UNIVERSIDAD MICHOACANA DE SAN NICOLÁS DE HIDALGO

Posgrado en Ciencias Biológicas

Biología reproductiva de especies exóticas y nativas de los manantiales y río Teuchitlán.

Tesis

Que presenta:

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ÍNDICE

I. RESUMEN GENERAL

La cuenca del río Ameca en el centro de México es de importancia biológica, ya que está identificado como centro de gran riqueza de ictiofauna. Sin embargo el río Teuchitlán, que pertenece a esta cuenca, ha sufrido impacto por actividades antrópicas, que han modificado el ecosistema acuático, produciendo una disminución de los peces nativos y un incremento de especies exóticas. Por lo que el objetivo de este estudio fue determinar la ecología reproductiva de dos especies exóticas (*Pseudoxiphophorus bimaculatus* y *Poecilia sphenops*) y tres especies nativas (*Goodea atripinnis*, *Ameca splendens* y *Zoogoneticus purhepechus*), presentes actualmente en el río Teuchitlán. La ecología reproductiva fue evaluada en términos de fertilidad, talla de primera madures, radio sexual, estadios de madures gonádica, índice gonadosomático, factor de condición, estructura de tallas y hábitat reproductivo. Estas variables reproductivas se relacionaron con variables ambientales utilizando un análisis de escalamiento no métrico multidimensional (NMDS). Un total de 2029 individuos de especies exóticas y 894 individuos de especies nativas fueron capturados con una red tipo chinchorro y electropesca de mochila. Los resultados mostraron que las especies exóticas presentan mayor fertilidad que las nativas. Las especies exóticas presentan múltiples desoves durante el año, contrario a las nativas que presentan dos picos reproductivos (marzo y julio). Respecto al radio sexual, para las exóticas fue mayor cantidad de hembras y una proporción 1:1 en las nativas. Las especies exóticas maduran a tallas más tempranas comparadas con las especies nativas. Los análisis multivariados mostraron que las especies exóticas se encuentran relacionadas con sitios con mayor cantidad de solidos disueltos, mayor concentración de clorofila a y mayor turbidez en el agua. Mientras que las especies nativas están relacionadas a los sitios con aguas más claras, mayor profundidad, mayor concentración de oxígeno disuelto y pH neutro.

Palabras clave: Teuchitlán, Ecología reproductiva, Peces Vivíparos, Peces Ovovivíparos.

II. ABSTRACT

The Ameca River basin in central of México has great biological importance. It is identified as a native center of ichthyofauna. However, the Teuchitlán River has suffered different anthropogenic activities that have modified the aquatic ecosystem, producing a decrease in native fish and an increase in exotic species. Therefore, the aim of this study was determine the reproductive ecology of two exotic species (*Pseudoxiphophorus bimaculatus* and *Poecilia sphenops*) and three native species (*Goodea atripinnis, Ameca splendens* and *Zoogoneticus purhepechus*) present in the Teuchitlán River, Jalisco, México. Reproductive ecology was evaluated with the variables of fertility, first maturity, sex ratio, gonadal stages, gonadosomatic index, condition factor, structure size and reproductive habitat. The ordering of the environmental variables was related to the reproductive variables of the species by means of a non-metric multidimensional scaling analysis (NMDS). A total of 2029 individual of exotic species and 849 individuals of native species were captured with a net type chinchorro and backpack electroshock. The results showed that the exotic species have higher fertility compared to the native species. Exotic species have multiple spawning during the year, while native species have two reproductive peaks (March and July). Females predominant in exotic species. Sex ratio was 1:1 in native species. Exotic species mature in earlier sizes compared to the native species. The multivariate analysis showed that the organism of the exotic species are related to sites where there is more dissolved solids in water, higher chlorophyll a and greater turbidity in water. Native species are related to sites with clearer water, greater depth, higher dissolved oxygen in water and neutral pH.

Keywords: Teuchitlán, Reproductive Ecology, Viviparous Fishes, Ovoviviparous Fishes.

III. INTRODUCCIÓN GENERAL

El centro de México alberga fauna de peces de agua dulce, la cual incluye varios grupos endémicos. Una de las familias más diversas es la familia Goodeidae, que habitan en el altiplano mexicano y su periferia. Esta familia comprende de 40 a 45 especies, la mayoría son vivíparos. La mayoría de las especies de goodeidos están en peligro crítico y algunas de ellas se consideran extintas en su hábitat natural (Domínguez-Domínguez *et al.,* 2005; 2008).

Las causas de la disminución de los peces vivíparos en México incluyen la sobreexplotación del agua, la introducción de especies invasoras, la destrucción del hábitat y la alta contaminación causada por diversas fuentes humanas (Contreras-Balderas, 2005). Otro más es el establecimiento de especies exóticas, considerada como una de las principales fuentes de pérdida de biodiversidad acuática y está entre los impactos humanos más importantes, menos controlados y menos reversibles de los ecosistemas del mundo (Lockwood *et al.,* 2007). Un ejemplo de esto son las especies de pecílidos, que han sido introducidos en diferentes sistemas de agua dulce en México, de manera accidental o por un fin determinado por el hombre (Lockwood *et al.,* 2007) la invasión se ha promovido debido a su estrategia reproductiva ovovivípara (Nelson, 2016).

El río Teuchitlán, ubicado en el centro de México, se encuentra en la parte alta de la cuenca del Ameca, en la cual se han llevado a cabo actividades antrópicas que han modificado el ecosistema acuático, incluyendo la construcción de la presa de La Vega, la extracción de agua, la contaminación municipal e industrial en la cuenca, y la introducción de especies exóticas. Esto ha derivado en una disminución significativa en los peces nativos del río Teuchitlán. La zona cuenta con un registro histórico de 20 especies nativas y seis especies exóticas, la mayoría de las cuales fueron descritas en la última década, actualmente solo cuenta con cuatro especies nativas y seis especies exóticas (López-López y Paulo-Maya, 2001; Dzul-Caamal, *et al.,* 2012). El río alberga a especies de peces microendémicos, *Ameca splendens*, *Skiffia francesae*, *Zoogoneticus tequila* (Goodeidae) y *Notropis amecae* (Cyprinidae), de los cuales *S. francesae*, *Z. tequila* y *N. amecae* no se encuentran actualmente en el río (De la Vega-Salazar, *et al.,* 2003, Domínguez-Domínguez, *et al.,* 2008, SEMARNAT, 2010, UICN, 2017). Mientras que la introducción de pecílidos en el río Teuchitlán sucedió a principios de 1977 (Webb y Miller 1998), actualmente se encuentran *Xiphophorus xellerii*, *Pseudoxiphophorus bimaculatus* y *Poecilia sphenops* (Mar-Silva, *et al*., en preparación).

Por otro lado, la reproducción es un aspecto importante ya que forma parte del ciclo de vida de las especies. Este proceso biológico en combinación con otros factores físicos y químicos, promueve la continuidad y la abundancia de las especies. El tamaño de las poblaciones depende del tamaño de la camada, la sobrevivencia (natalidad y mortalidad), las proporciones sexuales, tiempo en el que la especie alcanza la madures sexual, el tiempo de gestación y las enfermedades (Nikolsky, 1963).

Por lo tanto el éxito reproductivo de cada especie dependerá de la temporada y del sitio de reproducción y de cómo los recursos energéticos son canalizados. El cómo, cuándo y dónde se reproduce con relación a los efectos de los factores medioambientales es el objetivo básico del estudio de la ecología de la reproducción (Saborido, 2008). Por lo que, los factores ambientales pueden influir en la ontogenia de las historias de vida de las especies; Por ejemplo, la temperatura afecta la tasa de crecimiento corporal de los poiquilotermos. En segundo lugar, la selección natural puede haber dado forma a las historias de vida, para ello, dos conjuntos de hipótesis pretenden dar cuenta de la diversidad de las historias de vida, estrategias r y K (MacArthur y Wilson, 1967; Pianka, 1982). La reproducción es el vínculo entre las generaciones, el cual, a través del proceso de selección natural, puede ser visto como el objetivo último de la vida. Los organismos se seleccionan para maximizar el éxito reproductivo y, por tanto, la aptitud (es decir, el número de descendientes supervivientes), dentro de las limitaciones impuestas por la filogenia, el desarrollo, la genética y los entornos estocásticos. El éxito es una función de la estrategia reproductiva que un organismo individual adopta, incluyendo dónde y cuándo reproducirse y cómo asignar recursos dentro y entre los picos reproductivos. El entendimiento de tales patrones reproductivos es importante para la comprensión de la selección (Endler, 1987), la adaptación y la dinámica de la población (Judson, 1994).

Por lo tanto el objetivo de este estudio fue evaluar la ecología reproductiva de las especies nativas vivíparas: *Goodea atripinnis, Ameca splendens* y *Zoogoneticus purhepechus* y las especies invasoras ovovivíparas: *Poecilia sphenops* y *Pseudoxiphophorus bimaculatus,* describiendo la variación anual de la reproducción y sus relaciones con la condición ambiental del río Teuchitlán. El propósito fue comprender las tácticas reproductivas de las especies nativas para resistir los cambios en los ecosistemas, así como la alta capacidad de dispersión y establecimiento de las especies exóticas, para apoyar futuras acciones específicas de conservación para mantener la diversidad biológica en el río Teuchitlán. Esto servirá como modelo de estudio para este tipo de sistemas acuáticos antropizados.

IV. HIPOTESIS

Las especies exóticas (*Pseudoxiphophorus bimaculatus* y *Poecilia sphenops*) presentaran varios picos reproductivos a lo largo del año, sin importar las variables ambientales presente de cada sitio, mientras que las especies nativas (*Ameca splendens*, *Goodea atripinnis, Zoogoneticus purhepechus*) se verán afectadas en disminución de sus picos reproductivos, causados por ambientes antrópicos a lo largo del río.

V. OBJETIVOS

Objetivo general

Establecer la biología reproductiva de las especies nativas y exóticas en las diferentes condiciones temporales y de hábitats en los manantiales y río Teuchitlán.

Objetivos particulares

Describir los aspectos reproductivos de las especies exóticas en los diferentes sitios de colecta, evaluando criterios de fertilidad, estructura de tallas, talla de primera madures, estadios gonadales, proporción sexual y época reproductiva.

Describir los aspectos reproductivos de las especies nativas en los diferentes sitios de colecta, evaluando criterios de fertilidad, estructura de tallas, talla de primera madures, estadios gonadales, proporción sexual y época reproductiva.

VI. RESULTADOS

Capítulo 1

Reproductive biology of the invasive species *Pseudoxiphophorus bimaculatus* and *Poecilia sphenops* in the Teuchitlán River, México.

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Reproductive biology of the invasive species *Pseudoxiphophorus bimaculatus* and *Poecilia sphenops* in the Teuchitlán River, México

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Summary

Reproductive biology of invasive species is not often studied relative to the invasion process, although it may provide an accurate indicator of the invasion stage. We evaluated the reproductive biology of the exotic fish species *Pseudoxiphophorus bimaculatus* and *Poecilia sphenops* in the Teuchitlán River, Jalisco, Mexico by fertility, size at first maturity, sex ratio, gonad maturity stage, gonadosomatic index, condition factor, size-structure, and habitat. The reproductive variables were related to environmental characteristics using the non-metric analysis of multidimensional scaling. A total of 1374 specimens of *P. bimaculatus* and 571 of *P. sphenops* were captured by seine netting and electrofishing. Maximum fertility of *P. bimaculatus* was 15.99 ± 2.27 embryonated eggs and embryos and, for *P. sphenops*, 31.26 ± 4.17. Females predominated among *P. bimaculatus*, while in *P. sphenops* the sex ratio was ~1:1. We found mature female and male of *P. bimaculatus* in degraded sites and juveniles in the springs. *Poecilia sphenops* reproduced along the river. The establishment of both invasive species in the Teuchitlán River is evidence that they share the reproductive habitat with native fish species, and tend to spread and colonize new areas.

1 | INTRODUCTION

The reproductive biology of invasive fishes has not been extensively investigated, and it is necessary to expand such knowledge to provide a theoretical framework for reproductive constraints of females. More specifically, knowledge of reproductive biology requires an interpretation of biotic and abiotic factors based on the premise that the evolution of life histories involves selection for physiological mechanisms aimed at optimizing survival and reproductive effort.

The establishment of introduced exotic species is a major source of aquatic biodiversity loss and is the least controlled and least reversible of human impacts (Lockwood, Hoopes, & Marchetii, 2007). Physical and chemical anthropic effects on freshwater environments can foster success of exotic species Dudgeon et al., 2006); but they must establish self-sustaining populations, increase their abundance, and expand their distribution range (Williamson, 1996).

Poeciliid fishes have been introduced into freshwater systems in Mexico, mainly by aquarists (Mejía-Mojica, 1992) or mosquito control and its invasion has been facilitated by their ovoviviparous strategy (Nelson, 2016).

The molly *Poecilia sphenops* (Valenciennes 1846) is a popular aquarium species marketed in many countries worldwide. It is distributed naturally in the Atlantic slope in the southeast of Veracruz State and in the Pacific slope in Oaxaca State and Guatemala (Miller, Minckley, & Norris, 2005). Contreras-MacBeath, Gaspar-Dillanes, Huidobro-Campos, and Mejía-Mojica (2014) state that *P. sphenops* is native to Morelos State. It has been introduced into several ecosystems in Mexico, including the Teuchitlán River (TR) in Jalisco State, where its diet comprises mainly organic detritus (Trujillo-Jiménez & Toledo, 2007). Spawning occurs during the rainy season in artificial systems in Morelos State Gómez-Márquez, Peña-Mendoza, & Guzmán-Santiago, 2016).

Pseudoxiphophorus bimaculatus (Heckel, 1848), synonym of *Heterandria bimaculata* (Agorreta et al., 2013), is native to the Atlantic slope from the Misantla River in Mexico to the Prinzapolka River in Nicaragua (Miller et al., 2005). It has been introduced into several drainages in Mexico, including the upper basin of the Balsas River (Espinoza, Gaspar, & Fuentes, 1993), and the Teuchitlán River. Its diet comprises mainly Culicidae (Diptera) (Trujillo-Jiménez & Toledo, 2007) and multiple spawnings occur throughout the year (Gómez-Márquez, Guzmán-Santiago, & Olvera-Soto, 1999).

