis* y *C. humboldtinum* (anexo II). Los resultados muestran que ambas especies tienen proporciones sesgadas hacia las hembras. La especie *C. humboldtianum* presenta una fertilidad promedio de 1184 huevos, y *N. grandis* presenta una fertilidad promedio de 954 huevos por hembra. Respecto al periodo reproductivo, la especie *N. grandis* muestra valores altos del índice gonadosomático en las cuatro estaciones del año (correspondiente a los meses de mayo, julio, octubre y enero). Por su parte, *C. humboldtinum* presenta dos picos reproductivos, uno en enero, y un máximo en mayo y muestra disminución de la actividad reproductiva en julio y octubre. Ambas especies muestran valores constantes de robustez, de acuerdo con el factor de condición evaluado, lo que indica una buena salud de los organismos.

El periodo reproductivo de *N. grandis* es similar a lo reportado para otras especies del género en otros cuerpos de agua (Roberts et al., 2006), indicando múltiples óvulos durante un periodo prolongado, mayormente marcado de primavera a verano. Sin embargo, fue notoria la reducción de abundancia de esta especie a lo largo de las décadas en el lago Zacapu (capítulo II), por lo que se considera que *N. grandis* es resistente a perturbaciones menores a corto plazo, ya que presenta una estrategia oportunista (Winemiller y Rose, 1992), de corta vida sin cuidado parental, y presenta un esfuerzo prolongado para el periodo reproductivo con múltiples desoves a lo largo del año. Sin embargo, el éxito reproductivo de esta especie es vulnerable a disturbios crónicos, como es la eutroficación que podría persistir en el lago (Díaz-Argüero, 1997), o la ausencia de vegetación acuática, la cual es importante como hábitat de alimentación y crianza (Bouvier et al., 2010).

En cuanto la especie *C. humboldtianum*, se ha reportado que presenta puestas asincrónicas durante todo el año (Paulo et al., 2000; Blancas-Arroyo et al., 2003), con picos marcados, como se encontró en este estudio (anexo II). El número de huevos reportado en cautiverio oscila entre 120 y 1200 (Figueroa-Lucero et al., 2003), lo que concuerda con lo encontrado en este estudio. Dichos valores, en conjunto con las altas abundancias y dominancia de la especie en el lago (capítulo II), indican el éxito reproductivo de la especie. Sin embargo, se ha reportado para otros cuerpos de agua que especies de este género son sensibles a diferentes factores ambientales, como incrementos en la temperatura, contaminación, fluctuaciones en el nivel del agua, disminución de alimento y reducción o alteración del hábitat (Moncayo-Estrada et al., 2011; Mercado-Silva et al., 2015; Vital-Rodríguez et al., 2017), por lo que es importante tener en consideración que no aumenten los contaminantes al lago de Zacapu.

De manera general, las características del sistema permiten mantener las historias de vida de las especies presentes, se desarrollan tres estrategias reproductivas para las especies del lago: oportunista, de equilibrio y periódica. La estrategia oportunista, de maduración temprana, con tamaño del adulto pequeño, desove por lotes durante una temporada de reproducción extendida y rápido crecimiento temprano se presenta en especies como *N. grandis* y *C. humboldtianum*. Las especies con estrategias de equilibrio, de tamaño corporal pequeño, con fertilidad baja, pero con cuidado parental, las registran las especies de goodeidos. Finalmente, la estrategia periódica, se da en aquellas que presentan maduración tardía, un gran tamaño en la maduración sexual y altas fertilidad. Aunque Esta última se da en las especies no nativas, no fue posible evaluar aspectos reproductivos debido a los bajos registros de capturas de estas especies (capítulo II) al igual que para la especie *A. tincella*.

Otro aspecto importante que se aborda en el estudio es el papel de las especies no nativas en el lago Zacapu. Para este cuerpo de agua se han reportado dos especies no nativas, *C. idella* y *C. carpio*. Ambas especies presentaron abundancias relativamente bajas (capítulo II), y solo fue posible su captura mediante las redes agalleras de los pescadores (capítulo I).

La carpa común ha sido descrita como una de las peores plagas de vertebrados a nivel mundial (Gallardo et al., 2016). Se ha documentado que el comportamiento de *C. carpio* durante su actividad de alimentación puede provocar cambios en los ecosistemas (Zambrano et al., 2001; 2006), ya que resuspende el sedimento y aumenta la turbidez del agua. Este comportamiento se considera dañino en términos de alteración física y productividad del hábitat para otras especies (Özbay, 2008). Sin embargo, en el lago Zacapu, el corto tiempo de residencia del agua por su alto recambio en el lago mitiga el aumento en la turbidez del agua por efecto de estos organismos, esto concuerda con nuestros resultados de bajas concentraciones de sólidos suspendidos totales (capítulo I, II, III, y IV).

