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[Article]

Spatial and Temporal Distribution of the Asian Fish Tapeworm *Bothriocephalus acheilognathi* (Cestoda: Bothriocephalidea) in the Rio Grande (Río Bravo del Norte)

Megan G. Bean and Timothy H. Bonner*

Department of Biology/Aquatic Station, Texas State University–San Marcos, 601 University Drive, San Marcos, Texas 78666, USA

Abstract.—Recent collections of the Asian fish tapeworm *Bothriocephalus acheilognathi* in the Rio Grande have raised concern about the potential impacts on Rio Grande endemic and imperiled fishes. The objectives of this study were to determine distribution and definitive hosts of the Asian fish tapeworm within the Rio Grande drainage and to quantify occurrences and abundances. In total, 1,992 fish spanning 11 families were collected and examined for Asian fish tapeworms in the Rio Grande and the Pecos and Devils rivers. The parasite was collected from red shiners *Cyprinella lutrensis*, Tamaulipas shiners *Notropis braytoni*, sand shiners *N. stramineus*, river carpsuckers *Carpiodes carpio*, plains killifish *Fundulus zebrinus*, western mosquitofish *Gambusia affinis*, blue suckers *Cycleptus elongatus*, blacktail shiners *Cyprinella venusta*, proserpine shiners *Cyprinella proserpina*, and Manantial roundnose minnow *Dionda argentosa*, with the latter four species being new host records. Monthly collections of red shiners from Big Bend National Park exhibited prevalence levels above 15% in January–March and December and below 10% during April–June and October. With over 50% of the Rio Grande icthyofauna in Texas considered imperiled, the occurrence and pathological effects of the Asian fish tapeworm in combination with reduced water quantity and quality and increased habitat fragmentation are of concern for these taxa.

Introduction of exotic and invasive host taxa into new drainages facilitates the spread of potentially detrimental exotic parasites and pathogens (Hoffman and Schubert 1984) and contributes to the global spread of such parasites (Hoffman and Schubert 1984; Font 2003; Taraschewski 2006). Successful invaders often exhibit similar characteristics, such as physiological tolerance to a wide range of conditions, adaptation to harsh environments, and short generation times (Brown 1989; Elrich 1989). One such invader is the Asian fish tapeworm *Bothriocephalus acheilognathi* (Cestoda: Bothriocephalidea), which has been introduced worldwide, with one of the most recent findings in the Rio Grande (Río Bravo del Norte) of North America (Bean et al. 2007). The Asian fish tapeworm is a successful invader and colonizer in part because of its low specificity for definitive and intermediate hosts (Körting 1975; Dove and Fletcher 2000).

The natural geographic range of the Asian fish tapeworm is Japan (original description by Yamaguti 1934), China, and the Amur River basin in Russia (Bauer and Hoffman 1976; Pool and Chubb 1985; Pool 1987; Scholz 1997). The grass carp *Ctenopharyngodon idella* is one of the Asian fish tapeworm's native hosts (Choudhury et al. 2006), and worldwide shipments of grass carp for macrophyte control contributed considerably to the global introduction of the parasite (Hoffman 1980; Andrews et al. 1981). The Asian fish tapeworm is established on six continents and currently infects over 100 species of fish (Salgado-Maldonado and Pineda-López 2003). It is established in the USA, Canada, and Mexico (Heckmann and Deacon 1987; Brouder and Hoffnagle 1997; Ward 2005; Choudhury et al. 2006; Bean et al. 2007), with transfer into new drainages likely attributable to baitfish introductions (Heckmann et al. 1993; Choudhury et al. 2004).

Ease of Asian fish tapeworm colonization is partly a result of the short and relatively simple life cycle. The parasite requires as little as 2 weeks to complete its life cycle in an intermediate host (Körting 1975). Eggs are passed with fish feces, and mobile coracidia emerge after embryonation. Coracidia are consumed by an intermediate host, a cyclopoid copepod (e.g., *Acanthocyclops*, *Macrocyclops*, *Mesocyclops*, *Tropocyclops*, and *Diacyclops*; Körting 1975; Marcogliese and Esch 1989; Díaz-Castaneda et al. 1995). The life cycle is completed when fish ingest infected copepods. Water temperature has a discernable influence on the successful completion of each stage of the life cycle, with optimal temperatures for development and growth ranging between 20°C and 30°C (Liao and Shih 1956).