The TR is located in the upper Ameca River basin, in Jalisco State, where 21 fish species are reported, 15 native and 6 exotic (Dzul-Caamal, Olivares-Rubio, Medina-Segura, & Vega-López, 2012). Currently, only four native and six exotic species are present. The river harbored four microendemic fish species, *Ameca splendens*, *Skiffia francesae*, *Zoogoneticus tequila* (Goodeidae), and *Notropis amecae* (Cyprinidae), and the last three are may be extinct in the wild (De La Vega-Salazar, Ávila Luna, & Macías, 2003; IUCN, 2017). The reservoir formed by the La Vega Dam on the TR was designated a wetland of international importance (RAMSAR) in 2010 (SEMADET, 2014). Despite the conservation significance of the river, water pollution, flow alteration, and introduction of exotic ichthyofauna have been reported (Dzul-Caamal et al., 2012). *Poecilia sphenops* has been established in the Teuchitlán River since 1990 (Miller, Williams, & Williams, 1989), and *P. bimaculatus* was not reported before 1996 (López-López & Paulo-Maya, 2001). Studies assessing the reproductive potential of these species in TR are lacking. We hypothesized that the exotic species *P. bimaculatus* and *P. sphenops* undergo continuous reproductive cycles throughout the year, with high fertility and female predominance in the TR.

The aim of this study was to investigate the reproductive biology of the invasive species *P. sphenops* and *P. bimaculatus* and to describe the annual variation in their reproduction relative to environmental conditions in the TR.

2 | MATERIALS AND METHODS

The TR, 1274 m long with a mean width of 29.6 m, is in Jalisco State, Mexico and flows from its headwaters at the Ameca River to the La Vega Dam (Figure 1). Five study sites differing in habitat characteristics were selected. The habitat was characterized according to the visual bases habitat assessment proposed by Barbour, Gerritsen, Snyder, and Stribling (1999). The physical and chemical characteristics of water, including temperature (°C), depth (cm), transparency (cm), pH, dissolved oxygen (mg/L), total alkalinity (mg/L), chlorophyll a (μg/L), total hardness (mg/L), turbidity (NTU), sediments, and dissolved and total solids (mg/L), were measured following the APHA-AWWA-WEF (1995). Two springs located at the headwaters, (site A was highly impacted by anthropic activity that has modified the spring into a pool lacking aquatic vegetation that might serve as habitat for epifauna. Site B, with a concrete dam, contained litter, submerged tree trunks, and emergent and floating vegetation), a third in the upper stretch of the river (site C, contained abundant vegetation covering the left bank. The right bank was impacted by the construction of a bridge and the outskirts of the town of Teuchitlán. This site contained extensive ponds of varying depths), and two sites downstream (site D and E) that are polluted by sewage. The little substrate available for epifauna those sites was comprised primarily of silt and clay bottom. The sites includes bridges and ponds greater than 40 m wide, with low oxygenation. Physicochemical water characteristic show the headwater springs present highest water transparency, with clarity decreasing downstream. Water depth ranged from 87 to 101 cm in Site A, 31–47.5 cm in Site B, 39–59.5 cm in Site C, 58–110 cm in Site D, and 24–99.5 cm in Site E. Water temperature ranged from 24.3 to 27.1°C, and pH is 6.7–7.5. Moderate electrical conductivity is observed in the sampling site (E) near the La Vega Dam. Dissolved oxygen concentration ranged from 0.81 to 7.09 mg/L. Chlorophyll a concentrations ranged from 0.6 μg/L–7.1 μg/L. The total hardness value indicate soft water at all sites (Table 1).

The study was conducted from January through November 2015 with bimonthly sampling. Fish were captured by seine net (4.5 m wide, 2.3 m high, 1.3 mm mesh size) and electrofishing (Power ~200 W, peak voltage ~250 V, peak current ~10 amp). Fish were preserved in 70% ethanol and transported to the laboratory where they were identified, counted, measured (0.01 mm), and weighed following Gómez-Márquez et al. (1999).

The embryonated eggs (Nh) and embryos (Ne) were counted. A fertility model (F = Ne+Nh) was created following Schoenherr (1997) and Cabrera and Solano (1995). Standard Length (SL) at first maturity (L_{50}) was related to SL using the logistic regression model to fit sigmoid curves according to the equation:

$$M(L) = 1/(1 + e^{(-aL+b)})$$

Confidence limits were derived by Bayesian inference based on stochastic simulation. Sex ratio following Sparre and Venema (1997), and the significance of the sampling site ratios was determined by a fit to the Chi-squared test (χ^2), with $p < .05$. Gonad maturity was estimated according Contreras-MacBeath and Ramírez-Espinoza (1996) (Table 2). The GSI was calculated following Vargas and Sostoa (1996). The Fulton's condition factor (K) was assessed. The relationship between SL and weight was evaluated by linear regression, calculating the values of *a* and *b* in the equation $W = aL^b$, where, W= is the body weight, L= is the standard length, *b* is the growth exponent or length-weight factor, and *a* is a constant. The values of *a* and *b* were estimated using a linearized form (Froese, 2006). Population size-structure was analyzed by site, grouping the data into SL ranges following Sturges (1926). Analysis of variance for size and sex were made among sites. Tukey-Kramer test with $p < .05$ was significant.

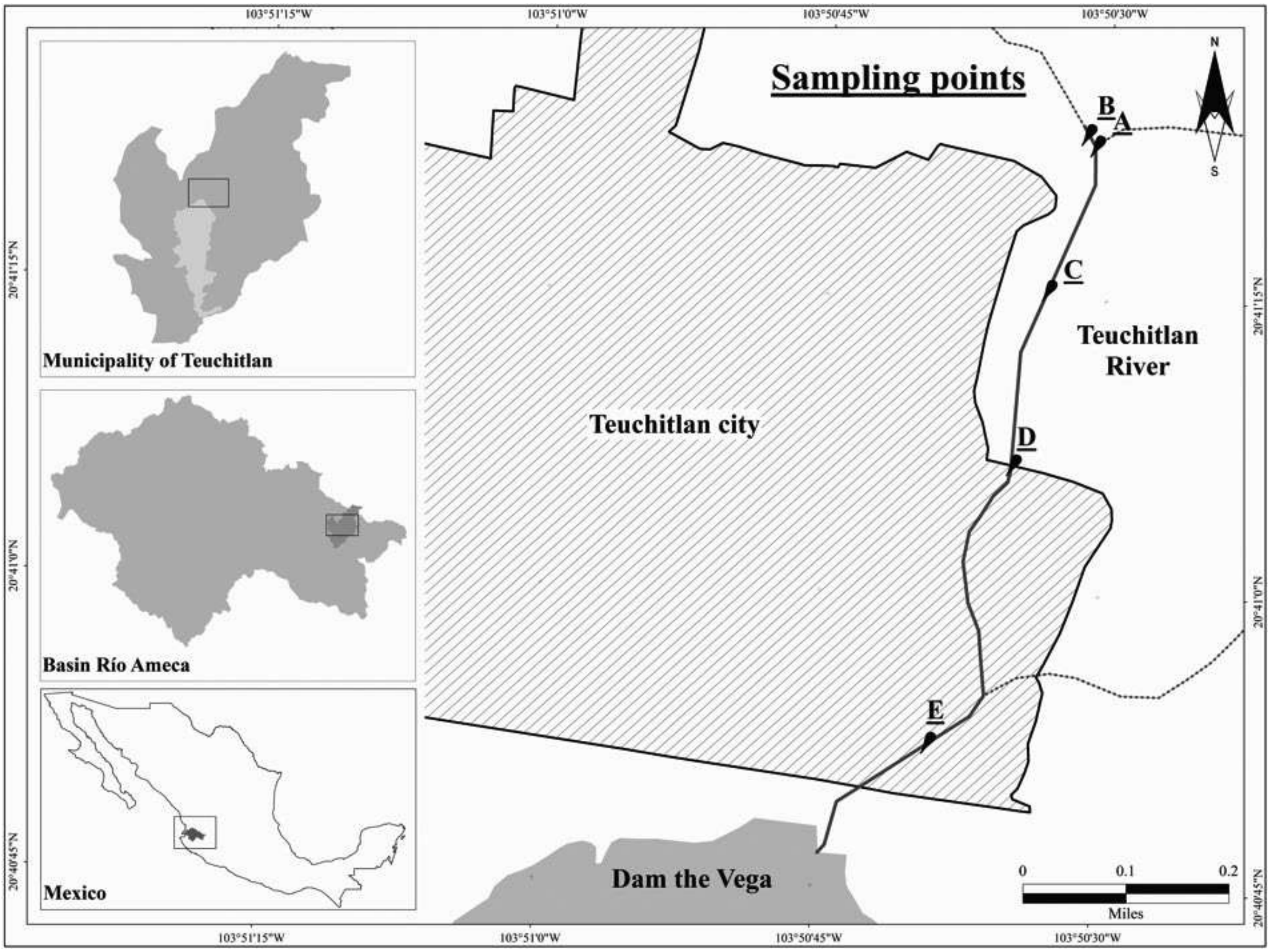

FIGURE 1 Location of Teuchitlán River and study sites (A, B, C, D, and E)

2.1 | Data analysis

The ordering of the environmental variables of sites with respect to the reproductive variables was carried out using the non-metric analysis of multidimensional scaling (NMDS) with Bray-Curtis distance. It was conducted using the meta MDS function of R (R Development Core Team, 2015) Vegan package (Oksabe et al., 2017).

3 | RESULTS

A total of 1374 fishes of *P. bimaculatus* and 571 of *P. sphenops* were examined (Table 3). The greatest standard length (Figure 2) for *P. sphenops* was 66.01 mm, and the smallest was 17.07 mm. The longest male fish was 52.76 mm, and the smallest was 21.77 mm. The smallest female *P. bimaculatus* was 5.17 mm and the longest was 76.09 mm. The smallest male was 11.40 mm and the longest male was 49.93 mm (Figure 2).

We found significant size differences among females (F = 18.24, p < .0001) and males (F = 18.24, p < .0001) of *P. sphenops*. Females in Site D were longer (SL = 43.99 ± 0.83), in site D males (38.25 ± 0.57) were longer than in site A (35.88 ± 0.58), C (33.25 ± 0.75), and E (33.84 ± 0.51) but not B (36.61 ± 0.69). For *P. bimaculatus*, males of all sites were similar-sized (F = 1.55, p = .1857), while females differed (F = 7.98, p < .0001). The smallest females were captured in site A (27.02 ± 0.96 mm).

The smallest L_{50} for male *P. bimaculatus* was 24.86 mm in Site D and, for females, was 25.28 mm at Site A. For *P. sphenops*, the smallest L_{50} was 31.70 mm for males at Site E and 35.48 mm for females at Site B (Table 4).

The species *P. bimaculatus* showed maximum fertility in site B (15.99 ± 2.27 embryonated eggs/embryos) and lowest in site C (9.15 ± 1.46). Highest fertility was observed in July (18.98 ± 9.46), and the lowest in May (6.04 ± 8.96). For *P. sphenops*, the lowest fertility was observed in site C (5.72 ± 5.72) and the highest in site D (31.26 ± 30.17). May showed the lowest values of fertility (6.44 ± 8.82), and the highest were in September (30.32 ± 32.51).

The sex ratio (female:male) of *P. bimaculatus* in all sites combined was 1.9:1 (χ^2 = 120.7 p < .0001), in the individual sites were A, 1.6:1 (χ^2 = 11.7 p < .0192); B, 3:1 (χ^2 = 33.4 p < .0001); C, 2.3:1 (χ^2 = 10.0 p < .0743); D, 2.8:1 (χ^2 = 27.9 p < .0001); and E, 6.2:1 (χ^2 = 20.2 p < .0011). *Poecilia sphenops* showed a ratio of 0.98:1 in the combined

TABLE 1 Physical and chemical water characteristics (mean ± standard deviation) for dry and wet season in each study site in the TR

Site	DO	BOD	AL	CL	HA	pH	TU	SE	DEP	TRA	TEMP	SOL-DIS	SOL-SUS
A													
Dry	6.2 ± 0.1	5.03 ± 1.2	141.1 ± 27.1	1.0 ± 1.0	48.3 ± 5.7	7.4 ± 0.3	0.9 ± 0.7	0.0 ± 0	97.0 ± 8.9	97.0 ± 8.9	26.5 ± 0.5	100.2 ± 1.5	3.9 ± 5.3
Wet	5.9 ± 0.2	3.75 ± 1.2	122.7 ± 22.5	0.6 ± 0.4	49.2 ± 3.8	7.2 ± 0.4	1.7 ± 0.7	2.2 ± 3.7	98.3 ± 3.1	98.3 ± 3.0	26.7 ± 0.3	97.3 ± 14.0	4.8 ± 3.6
B													
Dry	5.4 ± 0.6	6.59 ± 2.3	138.3 ± 34.0	2.7 ± 3.3	49.5 ± 9.5	7.3 ± 0.34	72.9 ± 71.0	1.1 ± 1.2	40.2 ± 2.6	29.8 ± 8.4	26.8 ± 1.0	99.2 ± 5.8	69.4 ± 83.6
Wet	5.9 ± 0.5	3.33 ± 0.5	123.3 ± 23.6	2.3 ± 2.0	50.8 ± 3.8	7.0 ± 0.4	14.9 ± 11.8	2.3 ± 3.9	38.8 ± 8.3	38.8 ± 8.3	27.1 ± 0.1	102.6 ± 5.4	16.3 ± 13.3
C													
Dry	6.1 ± 1.0	6.83 ± 1.4	140.0 ± 35.0	2.7 ± 1.5	44.7 ± 5.0	7.5 ± 0.1	12.0 ± 5.1	1.1 ± 1.4	52.7 ± 11.8	52.7 ± 11.8	26.4 ± 2.2	94.6 ± 9.1	10.1 ± 12.1
Wet	4.2 ± 0.4	4.61 ± 2.0	123.3 ± 14.4	7.1 ± 7.8	47.2 ± 2.6	6.9 ± 0.6	24.7 ± 9.8	3.4 ± 2.8	50.2 ± 4.7	38.5 ± 11.3	27.0 ± 1.5	103.5 ± 9.7	30.7 ± 21.7
D													
Dry	4.8 ± 1.1	5.67 ± 2.8	160.0 ± 30.4	1.9 ± 1.7	51.7 ± 2.9	7.3 ± 0.2	9.6 ± 3.7	1.0 ± 1.4	81.8 ± 24.7	81.8 ± 24.7	24.3 ± 3.2	89.3 ± 6.7	5.7 ± 6.3
Wet	4.1 ± 0.6	4.46 ± 1.5	133.3 ± 7.6	5.7 ± 5.1	58.3 ± 7.6	6.9 ± 0.6	17.1 ± 14.5	1.5 ± 2.6	61.7 ± 3.7	56.3 ± 12.5	26.9 ± 2.0	122.2 ± 4.7	14.3 ± 21.5
E													
Dry	3.3 ± 2.5	6.57 ± 2.8	153.8 ± 41.2	2.5 ± 0.7	53.3 ± 5.7	7.0 ± 0.3	12.3 ± 7.8	1.7 ± 2.5	55.2 ± 38.7	55.2 ± 38.7	24.7 ± 2.1	88.5 ± 7.6	11.7 ± 13.5
Wet	2.5 ± 1.0	4.46 ± 1.5	128.3 ± 12.5	2.7 ± 1.5	60.0 ± 10.0	6.7 ± 0.6	41.4 ± 40.6	0.1 ± 0.0	28.2 ± 4.0	25.5 ± 8.4	26.8 ± 1.0	113.1 ± 14.9	9.0 ± 1.9

Al, total alkalinity (mg/L); BOD, Biological oxygen demand (mg/L); Cl, Chlorophyll a (μg/L); DEP, depth (cm); DO, dissolved oxygen (mg/L); HA, total hardness (mg/L); Masl, meters above sea level; pH, pH; SE, sedimentation; SOL-DIS, total dissolved solids (mg/L); SOL-SUS, suspended solids (mg/L); TEMP, water temperature (°C); TRA, transparency (cm); TU, turbidity (NTU).

