

Helminth Parasites of Viviparous Fishes in Mexico

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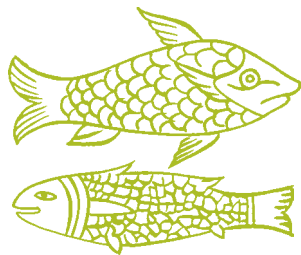
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Abstract

This study is aimed at collecting the extant published data on the helminth parasites of the Mexican Goodeidae and Poeciliidae, as well as contributing original data from the author's research, with the end of describing the taxonomic composition of this fauna and exploring their evolutionary and zoogeographic origins. The parasitological data in this study cover 9 goodeid species from 7 genera, and 20 poeciliid species from 6 genera, collected from the Lerma, Santiago, Pánuco, Balsas, Ayuquila, and Grijalva-Usumacinta basins as well as from the Yucatán Peninsula, Mexico. A total of 32 helminth species were recorded in the collected goodeid fish species. The data demonstrate that *Posthodiplostomum minimum* (MacCallum, 1921) and *Clinostomum complanatum* (Rudolphi, 1814) metacercariae are frequent in the goodeids. The most abundant helminth record in the collected goodeid host species was found in *Goodea atripinnis*, which had 16 helminth species, and in *Girardinichthys multiradiatus* and *Allophorus robustus*, which each had 13 helminth species. A total of 46 helminth species were recorded in the 20 collected poeciliid fish. The metacercariae of *Posthodiplostomum minimum* (MacCallum, 1921) and *Centrocestus formosanus* (Nishigori, 1924) are very frequent in Mexican poeciliids. The host species *Poecilia mexicana* was found to have the most abundant helminth community, with 24 species. The data indicate 4 components that determine helminth parasite community composition in these fish families, which are described below in order of the number of helminth species in each component. 1) Generalist, allogenic, mostly Nearctic helminth species. They have colonized goodeids and poeciliids as secondary intermediate hosts or paratenic hosts and conclude their lifecycle in birds. 2) Helminth species commonly associated with other fish species. Goodeid and poeciliid species have acquired these via sympatry with other fish species. 3) Anthropogenically introduced helminth species. 4) Specialist helminth species. These appear to restrict their parasitic relationship to goodeid or poeciliid fish. They have developed, or evolved, together with their hosts and are probably endemic or ancient species. The data presented here also indicate the numerical predominance of trematode and nematode species, the low representation of monogeneans and cestodes, and only a few species records for the acanthocephalan group. A large allogenic component is also characteristic of helminth communities in Mexican freshwater fish. The helminth communities recorded in Poeciliidae were notably richer than those observed in the Goodeidae.

Resumen

El presente estudio recaba datos bibliográficos y otros originados de nuestras propias investigaciones, para describir la composición taxonómica de las comunidades de helmintos parásitos de peces de las familias Goodeidae y Poeciliidae de México, y explorar sus orígenes evolutivos y zoogeográficos. Los datos parasitológicos que se presentan incluyen 9 especies de goodeidos de 7 géneros y 20 especies de poecílicos de 6 géneros, recolectados de las cuencas de los ríos Lerma, Santiago, Pánuco, Balsas, Ayuquila y Grijalva-Usumacinta, así como de los cuerpos de agua de la Península de Yucatán. Se registran un total de 32 especies de helmintos parásitos de goodeidos. Los datos demuestran que las metacercarias de *Posthodiplostomum minimum* (MacCallum, 1921) y las de *Clinostomum complanatum* (Rudolphi, 1814) son frecuentes entre los peces de esta familia. El registro helmintológico más abundante entre las especies de goodeidos examinadas lo presentó *Goodea atripinnis* con 16 especies de helmintos, en tanto que *Girardinichthys multiradiatus* y *Allophorus robustus*, presentaron cada una 13 especies de helmintos. En las 20 especies de poecílicos se registraron 46 especies de helmintos las metacercarias de *Posthodiplostomum minimum* (MacCallum, 1921) y de *Centrocestus formosanus* (Nishigori, 1924) son los helmintos más frecuentes entre los poecílicos de México. *Poecilia mexicana* es la especie de hospedero con mayor número de especies de helmintos, con 24 especies. Pueden distinguirse 4 componentes de estas comunidades, por orden del número de especies que incluyen, éstos son: 1) componente de especies generalistas, alogénicas, en su mayoría neárticas, que han colonizado a los goodeidos y poecílicos como hospederos intermediarios secundarios o bien, como hospederos paraténicos, y que concluyen su ciclo de vida en aves. 2) Especies de helmintos adquiridas por simpatria con otras especies de peces; estas especies son comunes en otros grupos de peces. 3) Especies introducidas antropogénicamente. 4) Especies especialistas de helmintos. Éstas se han desarrollado con sus hospederos y probablemente son endémicas y muy antiguas. Los datos también muestran la predominancia numérica de las especies de tremátodos y nemátodos; el número reducido de especies de monogéneos y céstodos, en tanto que sólo se registró una especie de acantocéfalo. Un componente numeroso de especies alogénicas es también una característica común entre los helmintos parásitos de peces de agua dulce de México. Finalmente, es notable que las comunidades de helmintos de los Poeciliidae son mucho más ricas que las de los Goodeidae.



Introduction

Viviparous fish in Mexico belong to the families Goodeidae and Poeciliidae, both in the order Cyprinodontiformes. The Goodeinae is endemic to the Mexican plateau and is currently composed of 16 genera, including: *Allodontichthys*, *Allophorus*, *Allotoca*, *Ameca*, *Ataenobius*, *Chapalichthys*, *Characodon*, *Girardinichthys*, *Goodea*, *Hubbsina*, *Ilyodon*, *Skiffia*, *Xenophorus*, *Xenotaenia*, *Xenotoca* and *Zoogoneticus*. The Poeciliidae are neotropical in origin and are widely distributed, ranging from the southern United States to Argentina. Several genera of Poeciliids have been recorded in Mexico: *Belonesox*, *Brachyrhaphis*, *Carlhubbsia*, *Gambusia*, *Heterandria*, *Phallichthys*, *Poecilia*, *Poeciliopsis*, *Priapella*, *Xenodexia*, and *Xiphophorus* (Espinoso-Pérez *et al.*, 1993).

Data on the helminth parasites of some Mexican goodeids and poeciliids have been published as part of the general inventories of helminths of freshwater fish (Moravec *et al.*, 1995a,b; Scholz *et al.*, 1995a,b, 1996; Salgado-Maldonado *et al.*, 2001a,b, 2004a,b; Aguilar-Aguilar *et al.*, 2004; Martínez-Aquino *et al.*, 2004). Taxonomic treatments of a particular helminth species have also been published (Pérez, 2001). The parasitology of these fish families, however, has not been addressed holistically, and the available data have not been analyzed as a whole. In response, this study is aimed at collecting the extant published data on the helminth parasites of the Mexican Goodeidae and Poeciliidae, as well as contributing original data from the author's research, with the end of describing the

taxonomic composition of this fauna and exploring their evolutionary and zoogeographic origins.

Materials and Methods

The data included in the results section comes from the freshwater fish helminth parasite database for Mexico assembled by the second author of this study and financed by the National Commission for Study and Exploitation of Biotic Resources (Comisión Nacional para el Estudio y Aprovechamiento de los Recursos Bióticos –Conabio). This database will be available on the Conabio webpage (www/http.conabio.xolo.mx), and portions of these data have been published previously as inventories (Scholz *et al.*, 1995a,b, 1996; Moravec *et al.*, 1995a,b; Salgado-Maldonado *et al.*, 2001a,b, 2004a,b; Aguilar-Aguilar *et al.*, 2004). Original data from the authors' own research is also included in the present study.

