Ecology

Helminth parasites of *Xiphophorus birchmanni* (Teleostei: Poeciliidae) from two localities of the Pánuco River drainage, Mexico

*Helmintos parásitos de Xiphophorus birchmanni (Teleostei: Poeciliidae) de dos localidades de la cuenca del río Pánuco, México*

Christian Elizabeth Bautista-Hernández a, Griselda Pulido-Flores a, Juan Violante-González b, Scott Monks a, *

a Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Apartado postal 1-10, 42001 Pachuca, Hidalgo, México
b Laboratorio de Ecología, Unidad Académica de Ecología Marina, Universidad Autónoma de Guerrero, Gran Vía Tropical Núm. 20, Fraccionamiento Las Playas, 39390 Acapulco Guerrero, México

*Corresponding author: monks.scott@gmail.com (S. Monks)*

Abstract

Specimens of *Xiphophorus birchmanni* (Teleostei: Poeciliidae) (55 individuals) (Sheepshead swordtail) were collected from 2 localities in the Pánuco River drainage from Hidalgo and Veracruz [at Atlatipa (n = 26) and Benito Juárez (n = 29), respectively], México. The structure of the parasite communities of fish from the 2 localities was examined and compared. Helminths from 10 taxa were recovered: 6 species of larval digeneans (*Posthodiplostomum* sp., *Uvulifer* sp., *Centrocestus formosanus*, *Ascocotyle* sp., *Haplorchis pumilio*, and *Echinostomatidae gen. sp.*); 2 adult monogeneans (*Urocleidoides vaginoclastrum* and *Gyrodactylus* sp.); 1 larval cestode (metacestode stage; *Glossocercus auritus*); and 1 larval nematode, *Eustrongylides* sp. *Urocleidoides vaginoclastrum* and *C. formosanus* were the most frequent and abundant species. The remaining taxa were rare and found at low mean abundance. Component community and infracommunity differences observed in this study could be attributed to abiotic and biotic environmental factors resulting from the geographic separation of these localities during the orogeny of the Sierra Madre Oriental that restricted fish to isolated localities.

Keywords: Component community; Infracommunity; Endemic species; Sierra Madre Oriental

Resumen

Se revisaron 55 ejemplares de *Xiphophorus birchmanni* (Teleostei: Poeciliidae) (espada del tempoal), recolectados de 2 localidades [Atlatipa (n = 26) y Benito Juárez (n = 29)] de la cuenca del río Pánuco pertenecientes a los estados de Hidalgo y Veracruz, México, respectivamente. La estructura de las comunidades de parásitos fue examinada y comparada. Se reportaron 10 especies de helmintos, 6 metacercarias *Posthodiplostomum* sp., *Uvulifer* sp., *Centrocestus*
formosanus, Ascocotyle sp., Haplorchis pumilio y Echinostomatidae gen. sp.; 2 monogeneans, Urocleidoides vaginoclastrum y Gyrodactylus sp.; 1 larva de céstodo (estadio metacéstodo), Glossocercus auritus, y una larva del nemáctodo Eustrongylides sp. Urocleidoides vaginoclastrum y C. formosanus fueron las más frecuentes y abundantes, mientras que el resto de las especies fueron raras y poco frecuentes. Las diferencias observadas a nivel de comunidad e infracomunidad entre las localidades estudiadas, pueden ser atribuidas a factores bióticos y abióticos resultado de la separación geográfica de las localidades durante la orogenia de la sierra Madre Oriental, que restringe y aísla a los peces.

Palabras clave: Comunidad componente; Infracomunidad; Especie endémica; Sierra Madre Oriental

Introduction

Poeciliidae Garman, 1895, a family of live bearing fishes, is among the 10 families with the greatest number of endemic species reported in Mexican river drainages (de la Vega-Salazar, 2003). The genus Xiphophorus, included in this family, has 26 species that are distributed along the coastal plain and the slopes of the Sierra Madre Oriental, and 21 of the 26 species of this genus are endemic to Mexico. Xiphophorus birchmanni Lechner & Radda, 1987 (Sheepshead swordtail) has a restricted distribution to the downstream portions of a few tributaries of the Pánuco River and Tuxpan River drainages (Rauchenberger et al., 1990). A number of studies have been conducted on the phylogeography, behavior and the life history of this species (Gutiérrez-Rodríguez et al., 2008; Kindsvater et al., 2012; Wilson et al., 2013; Wong & Rosenthal, 2005). However, the majority of studies of X. birchmanni have focused on the species’ sympathy with a close relative, X. malinche, because natural populations of hybrids of those 2 species occur in the intermediate zones between the boundaries of the distributions of the 2 species (Cumumber et al., 2011). Those studies mainly have been dedicated to examining aspects of behavioral ecology, physiology, and genetics (Cumumber & Rosenthal, 2013; Cumumber et al., 2012; Rosenthal et al., 2003; Willis et al., 2012). This study complements those works by comparing the helminth communities of these 2 species.