TABLE 2 Gonad maturity phases of viviparous fish (Contreras-MacBeath & Ramírez-Espinoza, 1996)

Phase	Description
Stage I (immature)	The ovaries were fusiform in shape and slightly thinner in their distal portions. The color of the ovaries ranged from white to white-yellowish.
Stage II (first reproduction)	The ovaries were flaccid and their colored ranged from white to yellow.
Stage III (ripening)	The ovaries were amber in color due to the ovules, which measured from 0.6 to 3 mm in diameter.
Stage IV (Ovules and embryos)	The ovaries had a mean width of 5.2 mm and weight of 0.37 g. Embryos of different developmental stages were present and were rolled over themselves and positioned randomly in the gonad. Small white ovules were also found in some ovaries. Frequently up to three broods at different stages of development were observed in a single female, thus indicating the existence of superfetation.
Stage V (pre-parturition)	These ovaries had a mean width of 5.4 mm and weight of 0.54 g. they were amber or brown-yellowish in color and had large, well developed embryos.
Stage VI (spent)	The ovaries were elongated, flaccid and white in color, without embryos or ovules.

TABLE 3 Number of specimens of female (♀) and male (♂) *Pseudoxiphophorus bimaculatus* and *Poecilia sphenops* captured per month, per site in the TR in 2015

Months	A♀	A♂	B♀	B♂	C♀	C♂	D♀	D♂	E♀	E♂	Total
P. bimaculatus											
January	28	25	15	11	75	44	86	80	119	51	53
March	33	45	118	20	25	4	21	6	21	8	30
May	21	8	25	5	0	0	12	12	0	0	8
July	21	9	21	10	16	6	20	6	21	9	13
September	20	20	23	26	19	9	25	5	29	1	17
November	18	12	18	7	13	14	22	8	12	16	14
Total	141	119	220	79	148	77	186	117	202	85	1374
P. sphenops											
January	5	10	3	1	19	23	13	20	11	12	117
March	13	13	46	23	21	9	14	16	13	17	185
May	21	9	0	8	0	0	6	8	0	0	52
July	6	9	4	4	1	1	5	1	18	11	60
September	2	18	7	4	0	0	25	4	7	23	90
November	1	1	0	3	3	3	13	13	15	15	67
Total	48	60	60	43	44	36	76	62	64	78	571

sites ($\chi^2 = 67.8$ $p < .0001$). Ratios in the individual sites were A, 0.92:1 ($\chi^2 = 18.6$ $p < .0022$), B, 1.3:1 ($\chi^2 = 18.7$ $p < .0021$); C, 0.69:1 ($\chi^2 = 5.6$ $p < .3465$); D, 1.7:1 ($\chi^2 = 7.3$ $p < .1968$); and E, 0.75:1 ($\chi^2 = 11.2$ $p < .0472$).

Immature fish predominant in sites A and B during dry season in *P. bimaculatus* (Figure 3). Maturity stages IV, V, and VI were present at low frequency, in site A. For *P. sphenops*, immature fish were predominant in site C during dry season and site E during wet season. Adult stages were frequent at site D during wet season. Site C presented the lower frequency of mature stages (Figure 3). Bimonthly variation of GSI showed that gonad growth began in May for *P. sphenops* and continued through September. The rainy season (July) marked the *P. sphenops* reproductive peak in all sites (Figure 4).

The GSI in *P. bimaculatus* females differed among sites, showing reproductive peaks along the year in all sites (Figure 4). The GSI values in males did not correlate temporally with females, and K did not show a clear relationship with the GSI. The growth coefficient *b* showed generally negative allometric growth in *P. bimaculatus*. *Poecilia sphenops* showed negative allometric growth in the headwaters (sites A, B, C) and positive allometric growth downstream (Table 5).

The NMDS for *P. bimaculatus* showed that depth, transparency, pH, and dissolved oxygen (Site A) were related to juvenile stages I and II. Mature fish stages IV and V tended to occur in sites of higher alkalinity, more dissolved solids, more mud, and a wider riparian vegetative zone (Site E). Higher fertility was associated with harder water and the

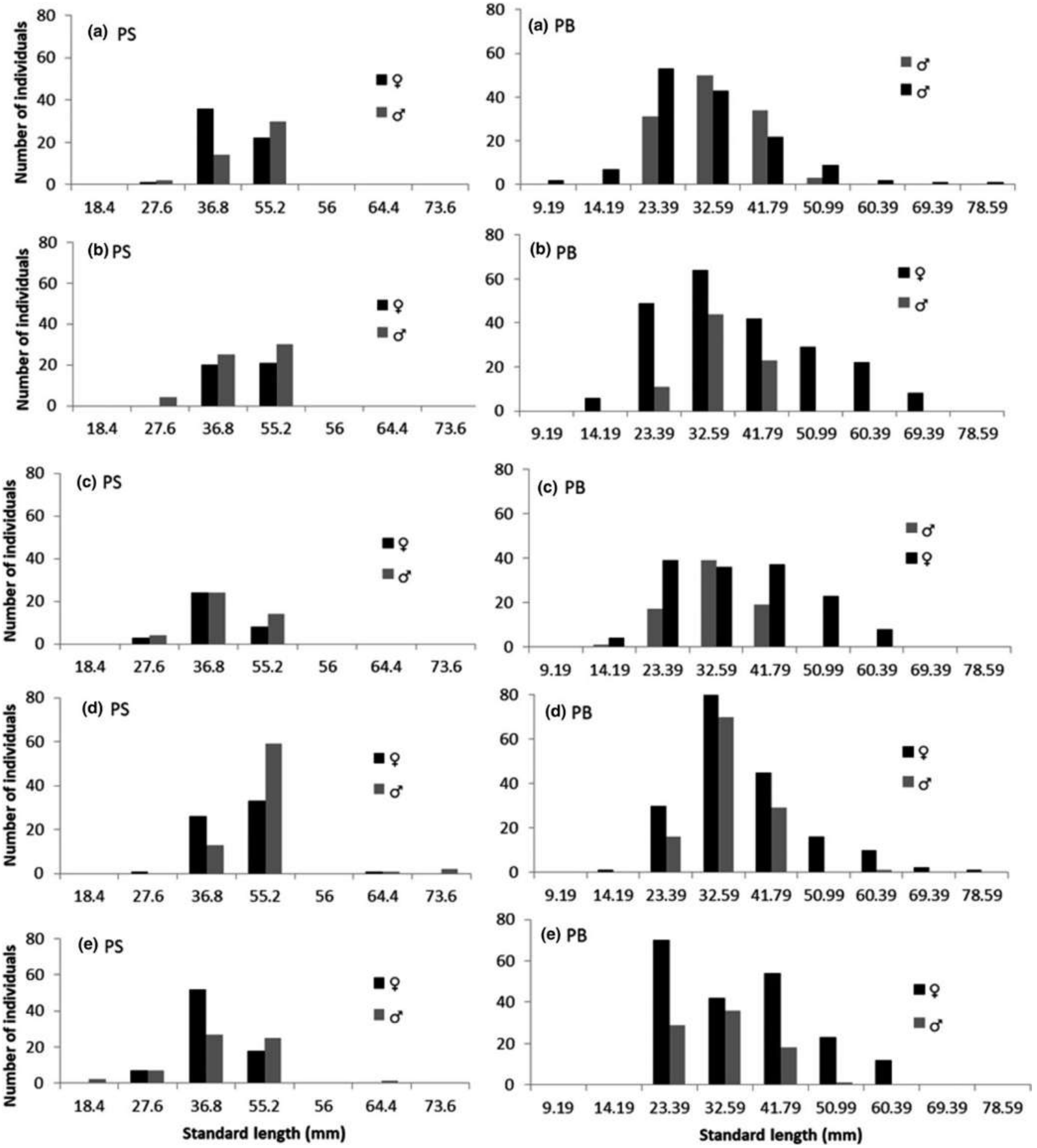

FIGURE 2 Size-frequency distribution (standard length) of female (♀) and male (♂) *P. bimaculatus* (Pb) and *P. sphenops* (Ps) by sampling site (A-E) in the TR

bank protected by vegetation (sites A, B). Higher GSI was observed at Site B, which had greater bank stability and high embeddedness (Figure 5).

Juvenile *P. sphenops* were found in Sites A and E, which had soft water, high turbidity, sediments, and vegetative protection on the left bank. Chlorophyll *a* is an important variable for fish at younger stages. Mature stages IV and V were found at sites A and E with more dissolved solids, high alkalinity, and areas of riparian vegetation. Fish in these sites showed higher GSI. Fertility was positively related to embeddedness and low dissolved oxygen (Site B) (Figure 5).

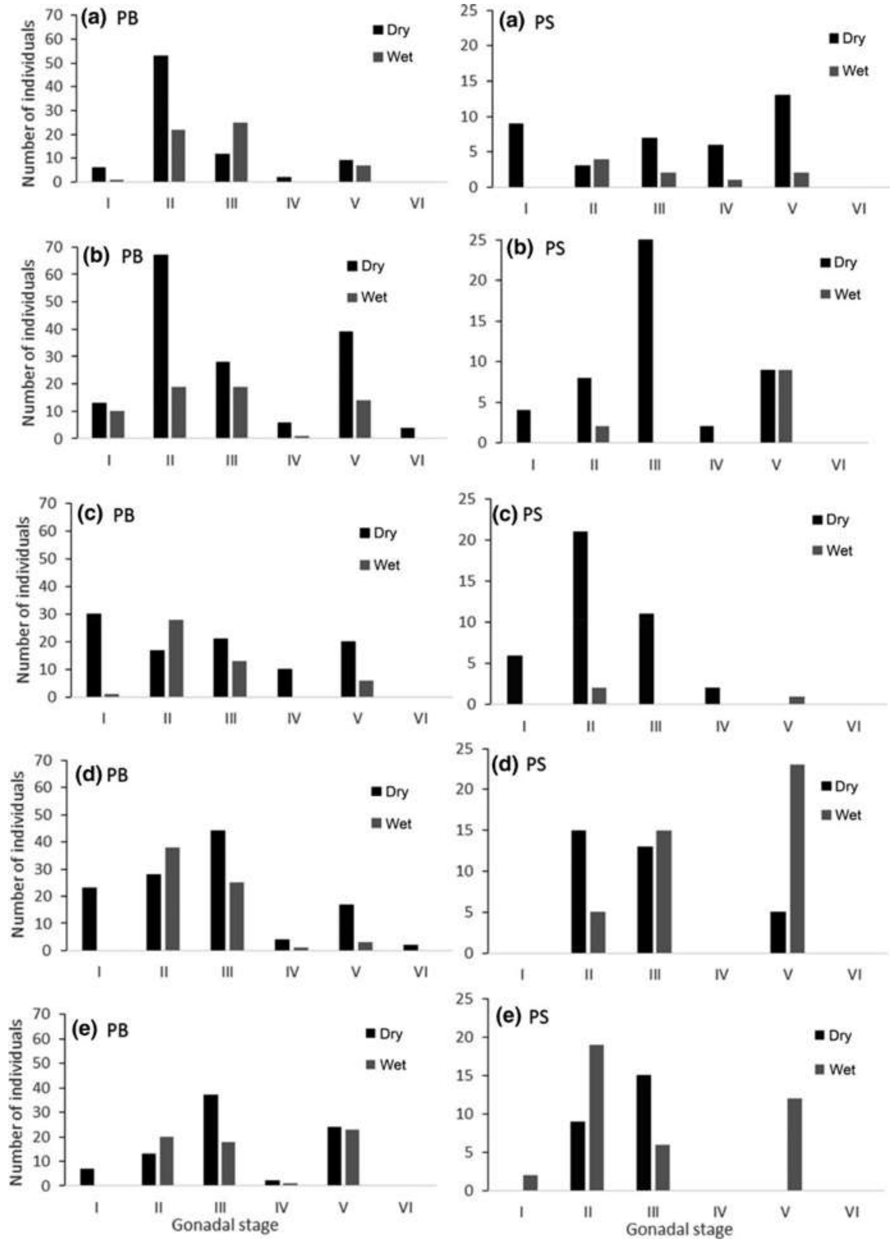

FIGURE 3 Relative frequency of gonad maturity stages in females of *P. bimaculatus* (Pb) and *P. sphenops* (Ps) in each study site (A, B, C, D, E) in dry and wet seasons in the TR

4 | DISCUSSION

This study documents the reproductive biology and seasonal changes in reproductive activity of the invasive species *P. bimaculatus* and *P. sphenops*.