Data were collected by catching goodeid and poeciliid fish in chosen locations in a number of the hydrological basins of Mexico, including the Lerma, Santiago, Pánuco, Balsas, Ayuquila in the Sierra de Manantlán, Grijalva-Usumacinta and surface waters of the Yucatán Peninsula. The collected fish were kept alive until helminthological examination was done 8 hours after capture. The examination included all organ systems, except the blood and bones. Data on the number of helminth species and number of helminth individuals per species were recovered during the examinations. Every helminth

found in every fish host was counted and samples were taken for morphological study and taxonomic determination (see Salgado-Maldonado, 1979). Details of the methodology, and collection dates and locations can be found in Salgado-Maldonado *et al.*, 2001a,b, 2004a,b; Aguilar-Aguilar *et al.*, 2004. Taxonomic determinations for monogeneans, trematodes, cestodes, nematodes and acanthocephalans were validated with the help of the taxonomic specialists E. Mendoza Franco (Cinvestav-IPN Unidad Mérida [monogeneans]), F. Moravec (nematodes), and T. Scholz (Academy of Sciences of the Czech Republic [cestodes and metacercariae]). Vouchers of all collected helminth species were deposited in the National Helminth Collection of the Institute of Biology, National Autonomous University of Mexico; the Parasite Collection of the Autonomous University of Querétaro; the Parasitological Collection of the Autonomous University Juárez of Tabasco; and the Parasitological Collection of the Academy of Sciences of the Czech Republic (IPCAS).

Results

The parasitological data in this study cover 9 goodeid species from 7 genera, and 20 poeciliid species from 6 genera, collected from the Lerma, Santiago, Pánuco, Balsas, Ayuquila, and Grijalva-Usumacinta basins as well as from the Yucatán Peninsula (Tables 1 and 2).

Goodeidae

A total of 32 helminth species were recorded in the collected goodeid fish species. These included 5 adult trematodes and 8 metacercariae; 1 monogenean; 2 adult cestodes and 6 metacestodes; 4 adult nematodes and 5 larvae, and 1 cystacanth (Table 1). Of these 32 species, 26 (81%) were found in the Lerma and Santiago, 11 (34%) in the Ayuquila, 4 (12%) in the Balsas, and only 1 (3%) in the Pánuco. All the helminths collected from goodeids in the Ayuquila, Balsas and Pánuco rivers were also present in the fish from the waters of the Lerma and Santiago basins. The only exception were five species recorded from the Ayuquila and not found in the Lerma-Santiago: the trematodes *Dendrorchis* sp., *Saccocoelioides* cf. *sogandaresi* Lumsden, 1961, *Magnivitelinum simplex* Kloss, 1966, *Ascocotyle* (*Ascocotyle*) *tenuicollis* Price, 1935, and the nematode *Capillaria cyprinodonticola* Huffman and Bullock, 1973.

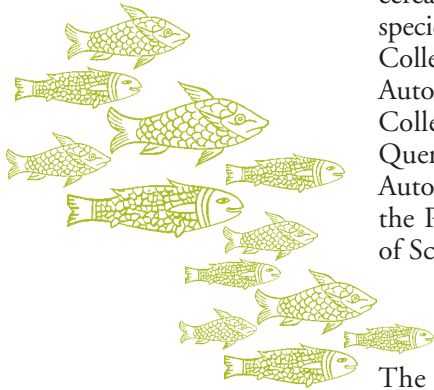
The data demonstrate that *Posthodiplostomum minimum* MacCallum, 1921, and *Clinostomum complanatum* Rudolphi, 1814, metacercariae are frequent in the goodeids, with the former parasitizing 7 fish species and the latter 6 fish species. The cestode *Bothriocephalus acheilognathi* Yamaguti, 1934, was recorded in 5 goodeid fish species, while the adult trematode *Margotrema bravoae* Lamothe-Argumedo, 1970, the nematode *Rhabdochona lichtenfelsi* Sánchez-Álvarez, García-Prieto and Pérez, 1998, and the *Spiroxys* sp. nematode larvae all parasitize 4 goodeid species. The nematode *R. lichtenfelsi* was recorded in goodeids from 4 of the studied hydrological basins.

The most abundant helminth record in the collected goodeid host species was found in *Goodea atripinnis*, which had 16 helminth species, and in *Girardinichthys multiradiatus* and *Allophorus robustus*, which each had 13 helminth species. The remaining goodeid species had from 2 to 10 helminth species (Table 1).

Of the 32 helminth species, 50% are autogenic, they complete their lifecycle in the same body of water, and the other 50% are allogenic, mainly maturing in birds. Almost all the helminths recorded in goodeids are widely distributed generalists and have been recorded in other host species. Two nominal helminth species are exclusive to goodeids: *Margotrema bravoae* and *Rhabdochona lichtenfelsi*. There is also a clearly distinguishable anthropogenically introduced component in the goodeids of the Mexican highland plateau, which includes *C. formosanus* metacercariae, the monogenean *Gyrodactylus* cf. *elegans* von Nordmann, 1832, the cestode *B. acheilognathi*, and the nematode *Pseudocapillaria tomentosa* Dujardin, 1843.

Poeciliidae

A total of 46 helminth species were recorded in the 20 collected poeciliid fish species, including 2 adult trematodes, 21 metacercaria, 5 monogeneans, 1 adult cestode, 6 metacestodes, 4 adult and 5 larval nematodes, 1 acanthocephalan, and 1 cystacanth (Table 2). Of the 46 helminth species, 23 (50%) were found in the Grijalva-Usumacinta, 20 (43%) in the Pánuco, 17 (37%) from the Yucatán Peninsula, 13 (28%) in the Balsas, 14 (30%) in the Papaloapan, 11 (24%) in the Ayuquila, and 10 (22%) in the Lerma-Santiago. Some of the helminth species collected from poeciliids from the Yucatán Peninsula are not present in other hydrological basins, includ-



ing *A. ? astorquii*, *A. (Leighia) megacephala*, *A. (Phagicola) diminuta*, *D. papillifera* and *Falcaustra* sp. The same is true of poeciliids from the Grijalva-Usumacinta basin, the only basin in which *P. bychowskyi*, *R. ondatrae*, *D. (Austrodiplostomum) compactum*, *E. leopoldinae*, *A. (Leighia) chandleri*, *A. (L.) mcintoshii*, *A. (Phagicola) macrostoma*, *A. (P.) mollienicolae*, Proterodiplostomidae, *S. seculus*, *U. reticulatus* and *Gnathostoma* sp. were recorded. Overall, 20 helminth species were only found in the poeciliids of southeast Mexico, *i.e.* those from the Yucatán Peninsula or Grijalva-Usumacinta basin (particularly in Tabasco), including the 17 listed above plus 3 species recorded in both regions (*G. tropica*, *S. minima* and *A. (Phagicola) nana*). There were also 2 helminth species found only in the poeciliids of the Papaloapan basin, including *Mexiconema cichlasomae* Moravec, Vidal-Martínez and Salgado-Maldonado, 1992; *Spinitectus mexicanus* Caspeta-Mandujano, Moravec and Salgado-Maldonado, 2000; and *Rhabdochona* sp. (a species distinct from others of the same genus and which are recorded in this study). The metacercariae of *Posthodiplostomum minimum* MacCallum, 1921, and *Centrocestus formosanus* Nishigori, 1924, are very frequent in Mexican poeciliids, the former parasitizing 12 poeciliid species and the latter 11. The cestode *Bothriocephalus acheilognathi* Yamaguti, 1934, was recorded in 10 host species as were *Uvulifer* sp. metacercaria. Other abundant species included the trematode *S. cf. sogandaresi* and *Contra-caecum* sp. larvae, both of which were recorded in 9 poeciliid host species.

The cestode *B. acheilognathi* and *Contra-caecum* sp. larvae were the most widely distributed helminths in poeciliids, as they were recovered in 6 of the sampled hydrological basins. The trematode *S. cf. sogandaresi*, and *P. minimum* and *C. formosanus* metacercaria were also widely distributed, all of them being recorded in 5 of the sampled basins.