Despite the interest in X. birchmanni, the helminth fauna of the species has received little attention. Bautista-Hernández, Monks et al. (2014), and Bautista-Hernández, Monks, & Pulido-Flores (2015) reported the parasite communities of 3 sympatric species, X. birchmanni, Pseudoxiphophorus bima culata and Amantitlania nigrofasciata, and compared the presence of species of helminth in terms of the origin of the fish (native or exotic) and niche and diet preferences, but did not provide detailed analyses of the structure of the populations of helminths. Bautista-Hernández, Violante-González et al. (2014) reported the helminths of a closely related congeneric species, X. malinche, from 2 populations in the upper streams of the Pánuco River drainage. The objective of the current study was to present the helminthological record for X. birchmanni from 2 localities different than those reported previously by Bautista-Hernández, Monks et al. (2014), and Bautista-Hernández, Monks, & Pulido-Flores (2015), to describe their helminth community structure, and to compare the results with corresponding data for X. malinche, sister taxa to X. birchmanni but living at opposite ends of the same drainages (upstream and downstream, respectively).

Materials and methods

A total of 55 adult specimens of X. birchmanni were collected using minnow traps. Fish were collected from 2 localities on separate rivers; the first locality, Benito Juárez, Veracruz (n = 29; 20°52'56.73” N, 98°12’14.55” W), is part of Río Zontecomatlán, and the second, Atlatipa, Hidalgo (n = 26; 21°2'17.78” N, 98°22’33.79” W), is part of Río Atlapexco. Fish were captured using minnow traps and taken alive to the laboratory of the Centro de Investigaciones Científicas de las Huastecas “Aguazarea” (CICHAZ), where they were sacrificed and internal and external organs were examined for helminths. Parasites were collected, counted, and processed according to Monks et al. (2005). Parasites were identified with the reference to original descriptions of species mentioned in previous studies of helminths of freshwater fish of the region (Arizmendi-Espinosa, 1992; Bautista-Hernández, Monks et al., 2014; Bautista-Hernández, Monks, & Pulido-Flores, 2015; Scholz & Salgado-Maldonado, 2001) and pertinent keys (Hoffman, 1999). Infection parameters were calculated and applied according to definitions proposed by Bush et al. (1997) and Bautista-Hernández, Monks, Pulido-Flores, & Rodríguez-Ibarra (2015); prevalence (percent of fish that were infected), abundance (number of helminths per examined fish ± standard deviation) and mean intensity (mean number of helminths per infected fish). Analyses were made at the levels of component community (i.e., all the helminths in all fish collected per site) and infracomunity [i.e., all the helminths in each individual host (Bautista-Hernández, Monks, Pulido-Flores, & Rodríguez-Ibarra, 2015; Zander, 2001)]. In order
to determine if the sample size was sufficient, accumulative species curve was plotted and the observed values fitted to the Clench Model to assess an asymptotic trend (Bautista-Hernández et al., 2013; Magurran, 2004). The non-parametric species richness estimator Bootstrap was calculated to estimate the number of missing species for each component community (Poulin, 1998). To describe the component community, the total number of species of helminth, the total number of individual helminths, the Simpson index (H), as a measure of diversity, and the Berger-Parker Index, as a measure of numerical dominance, were used (Magurran, 2004). We used the Jaccard index and Morisita-Horn index to compare the component communities between localities qualitatively and quantitatively (Magurran, 2004). Infracommunity level parameters were described by using the mean number of species of helminth per fish, the mean number of individual helminths, and the mean Brillouin Diversity Index value per host. Differences in abundance for species recorded in the 2 localities were evaluated using χ²-test.

Voucher specimens of helminths were deposited in the Colección Nacional de Helmintos (CNHE-11056-11063), Universidad Nacional Autónoma de México, México D.F.

