

HELMINTH PARASITES OF THE TROPICAL GAR, *ATRACTOSTEUS TROPICUS* GILL, FROM TABASCO, MEXICO

Guillermo Salgado-Maldonado, Frantisek Moravec*, Guillermina Cabañas-Carranza, Rogelio Aguilar-Aguilar, Petra Sánchez-Nava, Rafael Báez-Valé, and Tomás Scholz*

Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, CP 04510, Mexico D. F., Mexico. e-mail: gsalgado@mail.ibiologia.unam.mx

ABSTRACT: A total of 8 helminth species were recorded in an examination of 43 tropical gar, *Atractosteus tropicus* Gill, collected at the Pantanos de Centla Biosphere Reserve, Tabasco, Mexico. The parasite species included 1 adult trematode, 3 metacercariae, 1 cestode, 1 adult nematode, and 2 nematode larvae. Six of these 8 species were rare, with low prevalence (<17%) and abundance (<1.0 helminths per examined fish). The larvae of *Contraecaecum* sp. were the most abundant in the sample, constituting 60% of the total helminths (64% prevalence, 3.8 ± 5.2 abundance), followed by the cestode *Proteocephalus singularis*, constituting 18% of the worms (30.5% prevalence, 1.1 ± 3.0 abundance). Species richness, individual parasite abundance, and diversity were low in the infracommunities. The recording of 3 specialist species in the tropical gar confirms that the helminth fauna of gar has an appreciable degree of specificity. This study indicates the importance of ecological determinants of richness in helminth communities of the tropical gar.

The helminth parasite communities of freshwater fishes are generalized as being isolationist, poor, and of low diversity (Kennedy et al., 1986; Kennedy, 1990, 1995). In general, greater species richness and diversity are to be expected in tropical latitudes (Kennedy, 1995). Rich tropical helminth parasite communities of freshwater fishes have been described (Kennedy, 1995; Salgado-Maldonado and Kennedy, 1997; Vidal-Martínez et al., 1998; Vidal-Martínez and Kennedy, 2000). However, many other tropical freshwater fishes have species-poor helminth communities (Choudhury and Dick, 2000; Pérez et al., 2000; Salgado-Maldonado, Cabañas-Carranza, Caspeta-Mandujano et al., 2001; Salgado-Maldonado, Cabañas-Carranza, Soto-Galera et al., 2001; Aguilar-Aguilar et al., 2003; Salgado-Maldonado, Mercado-Silva et al., 2004; Salgado-Maldonado et al., 2003). Greater species richness is to be expected also in evolutionarily ancient host-parasite systems and in hosts that inhabit their geographic area of origin because they have had a long time to acquire their helminth fauna (Guégan and Kennedy, 1993; Kennedy and Bush, 1994; but see Choudhury and Dick, 1998). To investigate the species diversity patterns of helminths in an ancient tropical freshwater fish, an examination was made of the gar *Atractosteus tropicus*.

Extant gar comprise 2 phyletic lines dating back to at least the late Cretaceous period (75 mya) (Wiley, 1976) and are restricted to eastern North America, Central America, and Cuba (Berra, 1981; Nelson, 1994). The pejelagarto or tropical gar, *A. tropicus*, is a demersal freshwater species found in the Caribbean and Pacific drainages of southern Mexico and Central America. It is distributed in 3 separate populations within this region: (1) the Caribbean slope from the Usumacinta River basin in Guatemala to the Coatzacoalcos River in southern Mexico; (2) in lakes Managua and Nicaragua, the San Juan River, and the rivers of northwest Costa Rica to the Tortuguero River; and (3) the Pacific slope from southern Chiapas to the Negro River in Nicaragua (Bussing, 1987).

Information available on parasite communities in various Actinopterygii fishes (Choudhury and Dick, 1998) has shown that the helminth communities of these hosts display low species

richness, with the exception of *Amia calva* (Aho et al., 1991). Studies on the parasites of gar in the United States do not indicate richer helminth communities (Bangham and Venard, 1942; Castro and McDaniel, 1967). On the one hand, *A. tropicus* is a tropical species and is biologically ancient; one might, therefore, also expect that its parasite community in Mexico would be relatively rich. On the other hand, 2 characteristics of the tropical gar suggest it would have a relatively depauperate helminth fauna. First, *A. tropicus* in Mexico is not in its core geographic range but exists at the southern periphery. Kennedy and Bush (1994) suggested that as the distance at which a host species is removed from its heartland increases the parasite fauna becomes increasingly poor. Second, the tropical gar is an ambush predator, reportedly piscivorous throughout its life (Mora Janett et al., 1996) and near the top of the trophic chain. As such, its diversity of prey items is reduced, limiting potential parasite transmission (Aho et al., 1991; Guégan and Kennedy, 1993; Fiorillo and Font, 1996). To examine these hypotheses, this study focused on gathering data on the helminth parasite communities of *A. tropicus* from the state of Tabasco, Mexico.