The host species *Poecilia mexicana* was found to have the most abundant helminth community, with 24 species. This fish species was followed by *P. petenensis*, which had 20 helminth species, and *Gambusia yucatana*, with 17 species. The remaining poeciliid species hosted from 2 to 15 helminth species (Table 2).

Of the 46 helminth species recorded in poeciliids, 20 (43%) are autogenic, completing their lifecycle in the same body of water, and 26 (57%) are allogenic, mainly maturing in birds. Almost all the helminths recorded in the

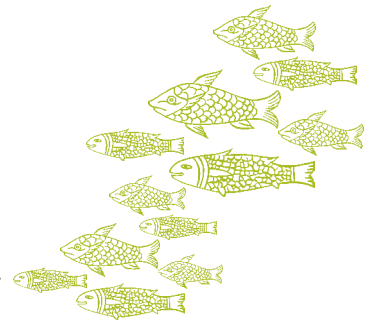
Poeciliids are widely distributed generalists and have been recorded in other host taxa. Three of the helminth species, however, appear to be exclusive to poeciliids: *Urocleidoides reticulatus*, *Spinitectus mexicanus* and *Rhabdochona xiphophori*. There is also a clearly distinguishable anthropogenically introduced component in Mexican poeciliids, including *C. formosanus* metacercaria and the cestode *B. acheilognathi*.

Discussion

The results highlight the need for more sampling and field work aimed at completing the helminth database for goodeids and poeciliids in Mexico. To date, only 7 goodeid genera and 9 goodeid species of the 19 known genera and 51 known species in Mexico have had any study done of their helminth fauna. The situation is similar for poeciliids, for which helminth studies have been done for 6 genera and 20 species of the 11 known genera and 95 known species in Mexico. Only the most common and accessible goodeid and poeciliid species have been examined, leaving a data gap for species with more limited distributions or from rarer populations.

The currently available data is from general fish samples and samples that only circumstantially report goodeid and poeciliid data. The data from the present study, in contrast, are based on the determinations of taxonomic specialists and the reference material has been deposited in stable institutional helminth collections to ensure its conservation and accessibility for future reference. To bring the level of knowledge on the helminth fauna of goodeids and poeciliids in Mexico to a comparable level of that currently available for cichlid (Cichlidae) parasite fauna (one of the best understood as far as helminths are concerned [Salgado-Maldonado *et al.*, 1997; Vidal-Martínez *et al.*, 2001]), sampling programs are needed that are directed at chosen goodeid and poeciliid species. This is particularly difficult since many of these species have very limited geographic distributions and consist of scarce populations. Many of the species in these families are also threatened and require special permits for research collection. Of the two families, the poeciliids are more widely distributed, though many of the species are small and live in microhabitats within bodies of water that are hard to access and sample, and thus require specialized collection tools and techniques.

The data indicate 4 components that determine helminth parasite community composi-



tion in these fish families, which are described below in order of the number of helminth species in each component. 1) Generalist, allogenic helminth species. These are transported by birds and have a wide geographic distribution, with most being Nearctic though some have world-wide distribution. They have colonized goodeids and poeciliids as secondary intermediate hosts or paratenic hosts and conclude their lifecycle in birds. 2) Helminth species commonly associated with other fish species. Goodeid and poeciliid species have acquired these by living in the same locations as other infected fish, that is, these are helminths acquired via sympatry with other fish species. 3) Anthropogenically introduced helminth species. 4) Specialist helminth species. These appear to restrict their parasitic relationship to goodeid or poeciliid fish. They have developed, or evolved, together with their hosts and are probably endemic or ancient species.

A total of 38% of the recorded helminths in goodeids, and 57% in poeciliids are allogenic, that is, widely distributed generalist species that reach sexual maturity in birds and are transported and dispersed by them. This component in the goodeids includes *C. complanatum*, *Diplostomum* sp., *P. minimum*, *Ligula intestinalis* Linnaeus, 1758, *Cyclostera* cf. *ralli* Underwood and Dronen, 1986, *Valipora campilancristrota* Wedl, 1855, *Contracaecum* sp., *Eustrongylides* sp., *Spiroxys* sp., *Falcaustra* sp., and *Polymorphus brevis* Van Cleave, 1916. In poeciliids it includes *C. complanatum*, *Diplostomum* (A.) *compatum*, *Diplostomum* sp., *P. minimum*, *Uvulifer* sp., *Contracaecum* sp., *Eustrongylides* sp., and *Polymorphus* sp., as well as 9 heterophyd and 5 dilepidid species. It also includes the more geographically restricted allogenic species *R. ondatrae*, *Apharangostrigea* sp., *E. leopoldinae*, and *Gnathostoma* sp. These allogenic helminth species have low host specificity and are widely distributed among freshwater fish in Mexico (Scholz *et al.*, 1995 a,b, 1996; Moravec, 1998; Scholz and Salgado-Maldonado, 2001b; Salgado-Maldonado *et al.*, 2001a,b, 2004a,b; Vidal Martínez *et al.*, 2001). Some are distributed throughout North America, and still others are found world-wide (Yamaguti, 1975; Gibson, 1996; Moravec, 1998; Hoffman, 1999). Metacercaria of the heterophyd *Ascocotyle* spp. are widely distributed in the fish of southeast Mexico and on the Gulf of Mexico slope (Scholz *et al.*, 1997, 2001). Metacercariae of the Dilepididae family are widely distributed in the

freshwater fish of the Mexican plateau (Scholz and Salgado-Maldonado, 2001b; Salgado-Maldonado *et al.*, 2001b).

The second component consists of helminth species that are infrequent in the parasite communities of goodeids and poeciliids and have invaded them from the parasite's primary preferred hosts, *i.e.* other fish species with which they live in sympatry. These include *M. simplex*, which is frequent in characids (mostly *Astyanax*) (see Jiménez Guzmán, 1973; Scholz *et al.*, 1995b; Salgado-Maldonado *et al.*, 2001a, 2004a,b, 2005); *Ascocotyle* (*Ascocotyle*) *tenuicollis*, a metacercaria frequently associated with cichlids (Scholz *et al.*, 2001; Vidal-Martínez *et al.*, 2001); *Proteocephalus pusillus* Ward, 1910, which parasitizes salmonids (Schmidt, 1986; Hoffman, 1999); *Capillaria cyprinodonticola*, which parasitizes cyprinodontids and poeciliids (Moravec, 1998), and *Ochetosoma brevicecum* (Caballero y Caballero, 1941) metacercariae, which parasitize amphibians (Jiménez-Ruiz *et al.*, 2002). This second helminth component in poeciliids includes *Genarchella tropica*, a parasite in characids; *A. ? astorquii*, *P. bychowskyi*, *S. minima*, *R. ondatrae*, which mainly parasitize various cichlid species in southeast Mexico (Salgado-Maldonado *et al.*, 1997; Vidal-Martínez *et al.*, 2001); *R. kidderi*, a parasite of cichlids; and *R. lichtenfelsi*, which parasitizes goodeids.

The third, anthropogenically introduced helminth component includes *Centrocestus formosanus* metacercariae, the monogenean *Gyrodactylus* cf. *elegans*, the cestode *Bothriocephalus acheilognathi*, and the nematode *Pseudocapillaria tomentosa*. All four are found in goodeids, but only the metacercariae and the cestode were recorded in poeciliids in this study.