Results

Ten species of helminth were recovered from fish inhabiting the 2 sampled sites. The helminthological record enlisted 6 species of larval digenean (metacercariae) (Posthodiplostomum sp., Uvulifer sp., Centrocestus formosanus, Ascocotyle sp., Haplorchis pumilio, and Echinostomatidae gen. sp.), 2 species of monogenean (Urocleidoides vaginoclaustrum and Gyrodactylus sp.), a larval cestode (metacestode stage; Glossocercus auritus), and a larval nematode (Eustrongylides sp.).

The cumulative species curve and the nonparametric species richness estimator value indicate that the inventory for both localities can be considered nearly complete (bootstrap: Benito Juárez = 10.95; Atlatipa = 3.12). In the locality of Benito Juárez, the non-parametric estimator predicted that 1 more species of helminth should be present in that population of fish. Statistical analysis showed no significant difference in either abundance of parasite species between localities or in the correlations with host size.

The fish of Benito Juárez harbored 10 species of helminths: Posthodiplostomum sp., Uvulifer sp., C. formosanus, Ascocotyle sp., H. pumilio, Echinostomatidae gen. sp., U. vaginoclaustrum, Dactylogyrus sp., G. auritus, and Eustrongylides sp. At the component community level, C. formosanus was the most abundant species, infecting 100% of the fish with a mean of 42 worms per host. The second most abundant species was U. vaginoclaustrum, with a prevalence of 100%, with 12.6 worms per fish. The remaining species were rare, infrequent, and with very low abundance values (Table 1). At the level of the helminth

| Table 1 |
| Ecological quantitative parameters for the helminths of Xiphophorus birchmanni from 2 localities in the Pánuco river drainage. Note: N = number of fish collected; n = total number of helminths collected; % = prevalence; Ab. = abundance; I.P. = mean intensity. |

<table>
<thead>
<tr>
<th>Helminths (site infection)</th>
<th>Benito Juárez (N = 29)</th>
<th>Atlatipa (N = 26)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval Digenea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centrocestus formosanus (gills)</td>
<td>1,263 96.6 42.1 43.5</td>
<td>291 84.6 11.1 13.2</td>
</tr>
<tr>
<td>Uvulifer sp. (skin and fins)</td>
<td>3 10 0.1 1</td>
<td>3 7.6 0.11 1.5</td>
</tr>
<tr>
<td>Ascocotyle sp. (intestinal wall)</td>
<td>9 6.6 0.3 4.5</td>
<td></td>
</tr>
<tr>
<td>Haplorchis pumilio (base of fins)</td>
<td>67 16.6 2.2 13.4</td>
<td></td>
</tr>
<tr>
<td>Echinostomatidae gen. sp. (mesentery)</td>
<td>6 20 0.2 1</td>
<td></td>
</tr>
<tr>
<td>Posthodiplostomum sp. (mesentery)</td>
<td>3 10 0.1 1</td>
<td></td>
</tr>
<tr>
<td>Larval Cestoda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glossocercus auritus (mesentery)</td>
<td>1 3.3 0.03 ---</td>
<td></td>
</tr>
<tr>
<td>Monogenea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gyrodactylus sp. (fins)</td>
<td>2 3.3 0.06 ---</td>
<td></td>
</tr>
<tr>
<td>Urocleidoides vaginoclaustrum (gills)</td>
<td>377 96.6 12.5 13</td>
<td>546 100 21 21</td>
</tr>
<tr>
<td>Larval Nematoda</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eustrongylides sp. (mesentery)</td>
<td>5.0 16.6 0.1 1</td>
<td></td>
</tr>
</tbody>
</table>
infracommunities, of the 29 fish that were necropsied, 8 individuals harbored at least 2 species of helminths, 16 fish were infected with 3 species of helminths, and 5 of the 29 fish harbored more than 4 species. The total number of individuals of all parasite species per host varied from 1 to 200, with a mean number of helminths per host of 60 ± 51. The mean number of species per host was 2.9 ± 0.75. The Brillouin index ranged from 0.25-1.08 with a mean diversity value of 0.58 ± 0.21. The Berger-Parker dominance index values ranged from 0.40-0.93 (0.68 ± 0.16).