Aunado a lo anterior, la carpa en este cuerpo de agua no es considerada como un competidor importante en los aspectos tróficos de los peces, debido a su posición trófica relativamente baja (capítulo IV), y las bajas abundancias de la especie en el lago (capítulo II). La población se encuentra regulada por las capturas de los pescadores, ya que es considerada como una de las especies con mayor importancia comercial para los habitantes de Zacapu (Joel Pimentel, presidente de la unión de pescadores del lago, comunicación personal; Centro Regional de Investigación Acuícola Pesquera, CRIAP-Pátzcuaro, 2019). Por lo que es importante que se tenga un control de la población de estas especies no nativas para que no aumenten sus abundancias.

CONCLUSIONES GENERALES

De 1995 a 2019-2020, el lago Zacapu ha tenido un cambio en la dominancia de especies que presentan preferencias de ciertos hábitats, y una reducción en la abundancia de especies consideradas sensibles. Sin embargo, las especies nativas son las dominantes en el sistema y las especies no nativas presentaron abundancias relativamente bajas. Aún se encuentran presentes todas las especies reportadas en 1995, por lo que las especies han persistido en el tiempo.

Las especies nativas en general presentan un alto éxito y tácticas reproductivas favorables, basadas principalmente en sexos sesgados hacia las hembras, madurez temprana y altas tazas de fertilidad, que en conjunto con sus estrategias reproductivas (vivíparas, ovíparas y ovovivíparas) ayudan a promover su reproducción, junto con las condiciones favorables que el lago Zacapu provee para las especies.

La mayoría de las especies fueron consumidoras secundarias y generalistas tróficas, la estructura de la red alimentaria no difirió significativamente entre los cuatro sitios de muestreo, respaldado por la gran cantidad de macroinvertebrados acuáticos presentes en el lago.

Siguiendo la hipótesis general planteada, el lago Zacapu es un sistema que presenta alta riqueza íctica, con un gran número de especies nativas y endémicas, las cuales han persistido a través de las décadas, además de una alta diversidad de otros grupos taxonómicos importantes en los flujos de energía. Esto se debe principalmente a las características del lago, indicando que la comunidad acuática se estructura por factores abióticos como la estabilidad ambiental y factores bióticos como los atributos de las especies (ej. estrategias, tácticas reproductivas, dieta y estructura trófica), lo cual les permiten subsistir a lo largo del tiempo en este pequeño lago del centro de México.

RECOMENDACIONES

A pesar de que las especies han persistido a lo largo del tiempo, es notorio el cambio de especies dominantes a de 1995 a 2019-2020, y la disminución de las abundancias de las especies sensibles, por lo que es de vital importancia implementar esfuerzos de conservación hacia el lago, a continuación, se mencionan algunas recomendaciones importantes.

La estructura del hábitat juega un papel esencial en el mantenimiento de las comunidades de peces en los sistemas acuáticos, por lo cual se recomienda proteger las plantas acuáticas, ya que son necesarias para las especies nativas, en términos de hábitat reproductivo, refugios y disponibilidad de alimento.

El análisis funcional del lago, evaluado por medio de la red alimentaria muestra un aprovechamiento integral de los recursos disponibles por las especies existentes, por lo cual se recomienda no introducir otras especies no nativas al sitio, ya que estas podrían competir con las especies nativas y desplazarlas, además de aportar enfermedades no existentes. Las especies no nativas (*C. carpio* y *C. idella*) ya establecidas en el lago deben seguir siendo controladas continuamente por la pesca comercial, para evitar que aumenten sus poblaciones.

El lago Zacapu presenta una gran cantidad de manantiales, ubicados principalmente en las zonas de recreación, los cuales son necesarios para la renovación hidráulica, por lo cual se recomienda evitar todo tipo de contaminantes, como descargas de agua de tipo doméstico, industrial y fertilizantes por parte de la agricultura, debido principalmente a que estos contaminantes podrían alterar las condiciones físicas y químicas del lago y por ende a las especies.

En las zonas de humedales no debe permitirse la construcción de casas habitación, acumulación de basura o desechos sólidos, para así evitar la disminución del espejo de agua del lago. Además, estas áreas son importantes para la alimentación, anidación, descanso y reproducción de las aves tanto residentes como migratorias del lago.

Es necesario elaborar una estrategia de educación ambiental encabezada por actores locales, con participación ciudadana en torno a la conservación de las especies nativas y endémicas del lago.

El lago Zacapu se encuentra en una zona de piedra volcánica, por lo que se recomienda evitar el cambio de uso de suelo en las partes altas de la cuenca, ya que puede afectar la carga de los mantos acuíferos y esto repercute la estabilidad hídrica del lago.

Ampliar el polígono del área natural protegida considerando las zonas de recarga de los mantos acuíferos y todas las zonas de humedales, así como actualizar el plan de manejo existente del lago, que fue publicado en 2005, para asegurar la conservación y protección de todo el ecosistema y sus especies.

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