Human-introduced helminths are a paradigm. They are the most successful helminth parasites of freshwater fish in Mexico based on the number of host species they infect and their wide distribution. The success of *Bothriocephalus acheilognathi*, for example, is directly favored by aquaculture policies carried out in central Mexico, especially in the highland plateau (see Salgado-Maldonado and Pineda-López, 2003). "Controlled" production and constant "sowing" of Asian carps is common aquaculture practice in the Mexican altiplano. These fish species are re-introduced year after year into natural bodies of water as well as into artificial ones such as reservoirs and "bordos" (artificial, temporary ponds used for storing water during the dry season) (Juárez-Palacios and Palomo-Martínez,

1985; Arredondo-Figueroa and Juárez-Palacios, 1986). This Asian cestode's current wide distribution and presence records clearly reflect this practice. The parasite's life cycle coincides nicely with the carp cultivation cycle. The helminth eggs are initially deposited with the host feces on the pond or reservoir bottom. These ponds are then fertilized to aid and increase the production of the plankton needed to feed the small carp raised there. This is generally done without disinfecting or applying any treatment to eliminate the cestode eggs in the muddy bottoms. This cycle ensures the conjunction in time and space of the parasite eggs, the zooplanktonic copepods that serve as intermediate hosts, and the fish, which is the definitive host. The introduction of infected carp into reservoirs and other large bodies of water in the Mexican altiplano favors the infection of native fish with this cestode. This parasite has a notable lack of host specificity, which complements the already propitious conditions for transmission between cultivated and wild fish populations. *Bothriocephalus acheilognathi* has been recorded in 49 freshwater fish species from 26 genera 7 families and 5 orders in Mexico (Salgado-Maldonado and Pineda-López, 2003).

These practices of repeated introduction and distribution of non-native carp have also favored other parasites such as *P. tomentosa* and *G. cf. elegans* (Moravec *et al.*, 2001; Salgado-Maldonado and Pineda-López, 2003).

Dispersion of *C. formosanus* metacercaria in Mexico appears to be related to distribution of its first intermediate host, the snail *Thiara tuberculata*. This species was initially introduced into the Caribbean, the southern United States, and South America to help in controlling other snail species that transmit schistosomiasis (see Scholz and Salgado-Maldonado, 2001a). *T. tuberculata* disperses actively and can establish populations in new environments with relative ease. It grows quickly and can reach sizable population densities in a short time. These intermediate host characteristics, coupled with the lack of host specificity in *C. formosanus* metacercariae, favor this trematode's transmission rate and it is spread to a wide variety of fish species (Scholz and Salgado-Maldonado, 2001a).

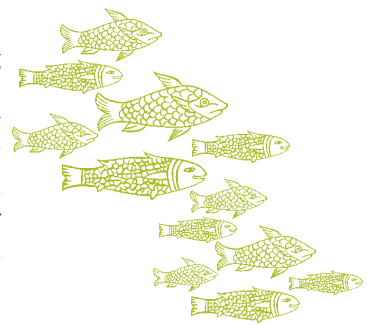
Introduced helminth species' aggressiveness and pathology in native fish species has been thoroughly documented (Hoffman, 1999; Scholz and Salgado-Maldonado, 2001a; Salgado-Maldonado and Pineda-López, 2003). However, the effect of these parasite species on

wild fish populations has not yet been reliably tested. Goodeids, and especially poeciliids, play a role in this dispersion because they are excellent distributors of introduced parasite species to other native fish species. Poeciliids are known to play this role in other parts of the world, such as Hawaii (Font, 1997), Australia (Dove, 2000), and in the sinkholes of the Yucatán Peninsula (Scholz *et al.*, 1996).

The fourth component in the helminth communities of Mexican goodeids and poeciliids consists of host-specific species, which have developed with these host families. Nematodes of the family Rhabdochoniidae, in particular, have widely diversified in Mexican freshwater fish (Salgado-Maldonado *et al.*, 2004b). *Rhabdochona lichthenfelsi* appears to have developed in association with goodeids in the Mexican highland plateau, as indicated by its host records in the present study. Trematodes of the genus *Margotrema* have also been collected only in goodeids from the Mexican highland plateau. Although a second species has recently been described for this genus (Pérez, 2001), the morphological variability of the *M. bravoae* Lamothe-Argumedo, 1970, type species is still not well studied. The differences between these two species are very tenuous and the arguments in favor of the second quite weak. None the less, the genus and type species validity are undisputed, meaning that in the Mexican altiplano some helminth parasites have speciated along with goodeids and are specific to these hosts.

To date, the two helminth species apparently host-specific to poeciliids are *Rhabdochona xiphophori* Caspeta-Mandujano, Moravec and Salgado-Maldonado 2000, and *Spinitectus mexicanus* Caspeta-Mandujano, Moravec and Salgado-Maldonado 2000, both of which have only been collected from poeciliids. It is also possible that the trematodes indicated as *Saccocoelioides cf. sogandaresi*, which includes a complex of species that have not yet been morphologically differentiated, is closely associated with poeciliids. This is supported by their presence in the records and their abundance data in the different basins (Salgado-Maldonado *et al.*, 2001a,b, 2004a,b, 2005).

The relative poorness of the endemic helminths of the Mexican highland plateau is likely due to their young geological age. Salgado-Maldonado *et al.* (2001b) suggest that helminth parasite communities of the Mexican altiplano, especially those in goodeids, are no more than 5 million years old. This, consequently, has con-



ditioned their poorness in terms of host species specificity, which makes them invadable by introduced species. The presence of only three nominal helminth species specific to this fish family is congruent with this proposal, especially if the geological age of the fresh water bodies in the altiplano and the evolutionary differentiation of the Goodeidae are taken into account (Barbour, 1973; Echelle and Echelle, 1984). This relative youth and consequent species poorness make these communities imminently invadable by allogenic, generalist and anthropogenically introduced helminth species.

Based on this, it is probable that the ancestral marine group from which the goodeids originated lost most of its parasites after being isolated in the freshwater bodies of the Mexican altiplano during the Pliocene, 5 million years ago (Barbour, 1973; Echelle and Echelle, 1984). However, some of these parasites persisted, such as the ancestors of the current genus *Margotrema*, which later differentiated in isolation with their hosts. Other parasites such as the *Rhabdochona* nematodes experienced an adaptive radiation process, dispersing themselves among the fish species of central Mexico, with various helminth species developing in different host groups (Caspeta-Mandujano *et al.*, 2000a, 2001; Salgado Maldonado *et al.*, 2004b, 2005). In the case of *R. lichtenfelsi*, the current data appear to indicate that this species differentiated in conjunction with the goodeids. During later evolutionary development, the helminth community of the goodeids, initially quite poor, was enriched by the invasion of allogenic generalist species and by the set of species acquired through sympatry with other fish groups. The current helminth community composition of goodeids now exhibits the effect of invasion by anthropogenically introduced helminth species.

The presence of allogenic generalist helminth species with wide geographic distribution, and transported by birds, are a constant in the Mexican freshwater fish studied to date (Salgado-Maldonado *et al.*, 2001b). In some hydrologic basins, the Lerma and the Santiago, for example, the allogenic species component is more significant in terms of number of species than in other

basins. This phenomenon is related to the small size of freshwater fish like the goodeids, and their habitat in shallow waters along the migration routes of Nearctic birds (Salgado-Maldonado *et al.*, 2001b). Like the allogenic species, the introduced helminth species are excellent colonizers and tend to occupy the “empty niches” (*sensu* Kennedy, 1990) they find in these species-poor helminth communities.

The geographic origins of the poeciliids are different than those of the goodeids, but the current conformation of helminth communities indicates that their development has followed a similar path. In other words, these young communities with few specialists are invadable by allogenic helminth species and species from other fish groups. For viviparous fish, populations can be started with a single founding female, suggesting a limited infection source in recently established, dynamic populations, and partially explaining these helminth communities’ species poorness.

The data presented here also indicate that by analyzing the taxonomic composition of helminth communities in a single host family, the same described patterns are reflected in the different studied hydrological basins (Salgado-Maldonado *et al.*, 2001a,b, 2004a,b, 2005). These patterns include the numerical predominance of trematode and nematode species, the low representation of monogeneans and cestodes, and only a few species records for the acanthocephalan group. A large allogenic component is also characteristic of helminth communities in Mexican freshwater fish.