TABLE 4 Size at first maturity (SL, mm, L50) by study site for *P. bimaculatus* (Pb) and *P. sphenops* (Ps) in the Teuchitlán River

Sites	♀Pb	♂Pb	♀Ps	♂Ps
A	25.28	25.77	39.66	33.72
B	36.27	27.40	35.48	36.39
C	34.55	28.21	40.07	32.77
D	30.50	24.86	41.34	34.99
E	32.51	25.97	36.41	31.70

♀ = female. ♂ = male.

Logistic model: $M(L) = 1/(1 + e^{(-aL+b)})$

The reproductive biology of exotic fish is seldom included in discussions of invasion processes, and its importance in geographic range expansion is often overlooked. Population growth is a basic requirement for the spread of an invasive species (Lockwood et al., 2007). Exotic species that establish in a new area may be r-strategists well-adapted to spread and colonizing new habitats but not to maintaining populations in highly competitive environments (Lockwood et al., 2007).

Winemiller (1989) stated that life-history strategies represent the endpoints of a triangular continuum arising from trade-off among the three basic demographic parameters of survival, fecundity, and onset and duration of the reproductive period. Our results showed females of both studied species to be larger than males. This size difference is typical of poeciliids, which exhibit rapid growth to maturity with little post-maturation growth (Snelson, 1984). The sex disparity may be related to the

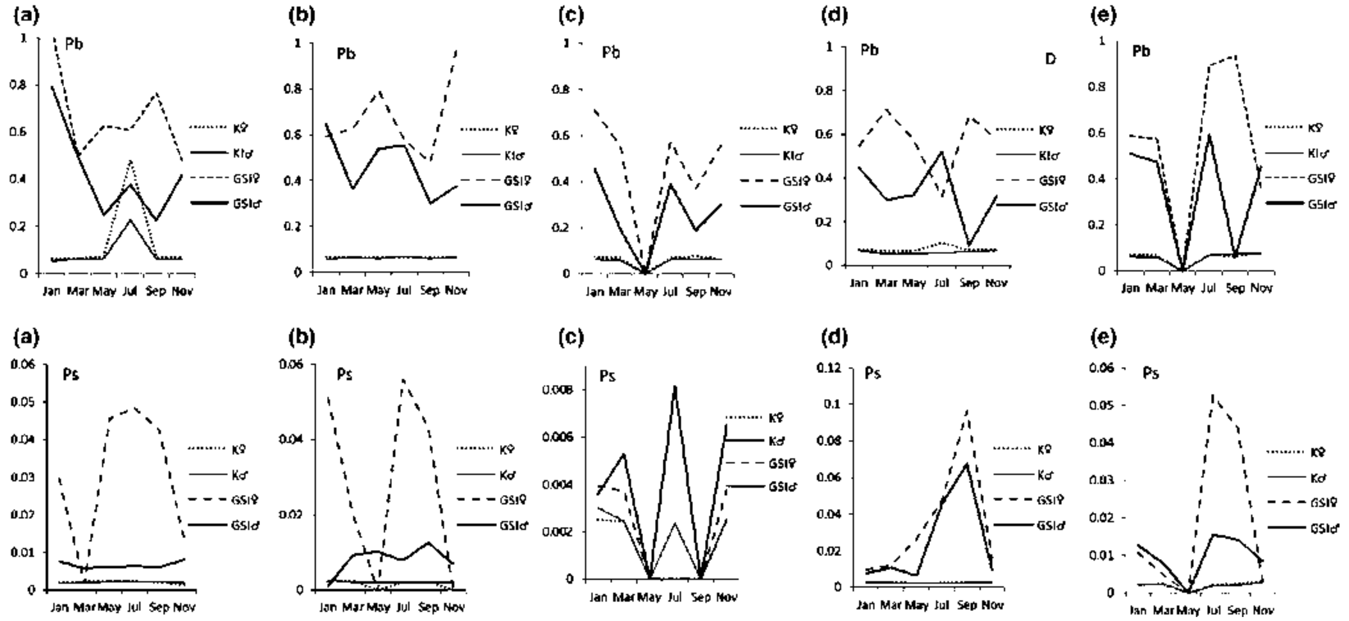

FIGURE 4 Bimonthly values of the GSI and K for each sampling site (A, B, C, D, E) in female (♀) and male (♂) *P. bimaculatus* (Pb) and *P. sphenops* (Ps) in the TR

reproductive capacity of females, with large abdominal cavities to accommodate embryos, and the maternal contribution to nutrition (Contreras-MacBeath & Ramírez-Espinoza, 1996). Male growth ceases when gonopodium are fully formed, and males do not live long after reaching sexual maturity (Snelson, 1984). Some studies suggest that the males are precocious compared to females (Gómez-Márquez et al., 2016; Ponce de León, Rodríguez, & León, 2013). The males reached first maturity at a smaller size than females. Gómez-Márquez et al. (1999) reported SL at first maturity of 22 mm in male of *H. bimaculata* and 27 mm in females. In this study, *P. sphenops* showed reproductive efficiency proportional to size, in agreement with several authors (Gómez-Márquez et al., 2016; Trujillo-Jiménez & Toledo, 2007). Sexual maturity is a function of size, and may be influenced by age, as well as abundance and availability of food, water temperature and day length (Nikolsky, 1978). Early reproduction favors the success of the species and implies a greater number of spawnings throughout life, favoring the increase of the population and colonization. *Pseudoxiphophorus*

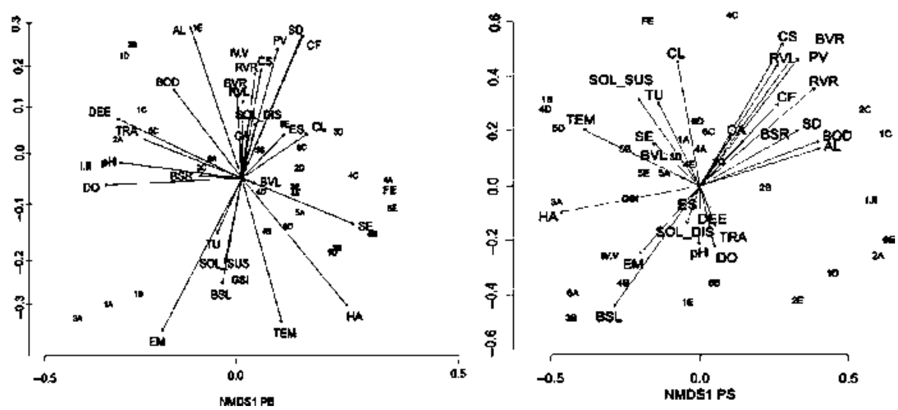

FIGURE 5 Non-metric analysis of multidimensional scaling (NMDS) for *P. bimaculatus* (PB) and *P. sphenops* (PS) from the Teuchitlán River. Sites (A, B, C, D, E), months (1 = January, 2 = March, 3 = May, 4 = July, 5 = September, 6 = November). Reproductive variables (I and II = immature and juvenile fish, IV and V = Mature fish, GSI = gonadosomatic index, FE = fertility). Physical and chemical water characteristic and attributes of visual based habitat assessment for each study site (DO = dissolved oxygen, BOD = Biological oxygen demand, Al = total alkalinity, Cl = Chlorophyll a, HA = total hardness, pH = pH, TU = turbidity, SE = sedimentation, DEE = depth, TRA = transparency, TEM = water temperature, SOL-SUS = suspended solids, SOL-DIS = total dissolved solids, ES = epifaunal substrate/available cover, EM = embeddedness, PV = pool variability, SD = Sediment deposition, CF = channel flow status, CA = channel alteration, CS = channel sinuosity, BSL = bank stability (left), BSR = bank stability (right), BVL = bank vegetative protection (left), BVR = bank vegetative protection (right), RVL = riparian vegetative zone width (left), RVR = riparian vegetative zone width (right))

TABLE 5 Standard length (SL, mm) and the relationship between SL and weight (g) for *P. sphenops* and *P. bimaculatus* in five study sites of TR

Site	Mean±SD	*a*	*b*	R^2 $^{**}p < .01$
P. bimaculatus				
A	36.61 ± 8.72	0.07	1.58**	0.75
B	45.36 ± 10.09	0.10	3.14*	0.89
C	42.16 ± 7.27	0.09	2.62**	0.89
D	41.30 ± 8.10	0.09	2.47**	0.92
E	39.41 ± 7.27	0.08	2.30**	0.92
P. sphenops				
A	42.01 ± 2.56	0.11	2.96**	0.72
B	40.46 ± 4.79	0.10	2.83**	0.71
C	35.29 ± 6.09	0.08	1.75**	0.99
D	45.28 ± 4.27	0.15	4.5*	0.81
E	44.34 ± 6.19	0.11	3.09*	0.95

R2, correlation coefficient. *positive allometry (b > 3), **negative allometry (b < 3).

bimaculatus showed higher fertility in springs, and *P. sphenops* downstream. Female poeciliids have been demonstrate to exhibit larger offspring as food resources become scarce.

Female of *P. bimaculatus* were dominant from ~2:1 to 6:1-. Difference in sex ratios are typically because the brightly colored males are susceptible to predation and vulnerable to hypoxia in high temperatures (Rodd & Reznick, 1997; Snelson, 1989). In this study, dissolved oxygen levels in water fell below 5 mg/L in site E, putting stress on aquatic organisms, further reducing the availability of energy for growth and reproduction (Kramer, 1987).

The sex ratio of *P. sphenops* was generally ~1:1, while studies have suggested the dominance of females in Poecilids (Lorán-Núñez, Martínez, Valdez-Guzmán, & Martínez-Lorán, 2013), although Urriola-Hernández, Cabrera-Peña, and Protti-Quesada (2004) reported the sex ratio of *P. reticulata* to be significantly male-biased. A higher proportion of females favors reproductive success, spread, and successful invasion. The GSI values indicated that *P. sphenops* and *P. bimaculatus* are iteroparous, which permits population increase and indicates effective exploitation of environmental resources, which is similar to those reported by Gómez-Márquez et al. (2016).

The condition factor follows the pattern of the gonadosomatic index in females; however, K values were low with respect to gonad maturation, and fish were in poor condition. Differential energy allotment versus reproductive tissue (female) and secondary sex characteristics (male), help explain disparity in K and GSI. *Poecilia sphenops* and *P. bimaculatus* showed allometry growth, however, they showed negative growth. The variability between the same species in different sites could be caused for differences in size or nutritional condition (Ricker, 1975). Other authors reported similar growth for species of Poecilids (Gómez-Márquez et al., 1999; Urriola-Hernández et al., 2004).

The structure of the channel of the Teuchitlán River has been modified, from a lotic to a lentic system and creating appropriate reproductive habitat for the invasive species. Both species were well-established along the river, but the juvenile of *P. bimaculatus* showed preference for the clear and highly oxygenated water of the headwaters. Mature fish were found downstream, in more turbid water with high dissolved solids and high alkalinity. These water characteristics are broadly related to the decomposition of organic matter, which could favor the availability of food resources.

Pseudoxiphophorus bimaculatus and *P. sphenops* in the Teuchitlán River showed the capability to growth and reproduce in several environmental conditions. Both species have established along the river; their reproductive strategy involves large number of small-highly fertile fish; they exhibit high reproductive yield with iteroparity. These characteristics are typical of fish species with high invasive potential (Lockwood et al., 2007). It is also necessary to study the reproductive strategies of native species to obtain conclusive results on interspecific competition for reproductive habitat.

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Capítulo 2

Reproductive biology of three native viviparous species in Teuchitlán River, México.

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Reproductive cycle of three native viviparous species in Teuchitlán River, México

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Running Title: Reproductive cycle of native fish

Abstract

The Ameca basin in central México contains a rich native and endemic ichthyofauna. We determined the reproductive cycle for three native goodeids (Goodeidae) from Teuchitlán River, *Goodea atripinnis, Ameca splendens* and *Zoogoneticus purhepechus*. This two-year study investigated the fertility, size at first maturity (L50), sex ratio, gonad maturity stage, gonadosomatic index, and size structure of the three species. Environmental variables was evaluated with respect to the reproductive variables using non-metric analysis of multidimensional scaling (NMDS). Three-hundred eighty seven specimens of *G. atripinnis*, 328 *A. splendens* and 179 Z. *purhepechus* were examined. *Goodea atripinnis* is widely distributed along the river, showing a complete structure of sizes. The endemic species (*A. splendens*, *Z. purhepechus*) show lower abundance downstream. Native species presented two reproductive periods, January to March and the second, July to September. Sex ratio is 1:1 (female: male), fertility is lower compared with other species in different basins. NMDS showed that native species are found associated with clean, deeper waters, more dissolved oxygen in water, and a neutral pH. These species have to adapt to the anthropogenic activities that have modified the river affecting their habitat. In spite there are not specific conservation actions to maintain biological diversity in Teuchitlán River.

Keys words: Gonadosomatic index, Goodeids, Fertility, NMDS, Sex ratio.

Resumen

La cuenca del Ameca en el centro de México contiene riqueza nativa y endémica de ictiofauna. Determinamos el ciclo reproductivo de tres goodeidos (Goodeidae) del río Teuchitlán, *Goodea atripinnis*, *Ameca splendens* y *Zoogoneticus purhepechus*. Un estudio de dos años, donde investigamos, fertilidad, talla de primera madurez (L50), proporción de sexos, estadios gonadales, índice gonadosomático y estructura de tallas de las tres especies. Evaluamos las variables ambientales respecto a las reproductivas utilizando un análisis no métrico de escalamiento multidimensional (MNDS). Se analizaron 387 especímenes de *G. atripinnis*, 328 *A. splendens* y 179 *Z. purhepechus*. *Goodea atripinnis* se distribuye a lo largo del río, mostrando una estructura de tallas completa. Las especies presentaron dos periodos reproductivos, enero a marzo y el segundo, julio a septiembre. Proporción de sexos 1:1, la fertilidad es menor en comparación con otras especies en diferentes cuencas. El NMDS mostro que las especies se encuentran asociadas con sitios que presentan el agua más clara y profunda, gran cantidad de oxígeno disuelto y pH neutro. Estas tienen que adaptarse a las actividades antrópicas que han modificado el río afectando su hábitat. A pesar de esto, no existen acciones de conservación específicas para mantener la diversidad biológica del río Teuchitlán.