MATERIALS AND METHODS

Forty-three tropical gar, *A. tropicus*, were collected from 3 localities in the Pantanos de Centla Biosphere Reserve in the state of Tabasco, Mexico (17°57'–18°39'N, 92°06'–92°47'W), in May 2001. The fishes were captured at each site using gill nets and then examined for helminth parasites. The number of fishes examined from each locality included 21 from the Nueva Esperanza Channel (18°23'77"N, 92°34'78"W), 15 from San Isidro Lake (18°21'55"N, 92°29'88"W), and 7 from Tabasquillo (18°47'N, 92°49'W). The Nueva Esperanza Channel opens into San Isidro Lake. These localities are contiguous and exhibited no significant difference in the helminth species found and their prevalence; thus, the data from these 2 localities were pooled. Tabasquillo was treated as a separate locality.

After capture, the fishes were taken live to the laboratory and examined within 8 hr of capture using standard procedures. In brief, all the external surfaces, gills, eyes, viscera, and musculature of each fish were examined using a stereomicroscope; we did not examine the inside of the mouth or the brain. All the helminths encountered in each fish were counted. Digeneans (adults and larvae), cestodes, and nematodes were fixed in hot 4% neutral formalin. Digeneans and cestodes were stained with Mayer paracarmine or Ehrlich hematoxylin, dehydrated using a graded alcohol series, cleared in methyl salicylate, and whole mounted. Nematodes were cleared with glycerin for light microscopy and stored in 70% ethanol. Voucher specimens of all taxa have been deposited in the National Helminth Collection (Colección Nacional de Helmintos), Institute of Biology, National Autonomous University of

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* Institute of Parasitology, Academy of Sciences of the Czech Republic, Branisovská 31, 370 05 České Budejovice, Czech Republic.

TABLE I. Prevalence, mean intensity, and site of infection of helminth parasites of the tropical gar, *Atractosteus tropicus*, from the Biosphere Reserve Pantanos de Centla, Tabasco, Mexico; data of 36 hosts from Nueva Esperanza Channel and Lake San Isidro (n = number of parasitized hosts).

Helminth species	Site	n (% prevalence)	Mean intensity (SE)
Adult Trematoda			
Acanthostomidae			
<i>Perezitrema bychowskyi</i> (Caballero y Caballero and Caballero-Deloya, 1975)*	Intestine	4 (11.1)	2.2 (1.5)
Metacercariae			
Clinostomidae			
<i>Clinostomum complanatum</i> (Rudolphi, 1814)	Stomach, mesentery	6 (16.7)	5.7 (4.8)
Diplostomidae			
<i>Diplostomum</i> sp.	Body cavity	1 (2.8)	2
<i>Posthodiplostomum minimum</i> (MacCallum, 1921)†	Free in intestine	1 (14.3)	4
Adult Cestoda			
Proteocephalidae			
<i>Proteocephalus singularis</i> La Rue, 1911*	Intestine	11 (30.6)	3.6 (4.6)
Adult Nematoda			
Cystoospiidae			
<i>Cystoopsis attractostei</i> Moravec and Salgado-Maldonado, 2003	Skin beneath scales	3 (8.3)	1 (0)
Nematoda larvae			
Anisakidae			
<i>Contracaecum</i> sp.*	Stomach and intestinal wall, liver, muscle, gall bladder, mesentery	23 (64)	5.7 (5.4)
Gnathostomatidae			
<i>Spiroxys</i> sp.	Mesentery	1 (2.8)	1

* Collected from 7 gar examined from Tabasquillo.

† Collected only from Tabasquillo.

Mexico, Mexico City, Mexico. Infection parameters used are those proposed by Margolis et al. (1982) and Bush et al. (1997), i.e., prevalence (percent infected) and mean intensity of infection (mean number of parasites per infected fish).