The helminth communities in poeciliids shown in the inventory exhibit variable richness (from 2 to 23 species). The host species with the fewest parasites, however, appear to show this trend because of insufficient sampling or geographically restricted distribution (*e.g.*, *P. latipunctata* from the Yucatán Peninsula, *P. reticulata* from the Balsas and *P. butteri* from the Ayuquila). Despite this, the helminth communities recorded in Poeciliidae were notably richer than those observed in the Goodeidae. This may result from the Poeciliidae being neotropical, their wider geographic distribution, and the density and contiguity of their populations.

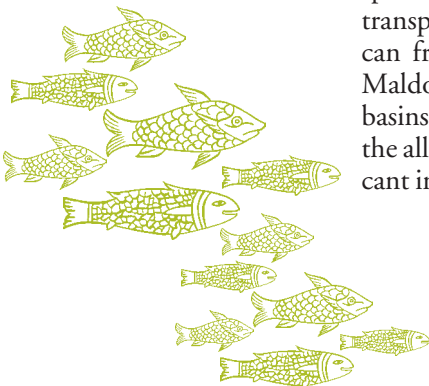
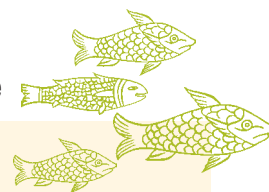


Table 1.

Parasite host list of helminths collected from viviparous fishes of Mexico:

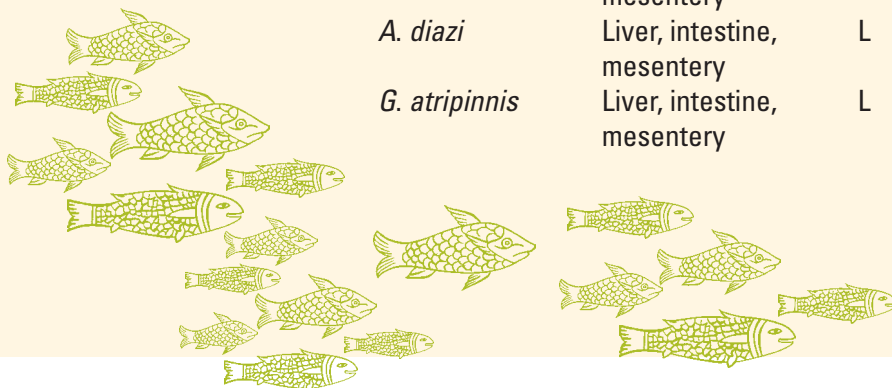
Goodeidae: *A.* = *Allophorus*, *G.* = *Girardinichthys*, *G.* = *Goodea atripinnis*, *I.* = *Ilyodon*, *X.* = *Xenotoca*;

Basin, BR = Río Balsas, L = Río Lerma, PS = Río Pánuco, SM = Río Ayuquila, Sierra de Manantlán.



Parasite	Host	Site of infection	Basin	Reference
Adult trematoda				
Family Gorgoderidae				
<i>Dendrorchis</i> sp.	<i>I. furcidens</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
Family Haploporidae				
<i>Saccocoelioides</i> cf. <i>sogandaresi</i>	<i>A. zonistius</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>I. furcidens</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>I. whitei</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
Family Macroderoididae				
<i>Magnivitellinum simplex</i>	<i>I. furcidens</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
<i>Margotrema bravoae</i>	<i>A. robustus</i>	Intestine	L	Pérez, 2001
	<i>A. diazi</i>	Intestine	L	Pérez, 2001
	<i>A. zonistius</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>G. multiradiatus</i>	Intestine	L	Sánchez-Nava <i>et al.</i> , 2004
<i>Margotrema guillerminae</i>	<i>A. robustus</i>	Intestine	L	Pérez, 2001
Metacercariae				
Family Clinostomidae				
<i>Clinostomum complanatum</i>	<i>A. robustus</i>	Liver, mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Liver, mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. zonistius</i>	Body cavity	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>G. atripinnis</i>	Liver	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>I. furcidens</i>	Body cavity	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>X. variatus</i>	?	L	Salgado-Maldonado <i>et al.</i> , 2001b
Family Diplostomidae				
<i>Diplostomum</i> sp.	<i>G. atripinnis</i>	?	L	Salgado-Maldonado <i>et al.</i> , 2001b
<i>Posthodiplostomum minimum</i>	<i>A. robustus</i>	Liver, mesentery muscle, eyes	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Liver, muscle, Mesentery	L	Pérez <i>et al.</i> , 2000
	<i>A. zonistius</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>G. multiradiatus</i>	Mesentery, liver	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>G. atripinnis</i>	Liver, muscle, mesentery, eyes	L	Salgado-Maldonado <i>et al.</i> , 2001b
		Muscle, liver, eyes, mesentery, body cavity	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>I. furcidens</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>X. variatus</i>	?	L	Salgado-Maldonado <i>et al.</i> , 2001b
<i>Tyloodelphys</i> sp.	<i>G. multiradiatus</i>	Body cavity, mesentery, eyes	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>G. atripinnis</i>	Body cavity	L	Salgado-Maldonado <i>et al.</i> , 2001b

Parasite	Host	Site of infection	Basin	Reference
Family Heterophyidae				
<i>Ascocotyle (Ascocotyle)</i>				
<i>tenuicollis</i>	<i>A. zonistius</i>	Heart	SM	Salgado-Maldonado <i>et al.</i> , 2004a
<i>Centrocestus formosanus</i>	<i>I. furcoidens</i>	Gills	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>I. whitei</i>	Gills	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>G. atripinnis</i>	Gills	L	Salgado-Maldonado <i>et al.</i> , 2001b
Family Plagiorchiidae				
<i>Ochetosoma brevicaecum</i>	<i>G. multiradiatus</i>	Mesentery	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>A. diazi</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. atripinnis</i>	Intestine	L	Pérez <i>et al.</i> , 2000
Monogenea				
Family Gyrodactylidae				
<i>Gyrodactylus cf. elegans</i>	<i>G. multiradiatus</i>	Fins	L	Sánchez-Nava <i>et al.</i> , 2004
Adult cestoda				
Family Bothriocephalidae				
<i>Bothriocephalus acheilognathi</i>				
	<i>A. robustus</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. multiradiatus</i>	Intestine	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>G. atripinnis</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>X. variatus</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
Family Proteocephalidae				
<i>Proteocephalus pusillus</i>	<i>G. atripinnis</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
Metacestodes				
Family Cyclophyllidae				
Cyclophyllidae gen. sp.	<i>A. diazi</i>	Gall bladder	L	Pérez <i>et al.</i> , 2000
Family Diphyllbothriidae				
<i>Ligula intestinalis</i>	<i>G. atripinnis</i>	Body cavity	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. multiradiatus</i>	Body cavity	L	Sánchez-Nava <i>et al.</i> , 2004
Family Dilepididae				
<i>Cyclusteria cf. ralli</i>	<i>G. multiradiatus</i>	Mesentery	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>X. variatus</i>	Mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
<i>Valipora campylancristrota</i>	<i>G. multiradiatus</i>	Gall bladder	L	Sánchez-Nava <i>et al.</i> , 2004
Dilepididae gen. sp.				
	<i>A. zonistius</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>I. furcoidens</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
Family Proteocephalidae				
Proteocephalidae gen. sp.				
	<i>A. robustus</i>	Liver, intestine mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Liver, intestine, mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. atripinnis</i>	Liver, intestine, mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b