Palabras clave: Goodeidos, Índice gonadosomático, Fertilidad, NMDS, Proporción sexual.

Introduction

The central region of México contains a depauperate freshwater fish fauna, but several endemic groups. The most diverse component of this region are the Goodeidae (Teleostei: Cyprinodontiformes). Goodeids comprise approximately 40 to 45 species, four of these are oviparous of the Great Basin of the United States belonging to the subfamily Empetrichthyinae, whereas the remaining species are viviparous belonging to the subfamily Goodeinae that inhabit drainages of the Mexican high plateau and its periphery. Goodeids fill many different ecological roles, and, as a result, possess unique and varied morphological and life-history specializations (Webb, Miller, 1987). Reproduction of the goodeids is unique in comparison to other co-occurring groups, for example, during gestation, most goodeids, develop structures termed trophotaeniae, an embryonic trophic adaptation consisting of a simple surface ephithelium surrounding a highly vascularized core of loose connective tissue. Trophoteniae are the chief sites of nutrients absorption in goodeid embryos. Through the uptake of nutrients, a massive gain in weight occurs during embryonic development (Hollenberg, Wourms, 1994).

Most of the species of goodeinds are critically endangered and some of them are considered extinct (Domínguez-Domínguez et al., 2005; Domínguez-Domínguez et al., 2008). The reasons for the decline of this group of viviparous fishes in México include the arid/semiarid conditions in the northern and central parts of México, water overexploitation, introduction of invasive species, habitat destruction, and water pollution caused by a diverse array of human activities (Contreras-Balderas, 2005).

The Ameca River basin in central México (Pacific Slope) is of great biological importance because it has been identified as one of the richest areas for native and endemic ichthyofauna in México (Miller, Smith, 1986). The upper part of the Ameca drainage, mainly the Teuchitlán River, is inhabited by several non-shared endemic species with other aquatic systems from central México (Domínguez-Domínguez et al., 2008). In contrast, the Ameca River basin ranks among the most heavily disturbed drainages by human activities in México. Water pollution, reductions in ground-water and surface water levels, basin deforestation, habitat modification and fragmentation, introduction of exotic species, and overfishing all have caused severe degradation of aquatic systems (Domínguez-Domínguez et al., 2008). In particular, the Teuchitlán River, in the upper part of the Ameca basin, has suffered anthropogenic activities that have modified the aquatic ecosystem, including reservoir construction, water extraction, and municipal and industrial pollution. Therefore, there has been a significant decrease in native fish species from Teuchitlán River. Historically, the area has twenty native and six non-native fish species, most of which were taxonomically described in the last decade. At present, the Teuchitlán River system harbors only four native fish species, including the endemic *Ameca splendens* and the natives *Zoogoneticus purhepechus* and *Goodea atripinnis*, as well as seven non-natives (López-López, Paulo-Maya, 2001).

Previous studies have provided some life-history information for each of the three goodeid species included in this study, but much information is still lacking. *Ameca splendens* has a restricted distribution, occurring in only two springs (Rincon and Almoloya). The species is mainly herbivorous, grazing on filamentous algae and diatoms, mosquito larvae, copepods, oligochaetes, small insects, and spiders falling on the water surface (Kingston, 1979). Reproduction occurs midwinter to early spring, but the reproductive period may be greatly extended. In aquarium stocks, their fecundity varies from 1 to 17. Maximum known length is 90 mm SL (Miller et al., 2005). *Goodea atripinnis* (Jordan, 1880) is the most widespread goodeid species occurring throughout central México. The species inhabits a variety of different habitats types including lakes, ponds, springs, outflows, and streams (Miller et al., 2005; De la Vega-Salazar, 2006). The diet consists of filamentous green algae, micro-crustaceans and mollusks (Miller et al., 2005). Reproduction is long, occurring from January to July, producing a large number of embryos (167) (Miller et al., 2005). Maximum length is 200 mm SL. *Zoogoneticus purhepechus* is a recent described species (Domínguez-Domínguez et al., 2008), formerly recognized as *Zoogoneticus quitzeoensis.* No autecological studies for this species have been conducted. This species is restricted to particular river drainages in the lower Lerma, upper Ameca, Armeria and Santiago rivers basins and Chapala Lake, México (Domínguez-Domínguez et al., 2008).

In spite of their high species richness and endemicity, goodeids have been largely ignored in conservation efforts. However, documented extinctions and extirpations have led to some level of legal protection, and these fishes have caught the attention of aquarists worldwide (De la Vega-Salazar et al., 2003; Domínguez-Domínguez et al., 2005). Understanding basic aspects of life-history, represents one of the first steps to develop conservation plans for any species. As a whole, little life-history information is known for most species of goodeids.

Therefore, the aim of this study was to conduct a comprehensive study to evaluate the reproductive cycle of three native goodeids (*G. atripinnis, A. splendens* and *Z. purhepechus*), and to describe annual variation in reproduction for each species and their relationships to habitat characteristics in the Teuchitlán River, México. The results of this study have relevant conservation implications and can be used to support specific conservation actions to maintain biological diversity in Teuchitlán River.

Materials and Methods

The Teuchitlán River, 1,274 m long with a mean width of 29.6 m (maximum shore), is located in Jalisco State, México, and flows from its headwaters springs to the La Vega Dam (Fig. 1). Five study sites differing in habitat characteristics were selected: two springs located at the headwaters, a third in the first stretch of the river, and two sites downstream that are polluted by sewage. This study was conducted over a bi-annual cycle with bi-monthly sampling occurring from January 2015 to November 2016.

Fish were captured with a seine net (4.5 m long, 2.3 m high and, 1.35 mm mesh size) and electrofishing (DC-backpack electrofisher model ABP-3, ETS electrofishing systems, LLC, average power ~200 watts, peak voltage ~250 V, peak current ~10 amps). Fish were preserved in 70% ethanol and transported in plastic containers to the laboratory where they were identified, counted, measured (0.01mm) and weight (0.001 g), following the criteria of Cruz-Gómez et al. (2013).

The reproductive variables including fertility, size at first maturity, sex ratio, gonad maturity stage, gonadosomatic index (GSI), condition factor (K), size structure, and reproductive habitat were assessed. The ovaries of each female were removed, and embryonated eggs and embryos were counted. The fertility model was obtained with the data from embryonated eggs and embryos, which was adjusted to the potential model F=

aL^b (Schoenherr, 1977). Size at first maturity (L_{50}) was related to the standard length using the logistic regression model to fit sigmoid curves according to the following equation: $M(L) = 1 / (1 + e^{(-aL+b)})$. Confident limits were derived by Bayesian inference based on stochastic simulation. The sexual ratio was described per site and season following the criteria of Sparre, Venema (1997). The statistical significance of the sampling sites ratio results was established by a fit to the Chi-squared test (X^2), using a $p < 0.05$ value. Gonad maturity was estimated with the criteria proposed by Ramírez-Herrejón et al. (2007) (Tab.1). The gonadosomatic index (GSI), an estimator of reproductive condition, was calculated by dividing the gonad mass by total body mass X 100 (both in grams; Zeyl et al., 2014). Condition factor was assessed with Fulton´s condition factor (K). Population length structure was analyzed by sampling site, grouping the data into standard length ranges following the criteria of Sturges (1926), a variance analysis allowed the identification of significant differences among sampling sites by size, species and sex. Tukey-Kramer test ($p < 0.05$) showed these significant differences. Model growth was evaluated by linear regression, calculating the values of *a* and *b* of the equation $W = aL^b$, where, W= is the body weight, L= is the standard length, *b* is the growth exponent or length-weight factor, and *a* is a constant. The values of *a* and *b* were estimated using a linearized form (Froese, 2006).

The physical and chemical characteristics of water, such as water temperature (°C), depth (mm), transparency (mm), pH, dissolved oxygen (mg/L), total alkalinity (mg/L), chlorophyll a (µg/L), total hardness (mg/L), turbidity (NTU), sedimentary, dissolved and totals solids (mg/L), were evaluated following the criteria of American Public Health Association, the American Water Works Association, and the Water Environment Federation (APHA-AWWA-WEF, 1995).

Data analysis

The ordering of the environmental variables of the sampling sites with respect to the reproductive variables of the species was carried out using the non-metric analysis of multidimensional scaling (NMDS) with Bray-Curtis distance. The NMDS was conducted using the metaMDS function of R (R Development Core Team, 2015) Vegan package (Oksabe et al., 2017).

Results

Three-hundred eighty specimens of *Goodea atripinnis*, 328 of *Ameca splendens*, and 179 of *Zoogoneticus purhepechus* were examined in this study (Tabs. 2-6).

Goodea atripinnis

The size structure of females of G. *atripinnis* ranged from 19 mm SL to 88 mm SL, with most individuals in the 37 to 54 mm SL size range. For males the range was 23 mm SL to 119 mm SL, with the greatest number of individuals between the sizes of 35 to 47 mm SL (Fig. 2). There were significant difference in size among sampling sites for females ($F = 15.42$, $p < 0.0001$) and males ($F = 6.05$, $p < 0.0001$). Site E (mean = 57.46±1.55) presented the longest size and site C (39.64±3.69) the smallest size for females; for males the site A (52.85±1.43) and E (52.60±2.42) presents similar mean of size but different from site B (42.97±1.84).

In all sampling sites, the fertility of *G. atripinnis* was 9±2.47, however, site B presented the highest (13±5.67) and site A the lowest (7±2.68). Females begin their reproduction at size of 43.02±8.9 mm SL. The average size of mature males is similar to females. However, across sampling sites, males of *G. atripinnis* reach the L50 at 36.01 mm SL and females at 30.09 mm SL, both in site C (Tab. 3). The sex ratio (female/male) was 1:1 in site A ($X^2 = 11.38$, $p > 0.0443$), 1.3:1 in site B ($X^2 = 14.72$, $p > 0.0116$), 2:1 in site C ($X^2 = 6.6$, $p > 0.2521$), 2.5:1 in site D ($X^2 = 10.08$, $p > 0.0729$) and 1.6:1 in site E ($X^2 = 14.64$, $p > 0.0119$). All gonadal stages were present for *G. atripinnis* at all sites, although few individuals were found in stage VI. Mature individuals (stages III, IV and V) were more frequent in the headwaters (site A). We found a higher frequency of immature individuals (stages I and II) in the middle portion of the river (sites C and D), (Fig. 3).

Bi-monthly variation of GSI for females varied among sites with a reproductive peak occurring in March in the headwaters, and downstream in September and November. The GSI for males was not consistent with the GSI for females and a reproductive peak in the headwaters in July to September, and downstream in March and September (Fig. 4). Condition factors did not show a clear relationship with GSI. K-condition data showed low values downstream (Fig. 4). Both sexes presented positive allometric growth (Tab. 4).

The non-metric analysis of multidimensional scaling (NMDS) for mature individuals showed a strong relationship with the environmental variables including higher pH, more suspended solids and higher turbid of the headwaters of the river (site A and B). Juveniles were related with the lower part of the river (site E) with highest values of mud, chlorophyll and temperature (Fig. 5).

Ameca splendens

Size structure for females was represented with a range of 15 mm to 57 mm SL, with most individuals between 26 to 31 mm SL. For males were between 15 mm to 53 mm SL, more frequency individuals between the sizes of 31 to 37 mm SL (Fig. 2). There were significant difference in size among sampling sites for females ($F = 33.55$, $p < 0.0001$) and males ($F = 18.22$, $p < 0.0001$). For females All sampling sites are statistical different in size from one another, site A (38.04±1.03), site B (30.61±0.90), site C (23.42±1.64) and site D (43.92±1.79). Males presented similar values in site D (42.24±2.33), and A (39.58±1.00), site B (32.82±0.89) and C (24.15±2.47) are different from another.

The endemic species *A. splendens*, across all sampling sites possessed a fertility value of 7 ±3.25 Site C showed the lowest value of fertility (5±9.95) and site A the highest (7±4.8). Reproduction began at an average size of 34.26±9.57 mm SL for females and 31.59±11.69 mm SL for males. Size at first maturity varied across sites with individuals reaching maturity at 27.04 mm SL for females in site C, and 31.95 mm SL for males in site B (Tab. 3). The sex ratio was 1.3:1 in site A ($X^2 = 13.27$, $p > 0.0209$), 1.14:1 in site B ($X^2 = 6.19$, $p > 0.2875$), 3.12:1 in site C ($X^2 = 2.20$, $p > 0.8119$) and 2.33:1 in site D ($X^2 = 2.60$, $p > 0.7603$). It was not possible to capture enough individuals in the lower section of the river (site E).

Site A showed the best structure of gonadic stages with high frequency of juvenile and mature stages. The immature individuals are dominant in the four sites (Fig. 3). The values of GSI for females showed a reproductive peak in March and July for site A, January and November for site B, March for site C and January for site D. Males showed a similar tendency in GSI values (Fig. 4). Condition factors showed a similar tendency during the peaks of the values of GSI in both sexes (Fig. 4). Both sexes presented negative allometric growth (Tab. 4).

The non-metric analysis of multidimensional scaling (NMDS) showed that the mature individuals (stage IV and V) were established in the headwaters of the river (site A) and downstream (in site D) where the environmental variable showed the largest values of transparency, depth, pH, and hardness. Juvenile organism (stages I and II) were related in sites D and E, with highest values of dissolved solids, mud and turbidity (Fig. 5).

Zoogoneticus purhepechus

Zoogoneticus purhepechus was most common in the headwaters (sites A, B and C) and we did not capture enough individuals from the downstream sites for analysis. Size structure for females were between 15 mm and 38 mm SL and 16 mm to 41 mm SL for males. Most individuals were between 24 mm to 27 mm SL (Fig. 2). There were significant difference in size among sampling sites for females ($F = 16.21$, $p < 0.0001$) and males ($F = 18.22$, $p < 0.0001$). All the sampling sites are statistical different in size from another in females, site A (31.88±1.00), site B (26.78±0.87) and site C (23.10±1.23). Males presented similar sizes in site B (25.43±0.76) and C (26.72±1.78), but different from site A (31.72±1.02).