Analysis of the helminth communities was carried out at the component and infracommunity levels (Holmes and Price, 1986), but we placed greater emphasis on the gar's infracommunities. Component community data will be included but not addressed in depth in the Discussion because of ambiguity in determining spatial limits to this level (Aho and Bush, 1993; Sánchez-Ramírez and Vidal-Martínez, 2002). To determine if sample size was sufficient to produce an accurate estimate of the pool of parasites using tropical gar in the sampled localities, a species-richness sample effort curve was used (Aho et al., 1991). This curve reached a maximum continuum level when sample size resulted in a high percentage of the total available parasite species in the host population. Cumulative species curves were then plotted using data from each site, Nueva Esperanza Channel and San Isidro Lake, and the observed values fitted to the Clench model to assess an asymptotic trend (Clench, 1979). The Tabasquillo sample is too small for any valid component comparisons to be made and was not considered further. The nonparametric species-richness estimator bootstrap was calculated from the observed data to extrapolate the number of missing species at the component community level (Poulin, 1998; Zeller and Esch, 1999). There are reports of various specialist helminth species in tropical fishes that do not inhabit the intestines but might nonetheless play a dominant role in the community. Most of the discussion on helminth community diversity in freshwater fishes, however, has emphasized on those that inhabit the intestine, therefore, the intestinal helminth communities were examined separately in this study. Infracommunities were described by the mean number of parasite species

per fish, the mean number of helminth individuals per fish, and the mean value of the Brillouin diversity index per fish.

RESULTS

Lengths of the 43 tropical gar examined in this study ranged from 270 to 680 mm (423 ± 83). Examination of the gonads demonstrated that all the collected specimens were sexually mature adults. Six helminth species were recorded from Nueva Esperanza Channel and 5 from San Isidro Lake (Table I). Based on cumulative species curves, more sampling is needed at each site to obtain a complete inventory of the helminth species. The present analysis indicates that 9 helminth species parasitize gar in Nueva Esperanza Channel and 10 in San Isidro Lake. However, values obtained from the nonparametric species-richness estimator (bootstrap = 6, for each of the 2 sites) suggest that the number of missing species is minimal.

The 7 fishes from Tabasquillo had 4 species of helminths (Table I), although 4 metacercariae of *Posthodiplostomum minimum* were found in the intestinal lumen of 1 host from this locality. These were considered accidental because they may have entered the fish with its prey, and were not included in further analyses.

The frequency distribution of helminth species prevalence shows 2 species groups, i.e., common parasites with prevalence

>30% included larvae (L₃) of *Contracaecum* sp. and the cestode *Proteocephalus singularis*. The 6 remaining species were rare, with prevalence <17%. Larvae (L₃) of *Contracaecum* sp. were the most abundant helminths recovered; this parasite accounted for 60% of the worms, followed by *P. singularis*, which accounted for 18%. The remaining species were not only infrequent but in low abundance.

No difference in prevalence or abundance of helminth infection between sexes of tropical gar was observed for any of the helminth species. Moreover, there was no significant correlation observed between the total number of species and the total number of individual helminths and host size; the same was true for the number of L₃ *Contracaecum* sp. and *P. singularis* versus host size.

Of the 36 tropical gar examined from the Nueva Esperanza Channel and San Isidro Lake localities, 30 had helminth parasites and 6 had none (Table I). The number of helminth species per individual host ranged from 1 to 5 in the 30 infected hosts. Fourteen of the 30 possessed only a single helminth species. Eleven of the infracommunities had 2 helminth species, 4 had 3, and only 1 had the maximum of 5 helminth species. The total number of helminths of all species (intestinal and nonintestinal) per host varied from 1 to 27, with a total of 219 worms collected from all hosts. The average number of species per host was 1.4 ± 1.0 , and the average number of individual parasites per host was 6.1 ± 6.4 . The Brillouin index calculated for total species varied between 0 and 1.1, with an average value of 0.2 ± 0.3 .

Among the 8 identified helminth species, 2, both specific to the gar, were intestinal. These were *Perezitrema bychowskyi* and *P. singularis*. The larvae (L₃) of *Contracaecum* sp. were most frequently found encysted and deeply embedded in the intestinal wall and thus were not considered as inhabitants of the intestinal lumen. Twelve of 36 hosts (33%) had at least 1 intestinal helminth, but only 4 (11%) had concurrent infections of both intestinal species. The number of intestinal helminths varied between 1 and 15, with a total of 52 intestinal helminths collected. The average number of intestinal helminth species per host was 0.4 ± 0.7 , and the average number of worms per host was 1.4 ± 3.2 . The Brillouin index for intestinal species varied between 0 and 0.5, with an average value of 0.04 ± 0.1 .