Parasite	Host	Site of infection	Basin	Reference
Adult nematodes				
Family Capillaridae				
<i>Capillaria cyprinodonticola</i>	<i>I. furcoidens</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
<i>Pseudocapillaria tomentosa</i>	<i>A. robustus</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. atripinnis</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
Family Rhabdochonidae				
<i>Rhabdochona lichthenfelsi</i>	<i>A. robustus</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. atripinnis</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
		Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
<i>I. furcoidens</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a	
Larval nematodes				
Family Anisakidae				
<i>Contraecaecum</i> sp.	<i>A. robustus</i>	Mesentery	L	Pérez <i>et al.</i> , 2000
	<i>G. multiradiatus</i>	Mesentery	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>G. atripinnis</i>	Mesentery,	L	Salgado-Maldonado <i>et al.</i> , 2001b
		body cavity		
<i>X. variatus</i>	Mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b	
Family Dioctophymatidae				
<i>Eustrongylides</i> sp.	<i>A. robustus</i>	Mesentery	L	Pérez <i>et al.</i> , 2000
	<i>G. atripinnis</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
Family Kathlaniidae				
<i>Falcaustra</i> sp.	<i>G. multiradiatus</i>	Mesentery, intestine	L	Sánchez-Nava <i>et al.</i> , 2004
Family Gnathostomatidae				
<i>Gnathostoma</i> sp.	<i>A. robustus</i>	Liver	L	Salgado-Maldonado <i>et al.</i> , 2001b
<i>Spiroxys</i> sp.	<i>A. robustus</i>	Mesentery, intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Mesentery, intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. multiradiatus</i>	Mesentery, intestine	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>X. variatus</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
Acanthocephala larvae				
Family Polymorphidae				
<i>Polymorphus brevis</i>	<i>A. robustus</i>	Mesentery, muscle	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>A. diazi</i>	Mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>G. multiradiatus</i>	Mesentery	L	Sánchez-Nava <i>et al.</i> , 2004
	<i>G. atripinnis</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>X. variatus</i>	Intestine	L	Salgado-Maldonado <i>et al.</i> , 2001b

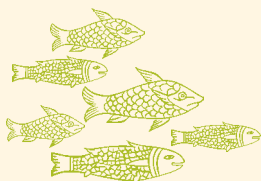


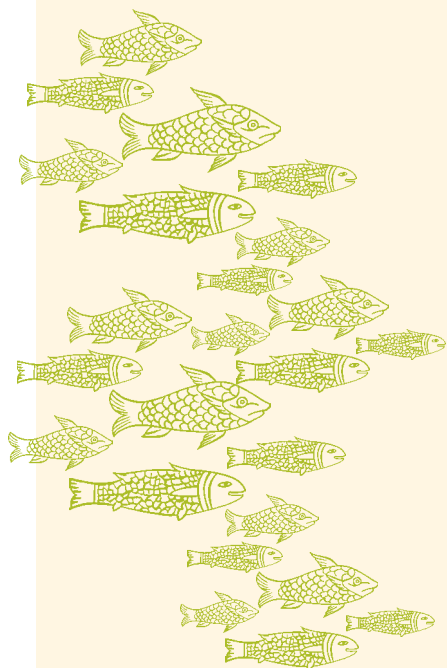
Table 2.

Parasite host list of helminths collected from viviparous fishes of Mexico: Poeciliidae

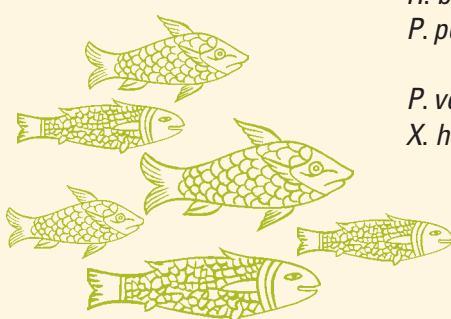
Basin: BR = Río Balsas, CY = Yucatán Peninsula, GU = Grijalva-Usumacinta basin, L = Río Lerma, PP = Río Papaloapan, PS = Río Pánuco, SM = Río Ayuquila, Sierra de Manantlán, S = Río Santiago, MO = Sierra Madre Oriental.

Parasite	Host	Site of infection	Basin	Reference
Adult trematoda				
Family Derogenidae				
<i>Genarchella tropica</i>	<i>G. yucatanana</i>	Intestine	CY	Scholz <i>et al.</i> , 1995a
	<i>P. petenensis</i>	Intestine	GU	Salgado-Maldonado <i>et al.</i> , 2005
Family Haploporidae				
<i>Saccocoelioides cf. sogandaresi</i>	<i>P. latipunctata</i>	Intestine	CY	Scholz <i>et al.</i> , 1995a
	<i>P. mexicana</i>	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
		Intestine	GU	Salgado-Maldonado <i>et al.</i> , 2005
		Intestine	PP	Present work
	<i>P. petenensis</i>	Intestine	GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. sphenops</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. gracilis</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. velifera</i>		CY	Scholz <i>et al.</i> , 1995b
	<i>Poecilia</i> sp.	Intestine	CY	Scholz <i>et al.</i> , 1995a
	<i>X. helleri</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
		Intestine	PP	Present work
	<i>Xiphophorus</i> sp.	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
Metacercariae				
Family Acanthostomidae				
<i>Atrophecaecum? astorquii</i>	<i>G. yucatanana</i>	Fins	CY	Scholz <i>et al.</i> , 1995b
	<i>P. latipunctata</i>	Fins	CY	Scholz <i>et al.</i> , 1995b
	<i>P. petenensis</i>	Fins	CY	Scholz <i>et al.</i> , 1995b
	<i>P. velifera</i>		CY	Scholz <i>et al.</i> , 1995b
<i>Perezitrema bychowskyi</i>	<i>G. yucatanana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
<i>Stunkardiella minima</i>	<i>G. yucatanana</i>	Fins	CY	Scholz <i>et al.</i> , 1995b
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
Family Cathaemasiidae				
<i>Ribeiroia ondatrae</i>	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
Family Clinostomidae				
<i>Clinostomum complanatum</i>	<i>H. bimaculata</i>	Mesentery	PR	Present work
	<i>P. mexicana</i>	Muscle	PR	Salgado-Maldonado <i>et al.</i> , 2004b
		Muscle	L	Present work
		Body cavity	PP	Present work
		eyes		
	<i>P. gracilis</i>	Mesentery	PR	Present work
	<i>P. infans</i>	Liver	L	Present work
	<i>X. helleri</i>	Gills	PP	Present work

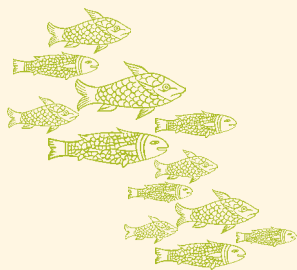
Parasite	Host	Site of infection	Basin	Reference
Family Diplostomidae				
<i>Diplostomum</i> (<i>Austrodiplostomum</i>)				
<i>compactum</i>	<i>P. mexicana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
<i>Diplostomum</i> sp.	<i>P. mexicana</i>	Eyes	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. sphenops</i>	Eyes, brain, body cavity	BR L	Salgado-Maldonado <i>et al.</i> , 2001a Salgado-Maldonado <i>et al.</i> , 2001b
	<i>P. reticulata</i>	Eyes, brain, body cavity	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. gracilis</i>	Eyes	PR	Salgado-Maldonado <i>et al.</i> , 2004b
<i>Posthodiplostomum</i>				
<i>minimum</i>	<i>B. belizanus</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>G. yucatanana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>G. vittata</i>	Mesentery, fat liver, muscle	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>H. bimaculata</i>	Muscle, eyes liver	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. butleri</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. mexicana</i>	Liver, mesentery, fat body cavity muscle, kidney, eyes, intestine Mesentery	PR L GU GU BR	Salgado-Maldonado <i>et al.</i> , 2004b Present work Salgado-Maldonado <i>et al.</i> , 2005 Salgado-Maldonado <i>et al.</i> , 2005 Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. mexicana</i>		L	Present work
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. sphenops</i>	Mesentery, body cavity	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		Mesentery	L	Present work
		Mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>P. gracilis</i>	Fat	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. infans</i>	Muscle, liver Liver, mesentery	BR L	Salgado-Maldonado <i>et al.</i> , 2001a Salgado-Maldonado <i>et al.</i> , 2001b
	<i>X. helleri</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>Xiphophorus</i> sp.	Muscle, eyes fat	PR	Salgado-Maldonado <i>et al.</i> , 2004b
<i>Uvulifer</i> sp.				
	<i>G. yucatanana</i>		CY	Scholz <i>et al.</i> , 1995b
	<i>P. butleri</i>	Skin	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. mexicana</i>	Skin	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. sphenops</i>	Skin, fins	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. petenensis</i>	Muscle	CY	Scholz <i>et al.</i> , 1995b
	<i>P. velifera</i>		CY	Scholz <i>et al.</i> , 1995b
	<i>P. baenschi</i>	Skin	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. gracilis</i>	Skin, fins Fins	BR PP	Salgado-Maldonado <i>et al.</i> , 2001a Present work
	<i>X. helleri</i>	Skin	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>Xiphophorus</i> sp.	Skin	PR	Salgado-Maldonado <i>et al.</i> , 2004b