The fertility in all the sampling sites was 8±3.17, however, site C showed the highest fertility (11±10.95), site B the lowest (5±2.64). Temporally, reproduction began at a size of 33.22±7.34 mm SL for females and 28.61±5.06 mm SL for males. Standard length at first maturity varied slightly by sites and was 28.03 mm SL for females and 25.03 mm SL for males at site B (Tab. 3). The sex ratio was 1.3:1 in site A ($X^2 = 16.21$, $p > 0.0062$), 0.97:1 in site B ($X^2 = 2.03$, $p > 0.8449$) and 2.6:1 in site C ($X^2 = 13.07$, $p > 0.0.0227$). Mature individuals were in higher frequency in the headwater sites (site A). Immature individuals dominated at site B (Fig. 3).

At site A, the GSI and K values for both sexes showed a similar tendency with two reproductive peaks, in March and November. For site B, two reproductive peaks also were present, but in July and November for females. March was the high GSI values for male, and the values for K showed a peak in May. Females showed two reproductive peaks during March and September, in site C, the values of GSI for males coincide with the reproductive peak of females in September, K values showed low in this site (Fig. 4). Both sex presented negative allometric growth (Tab. 4).

The results of NMDS showed that mature organisms were correlated with headwater site parameters (site A and B) with high values of depth, transparency, dissolved oxygen and pH. Juveniles were related with the site B, with high values of dissolved solids and high turbidity in the water (Fig. 5).

Environmental variables

The physicochemical variables show the lowest values of depth in site B in dry season and in the site E in wet season. The highest value of depth was in site A in the dry and wet seasons. Temperature ranged throughout the two years between 24.4±1.9~27.9±0.8 °C. The pH (6.3~6.9) indicates slightly acid water, with a moderate electrical conductivity in the sampling site near to the La Vega dam. The headwaters (springs) are the sites with greater transparency (site A and B) and the transparency decreases downstream. Dissolved oxygen concentrations ranged between 3.5 mg/L in site E (wet season) and 6.1 mg/L in site A (dry season). Chlorophyll a showed the minimal value of 0.6 µg/L in site A and the maximum value of 10.7 µg/L in site E, both in the wet season. The total hardness indicates soft waters (Tab. 5).

The habitat characteristics along the Teuchitlán River differ between sites. Site A showed high impacts by the anthropogenic activities that have modified the spring into a pool, which lacks emergent or floating vegetation, that can serve as a habitat or shelter for the epifauna. Site B contains organic material in different levels of degradation, submerged trunks, emergent and floating vegetation, it is a site that is dammed with masonry. Site C is the beginning of the river, showed abundant vegetation that covers the left bank, the right bank is impacted by the construction of an edge of land and the beginning of the settlement of the population of Teuchitlán, this site shows different kind of ponds, shallow (< 0.5 m) and deep (> 0.5 m). Sites D and E showed low and homogeneous substrate available for the epifauna, composed mainly by silt and clay covering the bottom. It can observed the construction of the bridges, however the ponds are very extensive of more than 40 meters width, which produces little oxygenation in the water. In spite, these sites are polluted by wastewater discharge.

Discussion

The present study documents the reproductive cycle of three native goodeids in the Teuchitlán River, México. The seasonal and inter-annual variation in the species spatial distribution, life history stages, and size structure are reflected and influenced by the anthropogenic activities along the Teuchitlán River.

Both *Ameca splendens* and *Zoogoneticus purhepechus* occurred in lower abundance than *Goodea atripinnis* throughout the river basin and their abundances decrease progressively downstream. The population density in the lower portion of the river was very low. Abundance differences can be explained by the greater environmental tolerance of *G. atripinnis*, which seems to be a generalist in regards to its habitat. Both, *A. splendens* and *Z. purhepechus* seem to be less tolerant to environmental stress, and are less abundant in more disturbed environments, such as was mentioned by López-López, Paulo-Maya (2001), Varela-Romero et al. (2002).

Fertility

The native fish species in Teuchitlán River show relatively low average fertility compared with the same species in other aquatic systems and also in comparison to other goodeid species. Other goodeids, such as *Alloophorus robustus*, *Allotoca diazi, G. atripinnis,* and *Ilyodon whitei* have averages of 20 to 50 embryos per female in other river basins (Mendoza, 1962; Uribe-Aránzabal et al., 2006). Furthermore, species of *Allodontichthys* had 11 to 30 embryos (Lyons et al., 2000) and *Zoogoneticus quitzeoensis, Hubbsinia turneri, Girardinichthys multiradiatus* have litter sizes averaging <20 embryos per female (Ramírez-Herrejón et al., 2007; Moncayo-Estrada, 2012; Cruz-Gómez et al., 2013).

Other exotic species in the Teuchitlán River, such as *Poecilia sphenops* and *Pseudoxiphophorus bimaculatus* produce a greater number of embryos (*P. sphenops* averages 31 embryos per female) than the native goodeids (Ramírez-García et al., 2017), which is likely contributing to an increase in exotic fish stocks. We hypothesized that the environmental degradation can cause a reduction of the number of embryos in livebearing species in Teuchitlán River, such as has been mentioned by Silva-Santos et al. (2016) under controlled conditions.

Size at First Maturity (L50)

Environmental variables (high values of dissolved oxygen, low values of alkalinity, high water temperature and low dissolved solids) are related directly with development of gonads (Salgado-Ugarte et al., 2005). We found that females mature earlier than males in the headwaters, which may be advantageous because maturation at a smaller size means greater production offspring throughout their life. At the same time this shows the reason because population decrease downstream in native species. Ramírez-García et al. (2017) mentioned that for exotic species (*P. bimaculatus* and *P. sphenops*) from the Teuchitlán River, males reached first maturity at a smaller size than females along the river but this phenomenon continues throughout all of the sampling sites because the exotics species are well-established along the river. Different sizes at first maturity are known for other goodeid species (*G. atripinnis*, *G. multiradiatus*, *Z. quitzoensis*, *H. turneri*, *A. robustus*, *A. diazi*) in different aquatic systems (Salazar-Tinoco et al., 2010; Cruz-Gómez et al., 2011; Ramírez-Herrejón et al., 2007; Moncayo-Estrada, 2001; Mendoza, 1962).

Sexual Ratio

Greater dominance by females was observed downstream (sites C, D and E), whereas, the headwater populations showed a nearly equal proportion for females and males. Ramírez-García et al. (2017) mentioned that for exotic species from the Teuchitlán River, female P. *bimaculatus* generally dominated throughout the year (~2:1), while, for *P. sphenops*, the sex ratio was generally ~1:1. Sex ratios tend to be 1:1 in cases where multiple factors in the aquatic system are in equilibrium (Valenzuela et al., 2003). Several authors have determined that sex ratios are equal for other species of goodeids (Silva-Santos, et al., 2016, Moncayo-Estrada et al., 2001; Ramírez-Herrejón et al., 2007). The pressures of natural selection directs populations to have equal sex ratios, providing an evolutionarily stable strategy (Maynard, 1978). However, several species in the family Goodeidae show the existence of female biased population structure (Moncayo-Estrada, 2012; Cruz-Gómez et al., 2010; Cruz-Gómez et al., 2011; 2013; Navarrete-Salgado et al., 2007). In goodeids and poeciliids (viviparous and ovoviviparous species), the sex ratio, in general, favors females in wild populations, which allows them to ensure reproduction.

Reproductive Period

The native fish species in the Teuchitlán River showed at least two reproductive peaks, depending on the portion of the river, as a reproductive strategy to adapt the variations of the habitat. However, native species presented lower abundances compared with exotic species present in the Teuchitlán River like *P. sphenops* and *P. bimaculatus,* which presented high reproductive output, and iteroparous spawning, which permits population increase and indicates effective exploitation of environmental resources (Ramírez-García et al., 2017).

Other goodeids species such as (*Alloophorus robustus, G. atripinnis, Allotoca diazi* and *Giraridinichthys multiradiatus*) the reproductive season were related to the increase in the water levels and temperature (Mendoza, 1962; Gómez-Márquez et al., 1999; Cruz-Gómez et al., 2013), as it occurs in the headwater of the Teuchitlán River.

Type of growth

The positive allometric growth of *Goodea atripinnis* and the negative allometric growth for *Z. purhepechus* and *A. splendens* can be related to variations in food availability, intra- and inter-specific competence, water temperature, and dissolved oxygen at the different sites, according to Hepher, Pruginin (1985). Exotic species present in the Teuchitlán River, *P. sphenops* and *P. bimaculatus* also showed allometric growth, however, in some sites of the river presented negative growth (headwater for *P. sphenops* and all the sites excepted B for *P. bimaculatus*) which indicate that the weight increases with a greater proportions in relation to the standard length, positive growth indicated that the organisms got highest increase in weight respect to standard length (Froese, 2006, Ramírez-García et al., 2017).

Environmental and Reproductive Variables

Gonadal maturity stages showed differences in habitat that are associated with ontogenic movements to deeper waters throughout individual development, whereas pH, and dissolved oxygen had stronger influences than temperature for mature organisms. Juveniles showed a persistent preference in downstream habitats throughout the season, which can be related to predator protection and food availability.

Goodea atripinnis is the best-established species along the river, showing a complete structure of sizes, and a frequency of gonadal stages at the five sites sampled in this study. This species matures earliest in the headwaters of the river, and later in downstream reaches, showing that the environmental conditions affect the reproduction of *G. atripinnis.* Mature individuals seem to prefer the headwaters (springs), while juvenile organisms are more frequent downstream where there is a higher proportion of mud, higher temperatures, and a higher concentration of chlorophyll a (Fig. 5).

Ameca splendens showed lower abundances in the lower portion of the river. Females mature earlier in the upstream reaches (site C), and the site D females mature in larger sizes. Males mature earliest in site B. Complete structures of sizes of *A. splendens* occurs along the river except in site E. However, mature organisms are more frequent in sites A, B and D. Two reproductive peaks in the springs and just one notable peak downstream (January to March). Immature organisms seem to prefer environmental conditions from sites A and B (clear waters, deep, more oxygen dissolved in water and pH neutral), whereas, mature organisms are related with sites D and A (higher transparency, higher depth, more hardness in water and neutral pH).

Zoogoneticus purhepechus was the least abundant species of the native species from the Teuchitlán River. Size at maturity only was evaluated in the springs, and showed that site B presented the best conditions for early maturity for both sexes. There were more mature individuals in site A, and more juveniles in site B and two reproductive peaks in site C (March to September). In the springs, one reproductive peak was from September to November. Mature organisms are related with clear and deeper waters, higher dissolved oxygen and neutral pH. Juveniles are related in sites with more turbid in water and solids dissolved in water. This is similar to the results of Ramírez-Herrejón et al. (2007), who described the reproductive habitat of Z. *quitzeoensis* in La Mintzita. This species prefers shallow waters, neutral pH, warm and clear waters with abundant vegetation. First occurs at 30 mmm SL, the sex ratio was 1:1, and fecundity ranged from 6 to 10 embryos per female and the reproductive peak was in winter.

The Teuchitlán River has been altered by the extraction of water for human uses, introduction the exotic species, which has caused habitat loss, reduction of the density of native fish populations, and low reproductive for many species in comparison to populations elsewhere. The endemic *A. splendens* and *Z. purhepechus* could be facing an elevated risk of extinction. However, our results offer a baseline data to design a management and conservation plan for the native species of the Teuchitlán River and to promote the aquaculture research of endemic species of México for conservation porpoises.

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TABLES

Tab. 1. Gonadal maturity stages of viviparous fish (Ramírez-Herrejón *et al.,* 2007).

Phase (female)	Description	Phase (male)	Description
Immature (I)	Small ovaries, length <6 mm, reaching 30-50% of the visceral cavity, with packed eggs.	Immature (I)	Fish larvae. Testis thin and yellowish occupying ~25% of the visceral cavity.
Developing eggs (II)	Ovaries longer than previous stage (10 mm), Eggs enclosed in ovarian tissue.	Developing Juvenile (II)	Turgid and yellow testis that occupy <25% of the visceral cavity.
Free eggs (III)	Ovary with free eggs and embryos (~2 mm in length). Enclosed within a common membrane.	Juvenile (III)	Turgid and yellow testis that occupy <50% of the visceral cavity.
With embryos (IV)	Ovary with embryos standard length >3.5 mm.	Immature (IV)	Whitish translucent testis that occupy ~50% of the visceral cavity. The fish reaches sexual maturation.
Ovaries after spawning (V)	The ovaries have flaccid walls and few visible eggs, with a rupture at the end of the gonad.	Mature (V)	Turgid, whitish opaque testis that occupy >50% of visceral cavity.
Ovaries in recess (VI)	Recovery after spawning, without embryos. Turgid ovaries >6 mm in length.	In recess (VI)	Flaccid and transparent testis that occupy >50% of visceral cavity. This stage corresponds to the semen ejaculation phase.

Tab. 2. Number of specimens of, *Ameca splendens*, *Zoogoneticus purhepechus* and *Goodea atripinnis* captured per site in Teuchitlán River in 2015 and 2016.

Site	*A. splendens*		*Z. purhepechus*		*G. atripinnis*	
	♀	♂	♀	♂	♀	♂
A	63	48	32	24	77	77
B	83	62	42	43	63	47
C	25	8	21	8	8	4
D	21	9	0	0	25	10
E	0	0	0	0	45	27
Total	192	127	95	75	218	165
Final total	319		170		385	

Tab. 3. First maturity size (SL, mm) by study site for *Goodea atripinnis* (Ga)*, Ameca splendens* (As) and *Zoogoneticus purhepechus* (Zp) in Teuchitlán River. ♀ = females. ♂ = males. ID= insufficient data. Logistic model: M (L) = 1 / (1 + $e^{(-aL+b)}$).