Objectives of this study were to determine the distribution and definitive hosts of the Asian fish tapeworm within the Rio Grande drainage and to

* Corresponding author: tbonner@txstate.edu

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TABLE 1.—Site information for fish sampling locations used to detect Asian fish tapeworm occurrence in the Rio Grande drainage, 2006 and 2007 (NM = New Mexico; TX = Texas).

Site code	Site location	Drainage	Coordinates	Dates sampled
RM1	Los Lunas, NM	Rio Grande	34°48′18″N, 106°43′02″W	Mar 2007
RM2	Highway 380, NM	Rio Grande	33°55′10″N, 106°51′02″W	Mar 2007
RM3	Presidio, TX	Rio Grande	29°33′23″N, 104°23′41″W	Jun 2006
RM4	Santa Elena Canyon, TX	Rio Grande	29°09′54″N, 103°36′35″W	Feb–Dec 2006
RT5	Terlingua Creek, TX	Rio Grande	29°09′58″N, 103°36′38″W	Mar–Dec 2006
RM6	Boquillas Canyon, TX	Rio Grande	29°11′57″N, 102°55′05″W	Feb–Dec 2006
RT7	Pinto Creek, TX	Rio Grande	29°11′20″N, 100°42′11″W	Mar 2007
RM8	Quemado, TX	Rio Grande	28°56′12″N, 100°38′36″W	Sep 2006–Oct 2007
RM9	Larado, TX	Rio Grande	27°41′56″N, 99°44′42″W	Feb 2007
RM10	San Ygnacio, TX	Rio Grande	27°02′58″N, 99°26′54″W	Apr 2007
PM11	Highway 84, NM	Pecos River	34°56′41″N, 104°42′09″W	Mar 2007
PM12	Fort Sumner, NM	Pecos River	34°28′24″N, 104°15′36″W	Mar 2007
PM13	Highway 70E, NM	Pecos River	33°34′18″N, 104°22′24″W	Mar 2007
PM14	County Road 507, NM	Pecos River	32°59′20″N, 104°19′27″W	Mar 2007
PM15	Artesia at Highway 82, NM	Pecos River	32°50′27″N, 104°19′26″W	Mar 2007
PT16	Independence Creek, TX	Pecos River	30°27′33″N, 101°45′23″W	Jun 2007
DM17	Dolan Falls, TX	Devils River	29°53′01″N, 100°59′38″W	Dec 2007

quantify prevalence, mean abundance, and mean intensity and assess patterns of occurrence at multiple sites on the Rio Grande. These parameters were then assessed to examine the spread and extent of this parasite species, possible source of introduction, and potential threat to the Rio Grande ichthyofauna.

Methods

Ten sites on the Rio Grande, six sites on the Pecos River, and one site on the Devils River were selected to assess Asian fish tapeworm prevalence, mean abundance, and mean intensity over a broad distribution within the Rio Grande drainage (Table 1; Figure 1). Codes were given to each site to reference drainage (R = Rio Grande, P = Pecos River, D = Devils River), main stem (M) or tributary (T), and a unique site number. Fish were collected monthly in Big Bend National Park from RM4 and RM6 during February–December 2006 and from RT5 during March–December 2006. The RM8 site was sampled seasonally during September 2006 through October 2007. All other sites were sampled opportunistically in 2007. At each site, up to 40 specimens of the red shiner *Cyprinella lutrensis* were randomly collected from all available geomorphic units with a 3- × 1.8-m seine (mesh size = 3.1 mm). At sites where red shiners exhibited low abundance or were not present, a congener (blacktail shiner *Cyprinella venusta*) was collected. These randomly collected fish were used to quantify site prevalence, mean abundance, and mean intensity. Other species exhibiting signs of infection (e.g., distended abdomens) were also retained from each site to determine the breadth of definitive hosts in the drainage but were not used to quantify prevalence, abundance, or intensity. All fish were anesthetized with a lethal dose of tricaine methanesulfonate (FINQUEL; Argent Chemical Laboratories, Redmond, Washington) and preserved in 4% formaldehyde solution.