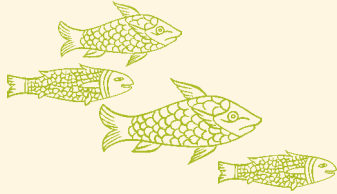
Parasite	Host	Site of infection	Basin	Reference	
Family Echinostomatidae					
<i>Echinochasmus leopoldinae</i>	<i>G. yucatanana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
	<i>P. mexicana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
Family Heterophyidae					
<i>Ascocotyle</i>					
<i>(Ascocotyle) tenuicollis</i>	<i>B. belizanus</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
	<i>G. yucatanana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
	<i>G. vittata</i>	Mesentery	PR	Salgado-Maldonado <i>et al.</i> , 2004b	
	<i>H. bimaculata</i>	Heart	PP	Present work	
	<i>P. butleri</i>	Heart, gills	SM	Salgado-Maldonado <i>et al.</i> , 2004a	
	<i>P. latipunctata</i>	Heart, mesentery	CY	Scholz <i>et al.</i> , 1995b	
	<i>P. mexicana</i>		Heart	PP	Present work
			Heart, mesentery	CY	Scholz <i>et al.</i> , 1995b
	<i>P. velifera</i>			GU	Salgado-Maldonado <i>et al.</i> , 2005
				CY	Scholz <i>et al.</i> , 1995b
	<i>X. helleri</i>	Fat	PP	Present work	
	<i>Ascocotyle</i>				
	<i>(Leighia) chandleri</i>	<i>G. yucatanana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
<i>Ascocotyle</i>					
<i>(Leighia) megacephala</i>	<i>P. velifera</i>	Intestinal wall	CY	Scholz <i>et al.</i> , 1995b	
			GU	Salgado-Maldonado <i>et al.</i> , 2005	
<i>Ascocotyle</i>					
<i>(Phagicola) diminuta</i>	<i>P. petenensis</i>	Gills	CY	Scholz <i>et al.</i> , 1995b	
			CY	Scholz <i>et al.</i> , 1995b	
<i>Ascocotyle</i>					
<i>(Phagicola) macrostoma</i>	<i>B. belizanus</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
<i>Ascocotyle</i>					
<i>(Phagicola) mollieniscicola</i>	<i>P. mexicana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
		<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
<i>Ascocotyle</i>					
<i>(Phagicola) nana</i>	<i>B. belizanus</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
	<i>G. yucatanana</i>	Mesentery	CY	Scholz <i>et al.</i> , 1995b	
	<i>H. bimaculata</i>	Intestinal wall	PP	Present work	
	<i>P. petenensis</i>	Mesentery	CY	Scholz <i>et al.</i> , 1995b	
				GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. velifera</i>		CY	Scholz <i>et al.</i> , 1995b	
	<i>X. helleri</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a	
		Intestinal wall	PP	Present work	


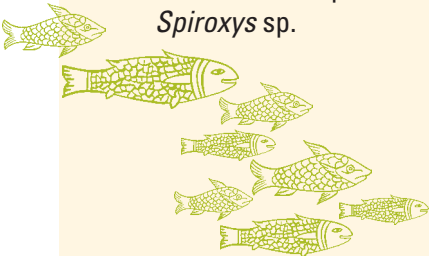
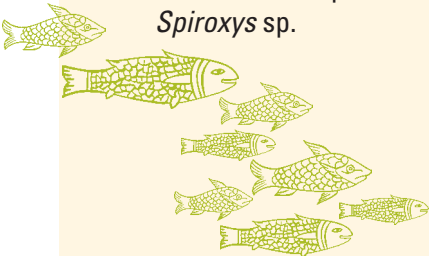


Parasite	Host	Site of infection	Basin	Reference
<i>Centrocestus formosanus</i>	<i>G. yucatanana</i>	Gills	GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>Heterandria</i> sp.	Gills	PP	Scholz and Salgado-Maldonado, 2001a
	<i>P. gracilis</i>	Gills	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		Gills	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. mexicana</i>	Gills	PR	Salgado-Maldonado <i>et al.</i> , 2004b
		Gills	GU	Salgado-Maldonado <i>et al.</i> , 2005
	Gills	L	Present work	
	Gills	PP	Present work	
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. reticulata</i>	Gills	PP	Present work
	<i>P. sphenops</i>	Gills	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		Gills	L	Salgado-Maldonado <i>et al.</i> , 2001b
	Gills	PP	Scholz and Salgado-Maldonado, 2001a	
	<i>P. baenschi</i>	Gills	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. butleri</i>	Gills	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. infans</i>	Gills	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>Poeciliopsis</i> sp.	Gills	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>X. helleri</i>	Gills	SM	Salgado-Maldonado <i>et al.</i> , 2004a
		Gills	PP	Scholz and Salgado-Maldonado, 2001a
	<i>Xiphophorus</i> sp.	Gills	PR	Salgado-Maldonado <i>et al.</i> , 2004b
Family Proterodiplostomidae				
Proterodiplostomidae gen. sp.				
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
Family Strigeidae				
<i>Apharingostrigea</i> sp.	<i>P. mexicana</i>	Body cavity	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. gracilis</i>	Body cavity	PR	Salgado-Maldonado <i>et al.</i> , 2004b
Monogenea				
Family Dactylogyridae				
<i>Salsuginus neotropicalis</i>	<i>B. belizanus</i>	Gills	CY	Mendoza-Franco and Vidal Martínez, 2001
<i>Salsuginus seculus</i>	<i>G. yucatanana</i>	Gills	GU	Salgado-Maldonado <i>et al.</i> , 2005
<i>Urocleidoides reticulatus</i>	<i>B. belizanus</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. mexicana</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>G. yucatanana</i>	Gills	CY	Scholz <i>et al.</i> , 1995a
<i>Urocleidoides</i> sp.	<i>P. mexicana</i>	Gills	PR	Present work
	<i>Xiphophorus</i> sp.	Gills	PR	Salgado-Maldonado <i>et al.</i> , 2004b
Dactylogyridae gen. sp.				
Family Gyrodactylidae				
<i>Gyrodactylus</i> sp.	<i>G. yucatanana</i>	Gills	CY	Scholz <i>et al.</i> , 1995a
	<i>P. mexicana</i>	Fins	PR, L	Present work
	Fins	PP	Present work	
	<i>P. sphenops</i>	Gills	L	Salgado-Maldonado <i>et al.</i> , 2001b
	<i>P. gracilis</i>	Gills	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	Fins	PP	Present work	
	<i>P. infans</i>	Gills	BR	Salgado-Maldonado <i>et al.</i> , 2001a