Sites	♀ Ga	♂ Ga	♀ As	♂ As	♀ Zp	♂ Zp
A	46.05	49.27	38.39	40.12	38.42	32.19
B	37.72	37.82	ID	31.95	28.03	25.03
C	30.09	36.01	27.04	ID	ID	ID
D	51.41	47.23	45.84	39.36	ID	ID
E	49.85	45.08	ID	ID	ID	ID

Tab. 4. Standard length (SL) and the relationship between SL and weight for *Goodea atripinnis*, *Ameca splendens* and *Zoogoneticus purhepechus* by females (♀) and males (♂). R^2= correlation coefficient, positive allometry* (b>3), negative allometry** (b<3).

Species	Mean±SD	*a*	*b*	R^2 $**p < 0.01$
G. atripinnis				
♀	47.26±8.2	0.13	4.11*	0.78
♂	49.59±11.75	0.12	3.89*	0.73
A. splendens				
♀	33.58±10.11	0.07	1.53**	0.80
♂	35.53±8.31	0.07	1.54**	0.81
Z. purhepechus				
♀	27.68±6.51	0.04	0.79**	0.84
♂	27.58±5.74	0.05	0.98**	0.90

Tab. 5. Physical and chemical water characteristics for dry and wet season in each study site in the Teuchitlán River, Jalisco, México, during 2015 and 2016. DO=dissolved oxygen (mg/L), Al= total alkalinity (mg/L), Cl= Chlorophyll a (µg/L), HA=total hardness (mg/L), pH=pH, TU= turbidity (NTU), SE=sedimentation, DEE=deep (cm), TRA=transparency (cm), TEM= water temperature (°C), SOL-SUS=suspended solids (mg/L), SOL-DIS=total Dissolved solids (mg/L), masl= meters over sea level.

Site	Altitude (masl)	DO	AL	CL	HA	pH	TU	SE	DEE	TRA	TEM	SOL-DIS	SOL-SUS
A	1266												
Dry		6.1±0.1	100.1±6.4	0.7±0.3	48.3±2.9	6.9±0.1	0.8±0.4	0.1±0	97.9±3.4	97.9±3.4	27.1±0.4	100.1±0.6	2.4±2.3
Wet		5.9±0.2	109.8±11.4	0.6±0.5	49.2±4.9	6.8±0.2	1.5±0.8	1.1±1.9	98.2±2.0	98.3±2.0	27.0±0.4	99.5±8.2	2.5±1.6
B	1266												
Dry		5.0±0.3	99.1±1.4	1.7±1.5	48.5±5.7	6.8±0.2	64.1±18.7	0.6±0.7	39.6±4.7	28.0±4.1	27.5±0.9	101.1±2.0	55.1±30.3
Wet		5.9±0.3	110.9±12.4	3.1±3.6	48.8±3.3	6.7±0.2	9.0±6.3	1.3±1.8	41.2±3.9	41.2±3.9	27.1±0.6	102.3±2.0	11.1±8.3
C	1266												
Dry		5.0±1.3	99.1.0±1.4	2.7±1.9	46.5±3.0	6.8±0.3	14.6±6.8	0.7±0.9	42.1±4.7	40.5±7.5	26.3±1.3	99.3±6.2	17.3±13.8
Wet		4.2±0.5	112.0±5.1	5.1±5.3	49.4±1.7	6.5±0.3	19.1±9.8	1.8±1.5	48.2±7.6	42.4±9.4	26.6±1.3	103.3±5.6	21.8±8.3
D	1265												
Dry		4.9±0.9	127.5±32.5	1.3±1.3	52.9±4.0	6.8±0.1	8.12±2.9	0.5±0.7	68.1±11.1	68.1±11.1	24.6±2.5	104.7±2.0	279.3±478.0

Wet		3.7±1.1	122.1±1.3	4.1±3.2	54.1±1.4	6.5±0.3	11.6±8.6	0.8±1.3	60.5±5.1	57.8±8.2	26.4±1.7	122.7±0.9	10.1±10.6
E	1265												
Dry		4.5±1.3	118.6±50.6	2.2±0.6	52.5±2.5	6.8±0.4	11.7±5.0	0.9±1.3	60.1±34.8	60.1±34.8	24.4±1.9	96.1±13.1	298.3±500.5
Wet		3.5±1.0	125.2±13.5	10.7±7.9	60.8±11.3	6.3±0.1	37.8±21.9	0.1±0.1	39.1±18.2	37.7±19.6	27.9±0.8	129.8±10.1	19.4±11.9

Tab. 6. Summary of reproductive cycle information on *Ameca splendens*, *Goodea atripinnis* and *Zoogoneticus purhepechus* in Teuchitlán River.

Characteristics	*Ameca splendens*	*Goodea atripinnis*	*Zoogoneticus purhepechus*
Size at reaching sexual Maturity	Females about 34.26±9.58 mm; males about 31.59±11.69 mm	43.02± 8.9 both sex	Females about 32.22±7.34 mm; males about 28.61±5.06 mm
Fecundity	6±2.66 embryos	7±1.49 embryos	6±1.59 embryos
Spawning period	March and July	March (springs) September and November (downstream)	March and November
Sex ratio (female: male)	1:1	1:1	1:1
Maximum size	Females 53.89 mm, males 52.00 mm	Females 74.89 mm, males 120.63 mm	Females 35.31 mm, males 37.95 mm
Type of growth	Negative allometric	Positive allometric	Negative allometric

Fig. 1. Location of Teuchitlán river and study sites (A, B, C, D and E).

Fig. 2. Size-frequency distribution (Standard-length) for females and males of *Goodea atripinnis* (Ga), *Ameca splendens* (As) and *Zoogoneticus purhepechus* (Zp) in Teuchitlán River.

Fig. 3. Relative frequency of gonadic maturity stages of *G. atripinnis* (Ga), *A. splendens* (As) and *Z. purhepechus* for each study sites (A,B,C,D,E) during 2015-2016 in the Teuchitlán River.

Fig. 4. Bimonthly variation in the gonadosomatic index (GSI) and condition index (K) values for each sampling sites (A, B, C, D, E) for females and males of *Goodea atripinnis* (Ga), *Ameca splendens* (As) and *Zoogoneticus purhepechus* (Zp) in Teuchitlán River.

Fig. 5. Non-metric analysis of multidimensional scaling (NMDS) for *Ameca splendens* (AS), *Zoogoneticus purhepechus* (Zp) and *Goodea atripinnis* (Ga) from Teuchitlán River. Sites (A, B, C, D, E), months (1= January, 2=March, 3=May, 4=July, 5= September, 6=November). Reproductive variables (I.II= immature and juvenile in growth fish, IV.V= Fish in mature and mature fish, GSI=Index gonadosomatic, FEC= fecundity). Physical and chemical water characteristic for each study sites (DO=dissolved oxygen, Al= total alkalinity, Cl= Chlorophyll "a", HA=total hardness, pH=pH, TU= turbidity, SE=, DEE=deep, TRA=transparency, TEM= water temperature, SOL-SUS=suspended solids, SOL-DIS=total Dissolved solids.

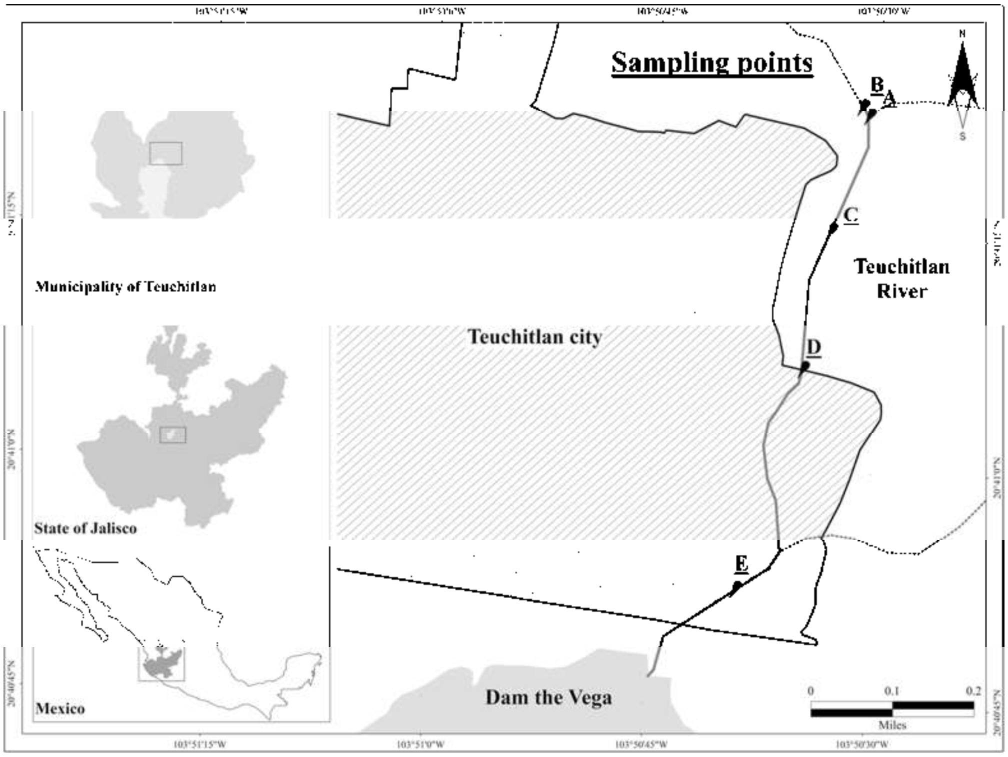

Fig. 1. Location of Teuchitlán river and study sites (A, B, C, D and E).

125x94mm (300 x 300 DPI)

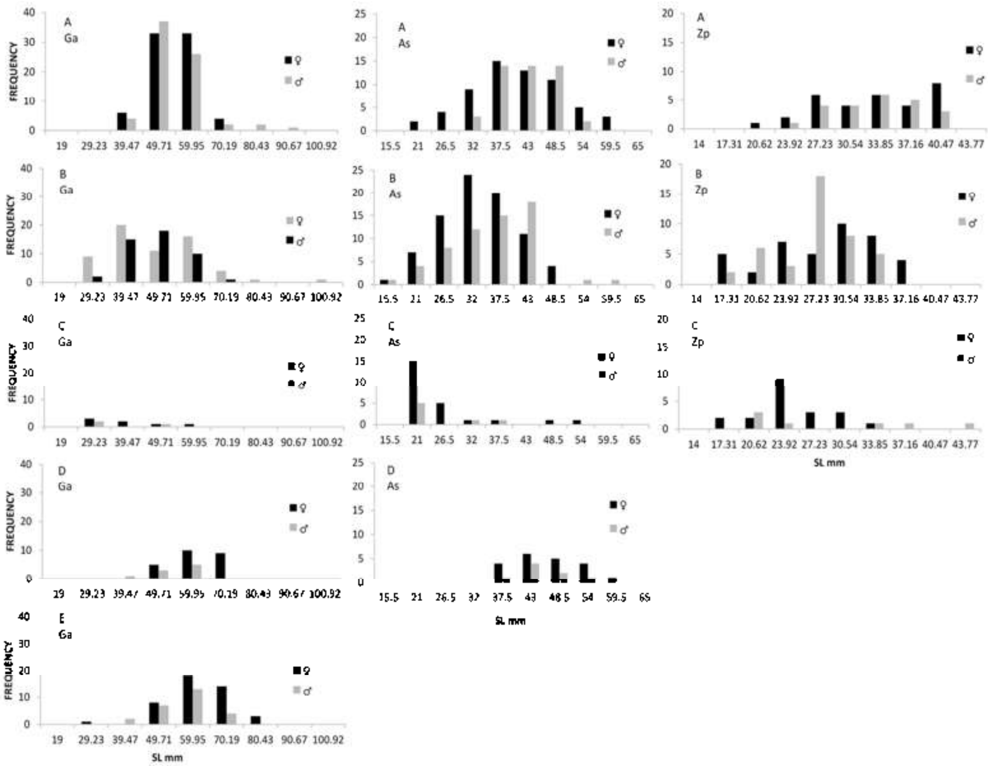

Fig. 2. Size-frequency distribution (Standard-length) for females and males of *Goodea atripinnis* (Ga), *Ameca splendens* (As) and *Zoogoneticus purhepechus* (Zp) in Teuchitlán River.

134x103mm (300 x 300 DPI)

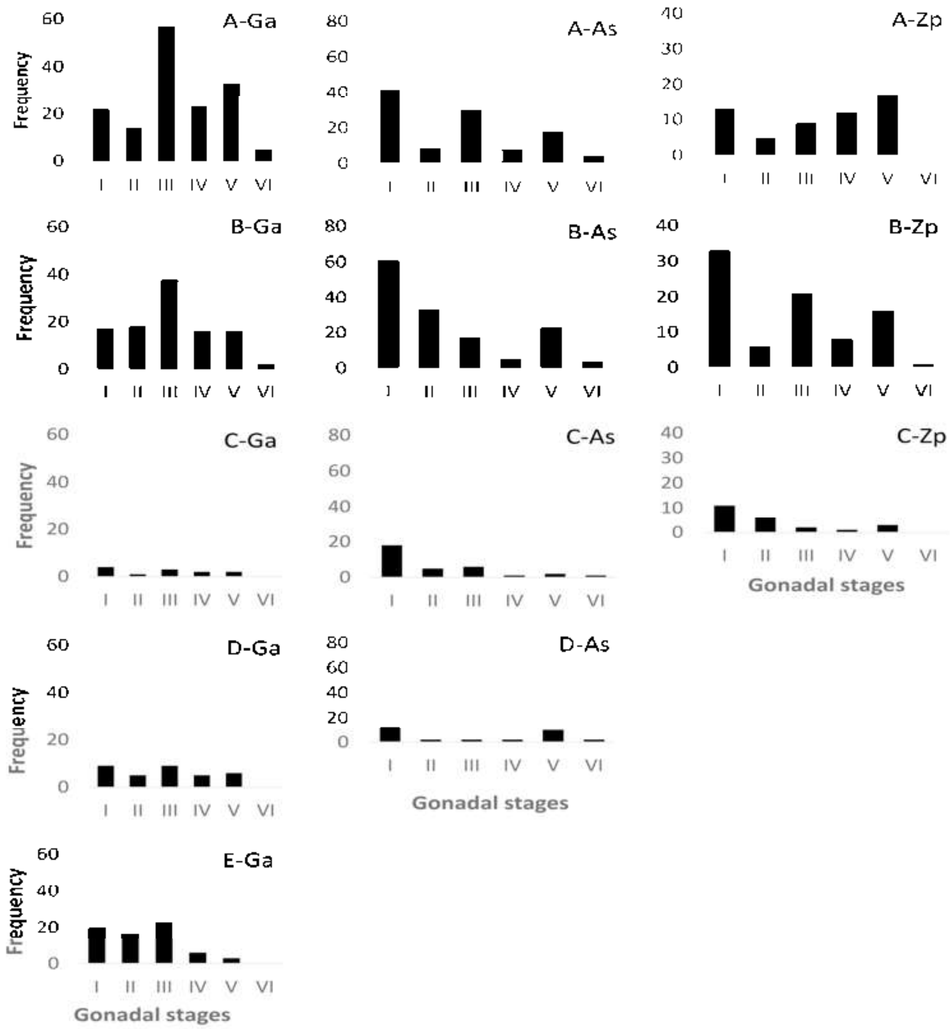

Fig. 3. Relative frequency of gonadic ma.turity stages of *G. atripinnis* (Ga), A. splendens (As) and *Z. purhepechus* for each study sites (A,B,C,D,E) during 2015-2016 in the Teuchitlán River.