In Atlatipa, fish were infected with only 3 species; *U. vaginoclastrum*, *C. formosanus*, and *Uvulifer* sp. (Tabla 1). The monogenean and the metacercarie of *C. formosanus* represent the species with the highest prevalence (100% and 84%, respectively). *Uvulifer* sp., was found rarely and infrequently. The total number of individual helminths per host ranged from 1 to 67, with a mean number of 32.3 ± 15.2 individuals per fish. At the infracommunity level, 3 of the 26 fish necropsied harbored 1 species of helminth, 22 were infected with 2 species of helminth and just 1 fish was parasitized with 3 species. The mean number of species per host was 1.9 ± 0.39. The Brillouin index values ranged from 0.00-0.64 with a mean diversity value of 0.43 ± 0.19 and the Berger-Parker dominance index values ranged from 0.5-1 (0.75 ± 0.15).

The fish studied herein belong to the same species, but we observed a difference in parasite richness between localities. Only 3 of the 10 species were shared between component communities: *U. vaginoclastrum*, *C. formosanus*, and *Uvulifer* sp., resulting in a Jaccard value of 0.3 and a Morisita-Horn value of 0.70. The Simpson index values were similar in both component communities (Benito Juárez = 0.42; Atlatipa = 0.45), despite the fact that the component community of Benito Juárez had the highest species richness and that fish from Atlatipa harbored only 3 species. The Berger-Parker dominance index (d) values were 0.72 in Benito Juárez, dominated by *C. formosanus*, and 0.65 in Atlatipa, dominated by *U. vaginoclastrum*.

**Discussion**

All species of helminths listed herein have been recorded previously in freshwater fishes of Mexican river drainages, including in fishes of the Pánuco River drainage (Bautista-Hernández, Monks et al., 2014; Salgado-Maldonado, 2006; Salgado-Maldonado et al., 2004) except the metacercarie of *H. pumilio*. This is the first time this species has been reported in the Pánuco River drainage and the first report of it infecting a species of *Xiphophorus*.

Eight of the 10 species reported in this study were represented by larval stages; as adults, all are parasites of fish-eating birds that serve as their definitive host. *Centrocestus formosanus* and *H. pumilio* are exotic species in México. These 2 species were introduced to Mexico along with the snail *Melanoides tuberculata* as a food resource for *Mylopharyngodon piceus*, a carp that also was introduced into the country for economic, fish-farming purposes (López-Jiménez, 1987). Many studies have focused on *C. formosanus* due to its importance as a widespread exotic species inhabiting many freshwater bodies in México, and for its relationship to fish aquaculture (Arizmendi-Espinosa, 1992; López-Jiménez, 1987; Scholz & Salgado-Maldonado, 2000). More recently, the metacercarie of *Haplorchis pumilio* have been found parasitizing native freshwater fishes in Mexico (Salgado-Maldonado et al., 2005; Scholz & Salgado-Maldonado, 2001; Vidal-Martínez et al., 2001). Until now, only 8 species of fish had been reported infected with this metacercarie; *X. birchmanni* now is added to this list. *Ascocotyle* sp., *Uvulifer* sp., and *Posthodiplostomum* sp. are generalists that are widely distributed in México due to the mobility of their final host, piscivorous birds. Salgado-Maldonado et al. (2004) found that *Posthodiplostomum minimum* was a common parasite of fishes in the Pánuco river drainage, infecting 10 species. *Uvulifer ambloplitis* has been found in just 4 species of fish of the region, and metacercarie of the *Ascocotyle* complex, *Ascocotyle* (*Ascocotyle*) *tenuicollis*, in just 1 species. Although the larvae Echinostomatidae gen. sp. could not be identified to the species level, digeneans of this family is known to use freshwater fishes as a second intermediate host, primarily through infection of fish-eating birds, as well as through mammals and reptiles (Hernández-Hernández, 2008).

*Glossocercus auriatus* and *Eustrongylides* sp. also are parasites of fish-eating birds, but they are less widely distributed than the metacercarie mentioned above. Metacestodes of *Glossocercus* have been recorded before in the state of Hidalgo (Monks et al. [2005] reported *Glossocercus* sp.; Scholz & Salgado-Maldonado [2001] reported *G. auriatus*) with a low prevalence and abundance (a mean of 1 worm per fish). Scholz & Salgado-Maldonado (2001) suggested that *G. auriatus* could have a narrow definitive host specificity, limited to herons (*Egretta* and *Casmerodius*); however, since our specimens could not be identified to species, no hypotheses about specificity can be made. This is the first record of a species of *Glossocercus* infecting a species of *Xiphophorus* from the Pánuco drainage. *Eustrongylides* sp. has a wider distribution in Mexican drainages, but in the Pánuco River drainage larvae of the species have been reported.
previously from only 2 species, *Herichthys labrideris* and *Poecilia mexicana* (Salgado-Maldonado et al., 2004).