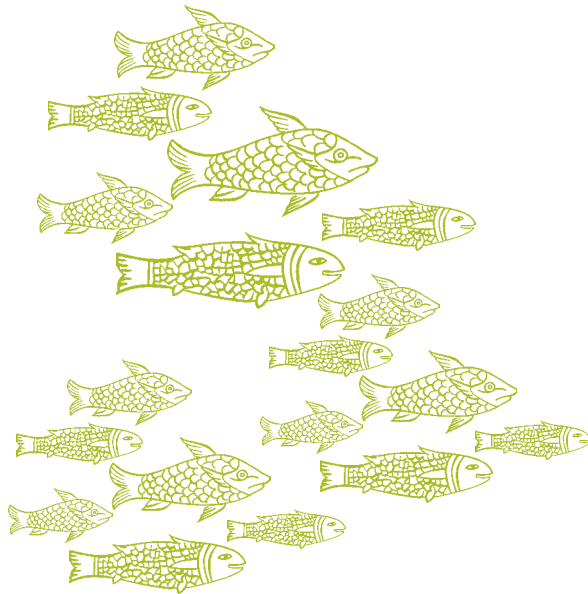
Parasite	Host	Site of infection	Basin	Reference
Adult Cestoda				
Family Bothriocephalidae				
<i>Bothriocephalus</i>				
<i>acheilognathi</i>				
	<i>G. vittata</i>	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>G. yucatanana</i>	Intestine	CY	Scholz <i>et al.</i> , 1996
		Intestine	GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>H. bimaculata</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		Intestine	L	Present work
	<i>P. butleri</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. mexicana</i>	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>P. reticulata</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. sphenops</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>P. baenschi</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a
	<i>P. gracilis</i>	Intestine	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>Poecilia</i> sp.	Intestine	MO	Aguilar-Aguilar <i>et al.</i> , 2004
Metacestoda				
Family Dilepididae				
	<i>Dendrouterina papillifera</i>		CY	Scholz <i>et al.</i> , 1996
	<i>Glossocercus auritus</i>	<i>P. catemaconis</i>	PP	Scholz and Salgado-Maldonado, 2001
		<i>P. mexicana</i>	PR	Salgado-Maldonado <i>et al.</i> , 2004b
			PP	Present work
		<i>P. sphenops</i>	BR	Salgado-Maldonado <i>et al.</i> , 2001a
			BR	Salgado-Maldonado <i>et al.</i> , 2001a
		<i>P. gracilis</i>	BR	Salgado-Maldonado <i>et al.</i> , 2001a
			BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>Glossocercus caribaensis</i>	<i>P. petenensis</i>	GU	Salgado-Maldonado <i>et al.</i> , 2005
	<i>Parvitaenia cochlearii</i>	<i>P. gracilis</i>	BR	Salgado-Maldonado <i>et al.</i> , 2001a
	<i>Valipora minuta</i>	<i>P. sphenops</i>	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		<i>P. gracilis</i>	BR	Salgado-Maldonado <i>et al.</i> , 2001a
			BR	Salgado-Maldonado <i>et al.</i> , 2001a
Family Proteocephalidae				
	Proteocephalidae gen. sp.	<i>P. infans</i>	L	Salgado-Maldonado <i>et al.</i> , 2001b
Adult nematoda				
Family Capillaridae				
	<i>Capillaria cyprinodonticola</i>	<i>P. mexicana</i>	PR	Salgado-Maldonado <i>et al.</i> , 2004b
		<i>P. sphenops</i>	BR	Salgado-Maldonado <i>et al.</i> , 2001a
Family Cystidicolidae				
	<i>Spinitectus mexicanus</i>	<i>H. bimaculata</i>	PP	Caspeta-Mandujano <i>et al.</i> , 2000b
		<i>P. mexicana</i>	PP	Present work
Family Daniconematidae				
	<i>Mexiconema cichlasomae</i>	<i>X. helleri</i>	PP	Moravec, 1998
Family Rhabdochonidae				
	<i>Rhabdochona kidderi</i>	<i>G. yucatanana</i>	CY	Moravec <i>et al.</i> , 1995a
		<i>P. mexicana</i>	PR, L	Present work
		<i>P. infans</i>	PR, L	Present work



Parasite	Host	Site of infection	Basin	Reference	
<i>Rhabdochona lichtenfelsi</i>	<i>P. mexicana</i>	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b	
<i>Rhabdochona xiphophori</i>	<i>Xiphophorus</i> sp.	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b	
Nematoda larvae					
Family Anisakidae					
	<i>Contraecaecum</i> sp.	<i>G. yucatanana</i>	GU	Salgado-Maldonado <i>et al.</i> , 2005	
		<i>H. bimaculata</i>	PP	Present work	
		<i>P. mexicana</i>	Mesentery, liver body cavity, Intestine	PR L	Salgado-Maldonado <i>et al.</i> , 2004b Present work
		<i>P. petenensis</i>	Mesentery	CY	Moravec <i>et al.</i> , 1995b
		<i>P. sphenops</i>	Liver, mesentery Muscle	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		<i>P. velifera</i>	Mesentery	CY	Moravec <i>et al.</i> , 1995b
		<i>P. baenschi</i>	Body cavity	SM	Salgado-Maldonado <i>et al.</i> , 2004a
		<i>P. gracilis</i>	Fat	PR	Salgado-Maldonado <i>et al.</i> , 2004b
		<i>P. infans</i>	Mesentery	L	Salgado-Maldonado <i>et al.</i> , 2001b
		<i>X. montezumae</i>	Mesentery, liver	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	Family Dioctophymatidae				
		<i>Eustrongylides</i> sp.	<i>H. bimaculata</i>	PR, L	Present work
		<i>P. butleri</i>	SM	Salgado-Maldonado <i>et al.</i> , 2004a	
		<i>P. mexicana</i>	Body cavity Mesentery	PR L	Salgado-Maldonado <i>et al.</i> , 2004b Present work
		<i>P. sphenops</i>	Muscle	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		<i>P. gracilis</i>	Muscle	BR	Salgado-Maldonado <i>et al.</i> , 2001a
		<i>X. helleri</i>	Mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
Family Gnathostomidae					
	<i>Gnathostoma</i> sp.	<i>B. belizanus</i>	GU	Salgado-Maldonado <i>et al.</i> , 2005	
	<i>Spiroxys</i> sp.	<i>G. yucatanana</i>	CY	Moravec <i>et al.</i> , 1995b	
		<i>P. butleri</i>	Body cavity, mesentery	SM	Salgado-Maldonado <i>et al.</i> , 2004a
		<i>P. mexicana</i>	Mesentery	PP	Present work
		<i>P. petenensis</i>	Body cavity, fat	PR	Salgado-Maldonado <i>et al.</i> , 2004b
		<i>P. gracilis</i>	Mesentery	PP	Present work
		<i>P. petenensis</i>	Mesentery	CY	Moravec <i>et al.</i> , 1995b
		<i>P. gracilis</i>	Intestine	PR	Salgado-Maldonado <i>et al.</i> , 2004b
	<i>X. helleri</i>	Mesentery	PP	Present work	
Family Kathlanidae					
<i>Falcaustra</i> sp.	<i>P. velifera</i>		CY	Moravec <i>et al.</i> , 1995b	
Adult acanthocephala					
Family Neoechinorhynchidae					
<i>Octospiniferoides chandleri</i>	<i>H. bimaculata</i>	Intestine	PP	Salgado-Maldonado <i>et al.</i> , 1992	
	<i>P. petenensis</i>		GU	Salgado-Maldonado <i>et al.</i> , 2005	
Acanthocephala (Cystacanth)					
Family Polymorphidae					
<i>Polymorphus</i> sp.	<i>X. helleri</i>	Intestine	SM	Salgado-Maldonado <i>et al.</i> , 2004a	

Acknowledgment

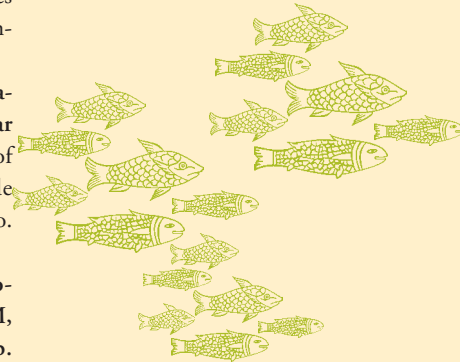
We acknowledge the Consejo Nacional de Ciencia y Tecnología (CONACyT) for funding this research through grant 31599-B: “Evaluación de la transferencia de parásitos exóticos entre peces nativos e introducidos”.



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