184x194mm (300 x 300 DPI)

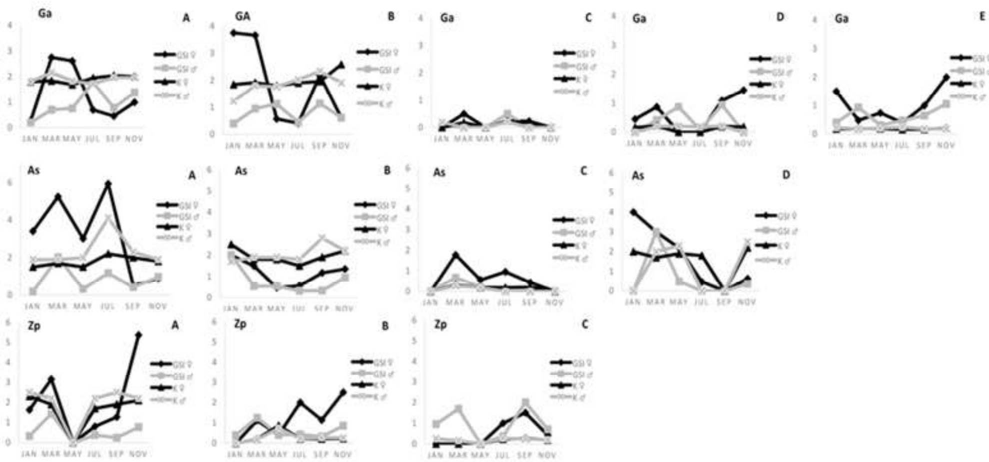

Fig. 4. Bimonthly variation in the gonadosomatic index (GSI) and condition index (K) values for each sampling sites (A, B, C, D, E) for females and males of *Goodea atripinnis* (Ga), *Ameca splendens* (As) and *Zoogoneticus purhepechus* (Zp) in Teuchitlán River.

83x38mm (300 x 300 DPI)

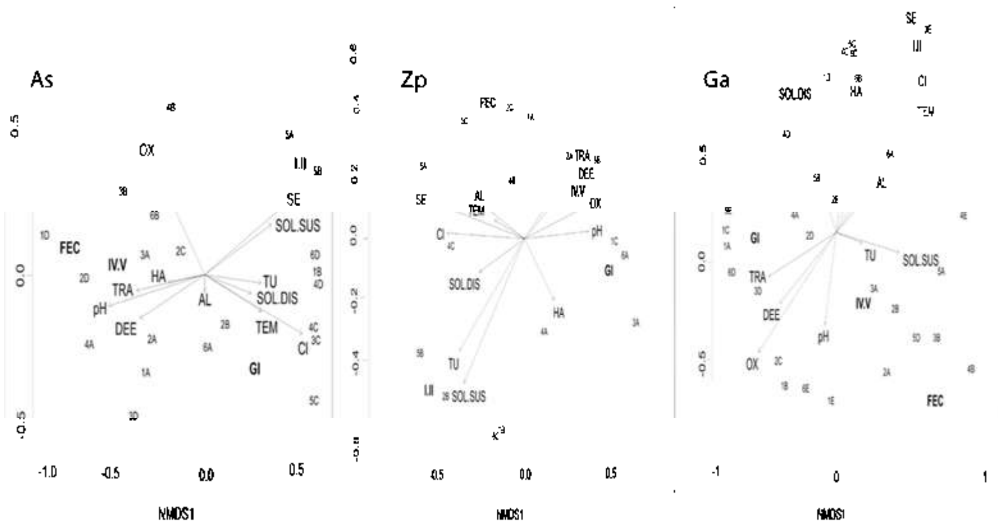

Fig. 5. Non-metric analysis of multidimensional scaling (NMDS) for *Ameca splendens* (AS), *Zoogoneticus purhepechus* (Zp) and *Goodea atripinnis* (Ga) from Teuchitlán River. Sites (A, B, C, D, E), months (1= January, 2=March, 3=May, 4=July, 5= September, 6=November). Reproductive variables (I.II= immature and juvenile in growth fish, IV.V= Fish in mature and mature fish, GSI=Index gonadosomatic, FEC= fecundity). Physical and chemical water characteristic for each study sites (DO=dissolved oxygen, Al= total alkalinity, Cl= Chlorophyll "a", HA=total hardness, pH=pH, TU= turbidity, SE=, DEE=deep, TRA=transparency, TEM= water temperature, SOL-SUS=suspended solids, SOL-DIS=total Dissolved solids.

90x46mm (300 x 300 DPI)

VII. DISCUSIÓN GENERAL

La reproducción es parte básica de la biología de todas las especies, especialmente de aquellas que se encuentran de manera nativa o endémica en su área de distribución, o especies que son exóticas dentro de un cuerpo de agua. Los peces muestran una gran variación de estrategias reproductivas y órganos reproductores únicos, tal como se encontró con las especies de este estudio. Las especies exóticas (pecílidos) son ovovivíparas, es decir, que se desarrollan dentro de la madre y su único alimento hasta la eclosión es el vitelo, se tratan de huevos provistos de yema, llamado desarrollo lecitotrofico. Mientras que los Goodeidos (especies nativas) presentan matrotrofia, en donde los embriones presentan una estructura llamada trofotenia (que son estructuras especiales que nacen de la región anal de la mayoría de las especies de esta familia) que después de que el embrión agota todo el vitelo, la madre brinda sustancias nutritivas para culminar su total desarrollo (Worms, 1981; Carrier *et al*., 2004). Otra de las diferencias entre las pecílidos y los goodeidos es el tipo de gestación, para los pecílidos el proceso embrionario se lleva a cabo dentro del fólico ovárico, (Gestación intrafolicular), mientras que para los goodeidos el proceso embrionario se lleva a cabo dentro del lumen ovárico, llamado intraluminar. Por otro lado los órganos copulatorios que usan estas dos familias es una característica que les permite el gran éxito reproductivo, para los Goodeidos es el andropodio, que es la modificación de la aleta anal que permite el paso de los espermatozoides hacia el ducto urogenital, sin haber penetración. Para los pecílidos el gonopodio, es el órgano copulatorio del macho, el cual es la modificación de los radios de la aleta anal.

Además de las estrategias reproductivas únicas de estas especies, cuentan con tácticas reproductivas que les permiten obtener mayor éxito dentro de un sistema acuático, por ejemplo, las variables reproductivas evaluadas en el presente trabajo demuestran que las especies exóticas (*Pseudoxiphophorus bimaculatus* y *Poecilia sphenops*) se encuentran bien establecidas a lo largo del río Teuchitlán, ya que fueron encontradas en todos los sitios, con una estructura de tallas bien definida y encontrando todos los estadios gonadales, desde organismo juveniles hasta organismo en reposo (es decir, que ya expulsaron las crías), las hembras alcanzan tallas más grandes que los machos, lo que es un patrón bien conocido entre organismos de la familia Pociliidae (Vargas & Sostoa, 1996). Mientras las especies nativas tienden a ser más vulnerables y menos resistentes a los disturbios antrópicos (López-López, & Paulo-Maya, 2001; Varela-Romero *et al*., 2002), produciéndoles una disminución en sus abundancias de las partes bajas (sitios D y E) del río. Respecto a las especies *Ameca splendens* y *Zoogoneticus purhepechus* únicamente presentan una estructura de tallas completa en las primeras partes del rio, manantiales (sitio A y B) y primera parte del río (Sitio C), sin embargo *Goodea atripinnis*, que es un goodeido más tolerante a los disturbios, mostro una estructura de tallas completa, desde ejemplares pequeños (crías) hasta ejemplares maduros en todo el río. La fertilidad evaluada para las especies del río Teuchitlán mostraron valores mayores para las especies exóticas (19 embriones con huevos embrionizados en promedio) comparada con las nativas (7 embriones con huevos embrionizados). Estos valores son muy bajos respecto a lo mencionado por diferentes autores para otros cuerpos de agua, como es el caso de pecílidos (Gómez-Márquez *et al.* (1999; 2011; 2016) y goodeidos (Ramírez-Herrejón *et al.,* 2007; Moncayo-Estrada 2012; Cruz-Gómez *et al.* 2013). Dentro de la proporción sexual, para los pecílidos encontramos mayor cantidad de hembras, característica de la familia poecilidae (Vargas y Sostoa 1996), siento valores similares con lo registrado por otros autores (Martínez-Trujillo, 1983; Gómez-Márquez *et al.,* 2008; Contreras-MacBeath y Ramírez, 1996; Zuñiga-Vega *et al*., 2012; Loran-Nuñez *et al*., 2013). Esta predominancia de las hembras se atribuye a la diferenciación basada en el sexo (Snelson, 1989), las hembras tienen mayores tasas de sobrevivencia debido a su mayor tamaño, peso, y color menos conspicuo que los machos, y la alta mortalidad de los machos se debe a la depredación, además que los machos presentan mayor susceptibilidad al estrés y un acelerado envejecimiento fisiológico (Rosenthal *et al.,* 2001). Para las especies nativas encontramos proporciones sexuales 1:1 en los manantiales (sitio A y B) y aguas abajo mayor cantidad de hembras (sitios C, D y E). Diferentes autores mencionan proporciones sexuales 1:1 para Goodeidos (Silva *et al.,* 2016, Moncayo-Estrada *et al.,* 2001, Ramírez-Herrejón *et al.,* 2007) lo que determinan como una población estable, sin embargo otros mencionan mayor cantidad de hembras, (Moncayo-Estrada *et al.,* 2012; Cruz-Gómez *et al.,* 2010; 2011; 2012; Navarrete-Salgado *et al.,* 2007) donde la población se encuentra en desequilibrio, a lo que atribuimos que nuestras especies nativas se encuentran en desequilibrio en las partes finales del río esto debido a la contaminación y los impactos antrópicos del sistema. Respecto a la época reproductiva, las especies exóticas presentan una táctica sorprendente, a lo largo del río y en los diferentes sitios de muestreo se están reproduciendo de manera distinta, es decir, para que sus poblaciones sean abundantes en todo el sistema, están presentando picos reproductivos en diferentes meses, estos picos están relacionados con las diferentes variables ambientales de cada sitio, mientras que las especies nativas solo presentan dos picos reproductivos al año, el más alto es el mes de marzo (primavera o estiaje), el mes donde se presentan los valores de temperatura más elevados, sin embargo, a diferencia de las especies exóticas, las especies nativas no presentan distintos picos en la época reproductiva con respecto a los sitios. Por otro lado, las especies exóticas, obtienen tallas de primera madurez entre los 25 a 30 mm de longitud patrón (LP), mientras que las especies nativas maduran entre 30 a 35 mm de LP, sin embargo a lo largo del río presentan distintos valores de maduración esto debido a que en cada sitio presenta temperaturas distintas que los hacen crecer y madurar más rápido que otras partes del río. Respecto a la relación de las variables ambientales del sistema, contra las variables reproductivas, mostro que los organismos en estadios juveniles (Estadios I y II) de las especies exóticas se ven relacionados con los manantiales (sitio A y B), donde presentan mayor claridad, profundidad y cantidad de oxígeno disuelto en agua, además de un pH neutro. Mientras los organismos maduros (estadios IV y V) se ven relacionados en la zona más baja de río (sitios D y E) donde hay menor transparencia del agua, alta cantidad de sólidos disueltos, alta turbidez y alcalinidad, la cual es producida por la descomposición de la materia orgánica, que a su vez produce gran cantidad de clorofila a, está siendo un indicador indirecto de la producción primaria, generando alimento, ya que los pecílidos son considerados como omnívoros multicadena de depredadores generalistas, lo que significa que aprovechan las cadenas alimentarias de los diferentes grupos funcionales primarios y productores, incluyendo el detritus. Esto indica la capacidad de estas especies para resistir a las fluctuaciones en la disponibilidad de alimento disponible en el medio acuático (Pollux y Reznick, 2011). Mientras que las especies nativas, tanto organismos juveniles como maduros están relacionadas con los manantiales (sitio A y B) que presentan aguas más claras, mayor profundidad, gran cantidad de oxígeno disuelto y pH neutro.

VIII. PRESPECTIVAS Y/O RECOMENDACIONES

Se ha observado que las características ambientales en el área de estudio han favorecido el desarrollo de las especies exóticas, mientras que las especies nativas tienen que adaptarse o responder a los disturbios por actividades antrópicas, por lo que estas se enfrentan a algún riesgo, pudiendo pasar a la lista de peces extintos. Nuestros resultados ofrecen una línea base para diseñar un plan de manejo y conservación de las especies nativas y control o erradicación de las especies exóticas. Ya que se han detectado sitios específicos donde hay mayor abundancia de crías e individuos maduros.

Sin embargo, se recomienda llevar acabo un monitoreo más extenso de las demás especies presentes del río, para evaluar sus aspectos reproductivos, ya que hay especies de estrategia reproductiva ovovivípara, que son tanto nativas como exóticas.

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