*Urocleidoides vaginoclaustrum* was originally described from introduced aquarium fish *X. hellerii* in India; however, recently studies had been expanded its distribution to others host in Mexican drainages. So far, it has been found infecting mainly poeciliids, such as, *X. hellerii* (Mendoza-Franco et al., 2015; Mendoza-Palmero & Aguilar-Aguilar, 2008), *Pseudoxiphophorus bimaculata* (Salgado-Maldonado et al., 2014), *X. malinche* (Bautista-Hernández, Monks et al., 2014) and *X. birchmanni* (present work), but recently it had been recorded from the profundulid *Profundulus labialis* (Mendoza-Franco et al., 2015).

*Gyrodactylus* is a widely distributed genus of monogeneans that infect freshwater fishes. Due to its strict host and niche specificity, this genus typically is highly diverse. García-Vásquez et al. (2015) and Rubio-Godoy et al. (2010) have worked extensively working in the description of new species of *Gyrodactylus* infecting poeciliids in Mexican drainages; to date, there are 11 known species, parasitizing 4 species of poeciliid (*Xiphophorus hellerii*, *Pseudoxiphophorus bimaculata*, *Poecilia mexicana*, and *Poecilopsis gracilis*). Furthermore, García-Vasquez et al. (2015) reported the presence of up to 6 species of *Gyrodactylus* in a single species of host, suggesting that there exists a vast hidden diversity of parasites infecting this family of freshwater fish. In the Pánuco River drainage, the only record is of *Gyrodactylus* sp., infecting *Astyanax mexicanus* (Salgado-Maldonado et al., 2004), but those authors suggested that this unidentified species could be specific to characids.

The specimens assigned to Echinostomatidae gen. sp. cannot be dealt with further because they could only identified to the family; we assume that they are members of the same species but the validity of this assumption was not tested. For the same reason, we also cannot provide comparative data because of the differences in life-cycles of the members of the genus in México. Further collections and identification using molecular markers would be necessary to identify the species reported herein.

Component communities of the same species of host often share species of parasites but rarely have an identical species composition (Valtonen et al., 2001). In the present study we found that *X. birchmannii* had a distinct component community in each locality. Fish from Benito Juárez harbored 10 species of helminth and fish from Atlatipa were infected with just 3 species. Although the Simpson index indicated similar diversity of the two populations (Benito Juárez = 0.42; Atlatipa = 0.45), the localities share only 3 parasite species (*J* = 0.3), emphasizing that the Simpson index was biased by the dominant species (Magurran, 2004). Thus, as suggested by Valtonen et al. (2001) these assemblages of component communities were influenced and maintained by the pool of both current and locally-available species of helminth, driven by the biotic and abiotic factors on the availability of intermediate and definitive hosts.

At the infracommunity level, *X. birchmannii* harbored species-poor infracommunities; each individual host had, on average, 2 species of parasites, and each was dominated by 1 species, an autogenic species (*U. vaginoclaustrum*) in Atlatipa and an allogenic species in Benito Juárez (*C. formosanus*). Previous studies (Martínez-Aquino et al. 2004, 2007; Pineda-López et al., 2005) suggested that species-poor infracommunities that are dominated strongly by an allogenic species is a common pattern in freshwater fish in Mexico due to the trophic position of the small fish in the food web as prey of many species of piscivorous birds that disperse the generalist parasite species. This is true for the host population of Benito Juárez, which is dominated by *C. formosanus*. However, this prediction does not fit the results found in Atlatipa, where the dominant species was an autogenic, specialist species, *U. vaginoclaustrum*; this demonstrates how parasite communities can be influenced by locally-available species.

The helminth fauna of fish of the Pánuco River drainage is interesting to parasitologists because of the complexity of the populations of fish; however, the majority of the studies have not gone beyond simple lists of helminths parasites of different species of fish from this region (Salgado-Maldonado et al., 2004), or the description of new species (Bautista-Hernández, Monks, Pulido-Flores, & Miranda, 2015; Caspeta-Mandujano et al., 2001; Falcón-Ordaz et al., 2015), and few studies have focused on the analysis of parasite communities.