Spatial and temporal patterns of habitat parameters were assessed with principal components analysis (PCA) using Canoco version 4.5 software (ter Braak 1986). Measurements of temperature (°C), specific conductance (S/cm), dissolved oxygen (mg/L), discharge (m^3/s), pH, and sulfate (mg/L) were averaged over sampling dates to obtain site estimates and then were *z*-score transformed (Krebs 1999) before PCA. Habitat parameters were collected at various gauges (International Boundary and Water Commission: gauges 13109, 13206, 13225, 13228, 13230, 13239, 13560, 15818, 15839, and 16730; Texas Commission on Environmental Quality: gauges C721, C757, C759, C764, and C768; U.S. Geological Survey: gauges 08331510, 08355490, 08382830, 08385522, 08396500, 08394024, and 08447020). Polygons were drawn around site scores by river section to assess similarities and differences among sections along linear combinations of physical habitats for the first and second principal component (PC) axes (PC-I and PC-II). Site habitat associations were then compared with Asian fish tapeworm prevalence to assess patterns of occurrence.

In the laboratory, the fish gastrointestinal tracts were examined and Asian fish tapeworms were identified from the heart-shaped scolex with a pair of deep bothria (Scholz 1997). Identification was based on previous morphological and genetic analyses by Bean et al. (2007). Voucher specimens have been deposited into the U.S. National Parasite Collection (collection number 98874) as well as the Institute of Parasitology at the Academy of Sciences of the Czech Republic (collection number C-15). Prevalence (number of infected fish of one species divided by the total

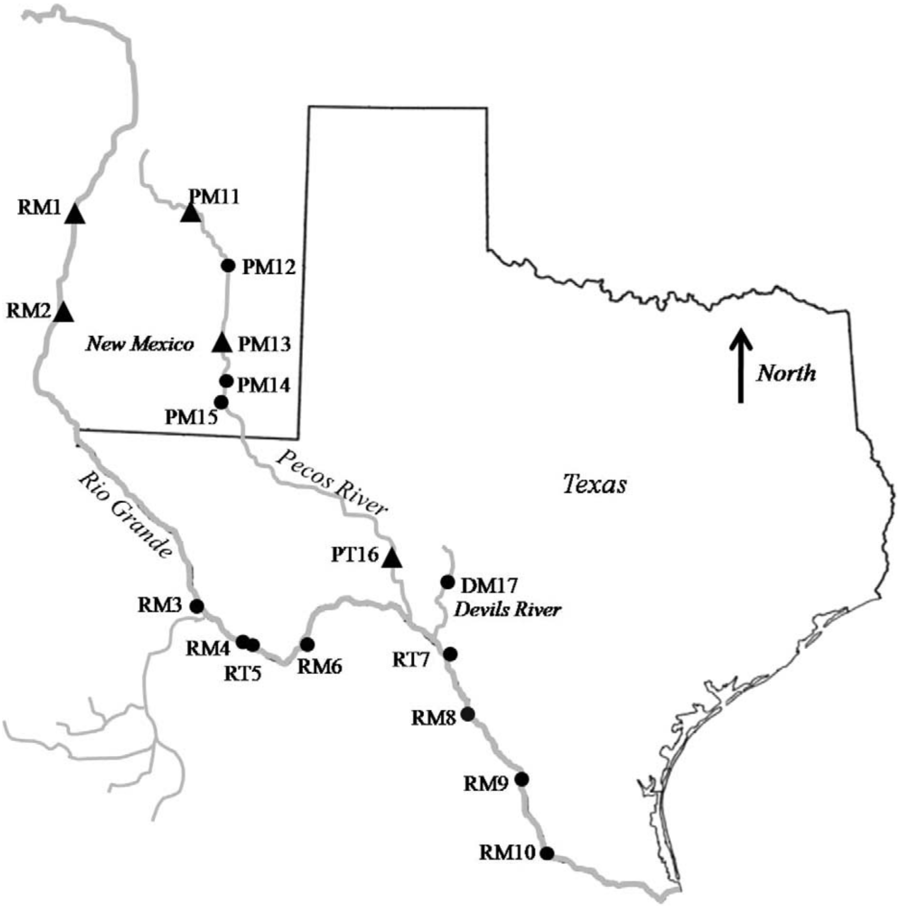

FIGURE 1.—Locations of fish collections from the Rio Grande and the Pecos and Devils rivers in 2006 and 2007 (site codes are defined in Table 1). Circles indicate sites of Asian fish tapeworm occurrence; triangles indicate sites where the parasite was not detected.