DISCUSSION

The analysis of the helminth parasites in the tropical gar, *A. tropicus*, showed impoverished, low-density infracommunities, with low to medium similarity provided by a dominant allogenic generalist species (Esch et al., 1988) and, to a lesser degree, an autogenic specialist species. An infrequent suite element of the helminth fauna is determined by sympatry with other fishes.

The most abundant species, *Contracaecum* sp. (L₃), is allogenic and a nonspecialist, and its presence reflects the abundance of these parasites in the freshwater fishes of the region (Salgado-Maldonado et al., 1997, 2004; Vidal-Martínez et al., 2001). Adults of *Contracaecum multipapillatum* (von Drasche, 1882) and *Contracaecum rudolphii* (Hartwich, 1964) have been recorded in the piscivorous birds *Nycticorax nycticorax* and *Phalacrocorax olivaceus* in Tabasco (R. Amaya-Huerta, unpubl.). Infections of these helminths in the tropical gar may

originate by consumption of intermediate host crustaceans during the early growth stages of this fish. These may also, however, be related to a lateral transfer of these larvae, as has been seen in other anisakids (Scott, 1954; Wootten and Smith, 1975). We examined only adult gar, which are predominantly piscivorous; only larvae (L₃) of *Contracaecum* sp. were present, and we did not find any evidence of cysts possessing dead worms. Thus, data suggest lateral transfer acquisition of *Contracaecum* sp. worms by the gar. The presence of *Contracaecum* sp. larvae is related to the sympatry of tropical gar with other fish species. However, *Contracaecum* sp. larvae provided most of the similarity observed between infracommunities.

The cestode *P. singularis* was the second most abundant species. This proteocephalid has been recorded previously in *Lepisosteus platostomus*, *L. osseus*, and *L. platyrhincus* from the United States (Freze, 1965; Schmidt, 1986), in *L. tristoechus* from Cuba (Barus and Moravec, 1967; Freze and Rysavy, 1976), and in *A. tropicus* from Tabasco (Osorio Sarabia et al., 1987). The life cycle of this cestode in Mexico is unknown, but we assume that a copepod serves as an intermediate host. Pleurocercoids of proteocephalids have been found in the viscera of several freshwater fishes in Tabasco (Salgado-Maldonado et al., 2003), and a similar pattern of limited transmission suggested for *Contracaecum* sp. may be true for this cestode. Based on these observations and assumptions, the most abundant helminths are most likely transmitted by way of piscivory to gar.

Two other infrequent specialist helminth species were recorded in the tropical gar. These included the trematode *P. bychowskyi*, and the nematode *Cystoopsis atractostei* (Moravec and Salgado-Maldonado, 2002, 2003). To date, *P. bychowskyi* adults have only been found in *A. tropicus*. Species of *Perezitrema* (Barus and Moravec, 1967) are typical of gar, i.e., *Perezitrema vigerasi* (Barus and Moravec, 1967) in *L. tristoechus* in Cuba and *P. bychowskyi*, a parasite of *A. tropicus* in Mexico and Nicaragua (Moravec and Salgado-Maldonado, 2002). The only other known *Cystoopsis* species is a parasite of acipenserids in the Holarctic. The presence of 3 specialist species in the tropical gar confirms that its helminth fauna has an appreciable degree of specificity.

The analysis also demonstrates the presence of an infrequent suite element in the helminth community of *A. tropicus* consisting of the allogenic metacercariae *Diplostomum* sp. and *Clinostomum complanatum* and the nematode larvae of *Spiroxys* sp. These 3 species are generalists, with records in a variety of hosts and a broad distribution in the hydrographic basins of Mexico, including the Yucatán Peninsula (Moravec et al., 1995; Scholz et al., 1995), the Grijalva–Usumacinta basin (Salgado-Maldonado et al., 2004), the Balsas River basin (Salgado-Maldonado, Cabañas-Carranza, Caspeta-Mandujano et al., 2001), the Lerma–Santiago drainage (Salgado-Maldonado, Cabañas-Carranza, Soto-Galera et al., 2001), the Ayuquila River (Salgado-Maldonado, Mercado-Silva et al., 2004), and the Pánuco River basin (Salgado-Maldonado, Cabañas-Carranza, Soto-Galera et al., 2004).