Bautista-Hernández, Monks et al. (2014), and Bautista-Hernández, Monks, & Pulido-Flores (2015) described the communities of 3 species, including *X. birchmannii*, contrasting the helminth communities of a native species of fish with an introduced species in sympathy. Those authors reported 3 species of helminth infecting *X. birchmannii*, a monogenean, *U. vaginoclaustrum*, and two metacercariae, *Uvulifer* sp. and *C. formosanus*, in communities that were highly dominated by the monogenean. However, the 2 localities that they sampled belong to streams of the Pánuco River drainage (San Pedro and Huiznopala), where it was discovered later that the identification of specimens of *X. birchmannii* was problematic due to the potential presence of hybrid specimens of *X. malinche* and *X. birchmannii* in those populations (Culumber et al., 2011; Rosenthal et al., 2003). The specimens of *X. birchmannii* (collected in 2008) for the study of Bautista-Hernández, Monks et al. (2014), and Bautista-Hernández,
Monks, & Pulido-Flores (2015) were identified using only morphological characters, which did not suggest evidence of hybridization at San Pedro nor at Huitznopala. However, in a study of reproductive and mating behavior of females using molecular markers, Paczolt et al. (2015) detected the presence of hybrid individuals at San Pedro.

Some studies have reported significant differences in parasite communities between parental species and their hybrids (El Gharbi et al., 1992; Moulia, 1999; Šimková et al., 2013). Since only morphological characters had been used for identification of the fish, we could not assume that the samples from 2008 were pure X. birchmanni. Thus, for this study we sought to add additional populations where hybridization was not probable, such as the localities studied herein. As such, the results of the present study of X. birchmanni and the comparisons with X. malinche, reported previously by Bautista-Hernández, Monks et al. (2014), represent records of parasite communities from pure populations of the parental species.

Bautista-Hernández, Monks et al. (2014) recently described the component communities of genetically-pure populations of X. malinche, a closely related species (Cui et al., 2013), in 2 localities in Hidalgo (Chicayotla and Malila). In Chicayotla, 4 species were reported (Uvulifer sp., U. vaginoclastrum, Schyzocotyle acheilognathi, and Rhabdocoelobora xiphophori) and in Malila, 3 species (Paracreptotrema rosenthali, R. xiphophori, and U. vaginoclastrum). Although populations of X. malinche and X. birchmanni inhabit the same streams of the Pánuco drainage, pure populations are confined to different altitudes; X. malinche is restricted to highland streams, while X. birchmanni is found at lower elevations (Culumber et al., 2011) (populations containing hybrids are found in the junction of the 2 species). As had been observed, these 2 species have distinct helminth communities as a result of more than just having different specific identities. The former species had communities harboring 4 adult species of the 5 species that were reported and the latter had communities comprised mostly of larval stages (8 of 10 species).

Garrido-Olvera et al. (2012) observed a positive correlation between the geographic distribution (range) of hosts and their helminth species richness and argued that one of the most important factors that determine the composition of helminth communities in freshwater fish in México is the geographic range of the host. Thus, species with broad distributions had richer assemblages than those with a limited distribution because the members inhabit more localities and feed on a wider variety of prey. As well, the latter populations are exposed locally to colonization by more species of parasite than fishes with a narrow distribution. Culumber et al. (2011) reported that X. malinche is confined to fewer localities in the Pánuco drainage than X. birchmanni. Thus, according to the hypotheses of Garrido-Olvera et al. (2012), the difference in the distribution of these 2 species of fish is an important factor contributing to the differences in the structure of their helminth communities.

Finally, it has been shown that there is a correlation between altitude and species richness in most taxa (Laakkonen et al., 2003); a factor that could contribute to the differences in the helminth communities of the 2 species is a greater availability of intermediate hosts in downstream localities compared to upstream ones. Blasco-Costa et al. (2013) observed a correlation between the abundance of digeneans infecting fish and river flow, and found that parasites were more abundant downstream, which they attributed to the downstream flow of water favoring the displacement and dispersion of invertebrates (including both intermediate hosts and infective stages of the helminths). The helminth communities in the Pánuco River drainage reflect this pattern; X. birchmanni (in Benito Juárez, a downstream locality) harbored a richer community of helminths than fish in the upstream locality X. malinche in Malila), as would be expected if there was a greater diversity of invertebrate intermediate hosts.

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