number of fish examined of the same species), mean abundance (total number of tapeworms in a fish species divided by the total number of fish examined of the same species), and mean intensity (the average number of tapeworms in a single fish host) were calculated for comparison among sites (terminology from Bush et al. 1997). Bootstrapped 95% confidence intervals (CIs) were constructed for mean abundance and mean intensity following Rózsas et al. (2000). To examine potential differences between Big Bend National Park main-stem and tributary parasite populations, prevalence was compared across months for main-stem (RM4 and RM6) and tributary (RT5) sites using a chi-square test for heterogeneity. Samples were pooled across main-stem sites within monthly collections based on the close proximity and similar habitat availability of the sites.

Results

Overall, 1,993 fish spanning 11 families and 31 species were collected from 17 sites within the Rio Grande drainage (Table 2). Ten species in four families (Cyprinidae, Catostomidae, Fundulidae, and Poeciliidae; 32% of the total number of species collected) were definitive hosts for the Asian fish tapeworm. Definitive hosts were the red shiner, blacktail shiner, proserpine shiner, Manantial roundnose minnow, Tamaulipas shiner, sand shiner, river carpsucker, blue sucker, plains killifish, and western mosquitofish. Infected fish were taken from the main-stem Rio Grande in Texas at sites RM3–RM10; the Pecos River at sites PM12, PM14, and PM15; and the Devils River at site DM17. The parasite was not found in fish taken from the main-stem Rio Grande in New Mexico.

Across all sites, prevalence ranged from 3% (site

TABLE 2.—List of fish species collected to determine Asian fish tapeworm occurrence in the Rio Grande drainage, 2006 and 2007. Species documented as definitive hosts are indicated by an X.

Family	Species	*N*	Definitive host
Cyprinidae	Red shiner *Cyprinella lutrensis*	1,411	X
	Blacktail shiner *Cyprinella venusta*	257	X
	Proserpine shiner *Cyprinella proserpina*	1	X
	Common carp *Cyprinus carpio*	1	—
	Manantial roundnose minnow *Dionda argentosa*	1	X
	Roundnose minnow *D. episcopa*	3	—
	Plains minnow *Hybognathus placitus*	4	—
	Speckled chub *Macrhybopsis aestivalis*	31	—
	Texas shiner *Notropis amabilis*	3	—
	Tamaulipas shiner *N. braytoni*	91	X
	Arkansas River shiner *N. girardi*	1	—
	Sand shiner *N. stramineus*	72	X
	Fathead minnow *Pimephales promelas*	3	—
	Bullhead minnow *P. vigilax*	1	—
Catostomidae	River carpsucker *Carpiodes carpio*	3	X
	White sucker *Catostomus commersonii*	4	—
	Blue sucker *Cycleptus elongatus*	22	X
	Gray redhorse *Moxostoma congestum*	1	—
Characidae	Mexican tetra *Astyanax mexicanus*	4	—
Ictaluridae	Blue catfish *Ictalurus furcatus*	1	—
	Channel catfish *I. punctatus*	3	—
Atherinopsidae	Inland silverside *Menidia beryllina*	26	—
Fundulidae	Gulf killifish *Fundulus grandis*	3	—
	Plains killifish *F. zebrinus*	3	X
Poeciliidae	Western mosquitofish *Gambusia affinis*	9	X
	Largespring gambusia *G. geiseri*	1	—
Cyprinodontidae	Sheepshead minnow *Cyprinodon variegatus*	1	—
Centrarchidae	Longear sunfish *Lepomis megalotis*	1	—
	Largemouth bass *Micropterus salmoides*	1	—
Percidae	Rio Grande darter *Etheostoma grahami*	4	—
Cichlidae	Rio Grande cichlid *Cichlasoma cyanoguttatum*	1	—