At the component community level, the core suite of 3 specialist helminth species, i.e., *P. bychowskyi*, *P. singularis*, and *C. atractostei*, which accounts for 43% of the helminth recorded in this host, seems to vary spatially because of the presence of the generalists acquired through food web links. Although the nonspecific parasites of the tropical gar occur sporadically,

Contracaecum sp. larvae are a persistent structural component of these communities. Data from this study show that a considerable proportion of the helminths that are not specific to the tropical gar are allogenic larvae, which do not mature in this host, a common aspect of freshwater fishes in Mexico (Moravec et al., 1995; Scholz et al., 1995; Salgado-Maldonado et al., 1997, 2004; Salgado-Maldonado, Cabañas-Carranza, Caspeta-Mandujano et al., 2001; Salgado-Maldonado, Cabañas-Carranza, Soto-Galera et al., 2001; Salgado-Maldonado, Cabañas-Carranza et al., 2004).

The data in this study are notable in that even though the available literature indicates that the infracommunities in basal actinopterygian fishes, with the exception of *A. calva* (Aho et al., 1991), have low average species richness, infracommunities of tropical gar are among the poorest. The impoverished and low-density characteristics of the component and infracommunities are probably related to the tropical gar's feeding habits. Gar are top predators, and *A. tropicus* fits this pattern in being primarily piscivorous (Mora Janett et al., 1996). The comparison between the species richness of *A. tropicus* and that described for bowfin, *A. calva*, in South Carolina (Aho et al., 1991) is of interest. The broad feeding preferences of *A. calva* were suggested to favor a rich helminthological community, whereas the strict piscivorous diet of *A. tropicus* limits the acquisition of helminth parasites (see also Guégan and Kennedy, 1993). A generalist feeder is exposed to a greater number of potential intermediate host species, resulting in a greater helminth richness than that of a specialized predator (Fiorillo and Font, 1996). For example, the broad, opportunistic diet of the tropical cichlid *Cichlasoma urophthalmus* favors a rich helminthological community (Salgado-Maldonado and Kennedy, 1997).

The data from this study also indicate that the helminth component community of *A. tropicus* has persisted for the past 30 yr, at least, because all the observed helminths have been reported previously (Caballero y Caballero and Caballero-Deloya, 1975; Reséndez-Medina and Salvadores, 1983; Osorio-Sarabia et al., 1987).

Bangham and Venard (1942) recorded 6 helminth species parasitizing the short-nosed gar, *L. platostomus*, of Reelfoot Lake, Tennessee. Each of the 6 hosts examined was parasitized at least by 2 species of gar specialists, i.e., the trematodes *Macroderoides spiniferus* Pearse, 1924, and *Paramacroderoides echinus* Venard, 1941; a third gar specialist, *P. singularis*, was also recorded with a high prevalence (83%). Compared with the helminth communities of 3 *Lepisosteus* species described from Texas (Castro and McDaniel, 1967), the helminth communities of *A. tropicus* are richer but not as clustered. In the Texas study, fewer numbers of helminth species were found. There were also fewer parasite-free hosts, a greater number of worms, and a higher average number of individuals per host, even though the number of fishes examined for each of the 3 host species was lower than that in this study. However, dominance of the bass tapeworm, *Proteocephalus ambloplites* (Leidy, 1887) Benedict, 1900, in the gar species examined from Texas was very high. In addition, only 3 of the helminth species recorded by Castro and McDaniel (1967) can be considered as gar specialists, i.e., *Dichelyne lepisosteus* Castro and MacDaniel, 1967, *M. spiniferus*, and *P. echinus* (Yamaguti, 1971; Gibson, 1996). The taxonomic status of *D. lepisosteus*, how-

ever, is doubtful because it may be accidentally acquired by gar while feeding on other fishes.

One of the expectations at the outset of this study was that helminth communities in freshwater fishes from areas far from the host's evolutionary point of origin would be poorer and include fewer specialist species compared with those from geographic areas closer to the host's point of origin. This would conform to the suggestions of Kennedy and Guégan (1999) and to Brown's (1984) hypothesis as extrapolated to parasites by Fedynich et al. (1986) and Radomski et al. (1991). The lepisosteids of Mexico are a Nearctic-derived component inhabiting a site distant from their point of origin. According to Brown's hypothesis (1984), this should contribute to a relatively poor helminth community and a lower number of specialist species when compared with lepisosteids from northern latitudes. The data in this study do not support this hypothesis and, indeed, confirm host specificity as an important process in parasite community composition, as suggested by other authors (Dogiel, 1962; Holmes, 1990; Choudhury and Dick, 1998).

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