RM8: $N = 38$ red shiner and blacktail shiner) to 28% (RM6: $N = 25$ red shiner; RT5: $N = 39$ red shiner) during months when mean monthly temperatures were within the Asian fish tapeworm's optimal growth range of 20–30°C. Overall, prevalence was highest in Big Bend National Park (RM4, RT5, and RM6) and was lowest on the lower Rio Grande at RM8. Within the Big Bend National Park reach of the Rio Grande, 790 red shiners were taken across monthly collections from two main-stem sites (RM4 and RM6), and 306 red shiners were taken across monthly collections from one tributary site (RT5). Prevalence differed ($\chi^2 = 32.88$, df $= 8$, $P < 0.01$) between main-stem and tributary sites across months. Main-stem prevalence was over 15% in January–March and December, with the highest prevalence (27%) recorded in January ($N = 115$ red shiner; Table 3). Prevalence was less than 10% during April–November, with the lowest prevalence (7%) observed in April ($N = 55$ red shiner). Parasite prevalence at tributary sites was less than 10% for the duration of the year except in June (28%; $N = 40$ red shiner) and November (16%; $N = 38$ red shiner). Mean abundance for RM4, RT5, and RM6 ranged from 0.10 (95% CI = 0.00–0.25) to 0.73 (95% CI = 0.35–1.25; Table 3). Mean intensity ranged from 1.17 (95% CI = 1.00–1.33) to 7.5 (95% CI = 1.33–25.00). Highest intensity observed was 37 in a 43-mm fish.

The PC-I and PC-II axes explained 66.8% of the total variation in habitat among all rivers. Axis PC-I explained 46.4% of the total variation and described a temperature, discharge, pH, and dissolved oxygen gradient (Figure 2). Sites with strong positive sample scores were associated with greater discharge, dissolved oxygen, and pH, whereas sites with strong negative sample scores were associated with higher temperatures. Axis PC-II described a specific conductance and sulfate gradient. Sites with strong positive sample scores were associated with greater specific conductance and dissolved oxygen, whereas collections with strong negative sample scores were associated with greater sulfate concentrations and pH. With sample scores grouped by river section, Rio Grande sites in New Mexico (RM1 and RM2) had greater discharge and pH, Big Bend National Park sites (RM4, RT5, and RM6) had higher temperatures and sulfate concentrations, lower Rio Grande sites (RM8) were associated with higher temperatures, and Pecos River sites in New Mexico (PM11–PM15) were associated with greater specific conductance, dissolved oxygen, pH, and discharge.

TABLE 3.—Monthly prevalence (number of infected fish divided by the total number of fish), abundance (total number of tapeworms divided by the total number of fish examined), and intensity (average number of tapeworms in an individual fish) of Asian fish tapeworms collected from red shiners in Big Bend National Park during January–December 2006. Abundance and intensity estimates include 95% confidence intervals. January data are from Bean et al. (2007).

	Main stem				Tributary			
Month	*N*	Prevalence (%)	Mean abundance	Mean intensity	*N*	Prevalence (%)	Mean abundance	Mean intensity
Jan	115	27	0.52	1.9	—	—	—	—
Feb	76	18	0.37 (0.20–0.63)	2.0 (1.4–2.6)	—	—	—	—
Mar	46	22	0.41 (0.17–0.74)	1.9 (1.2–2.6)	11	9	0.18 (0.00–0.55)	2.0
Apr	55	7	0.11 (0.02–0.24)	1.5 (1.0–2.0)	38	0	—	—
May	65	9	0.69 (0.08–3.06)	7.5 (1.3–25.0)	40	8	0.10 (0.00–0.25)	1.3 (1.0–1.7)
Jun	66	8	0.11 (0.03–0.24)	1.4 (1.0–1.6)	40	28	0.73 (0.35–1.27)	2.6 (1.7–3.6)
Jul	64	11	0.2 (0.06–0.45)	1.9 (1.0–3.0)	—	—	—	—
Aug	58	14	0.31 (0.10–0.84)	2.3 (1.1–4.8)	38	8	0.58 (0.05–2.39)	7.3 (1.0–12.67)
Sep	61	11	0.26 (0.10–0.57)	2.3 (1.6–3.3)	25	0	—	—
Oct	66	8	0.21 (0.05–0.71)	2.8 (1.0–5.6)	38	5	0.32 (0.00–0.87)	6.0 (5.0–7.0)
Nov	55	13	0.25 (0.09–0.47)	2.0 (1.3–2.4)	38	16	0.18 (0.05–0.34)	1.2 (1.0–1.3)
Dec	63	17	0.40 (0.19–0.70)	2.3 (1.6–3.0)	38	5	0.34 (0.00–1.45)	6.5 (2.0–11.00)

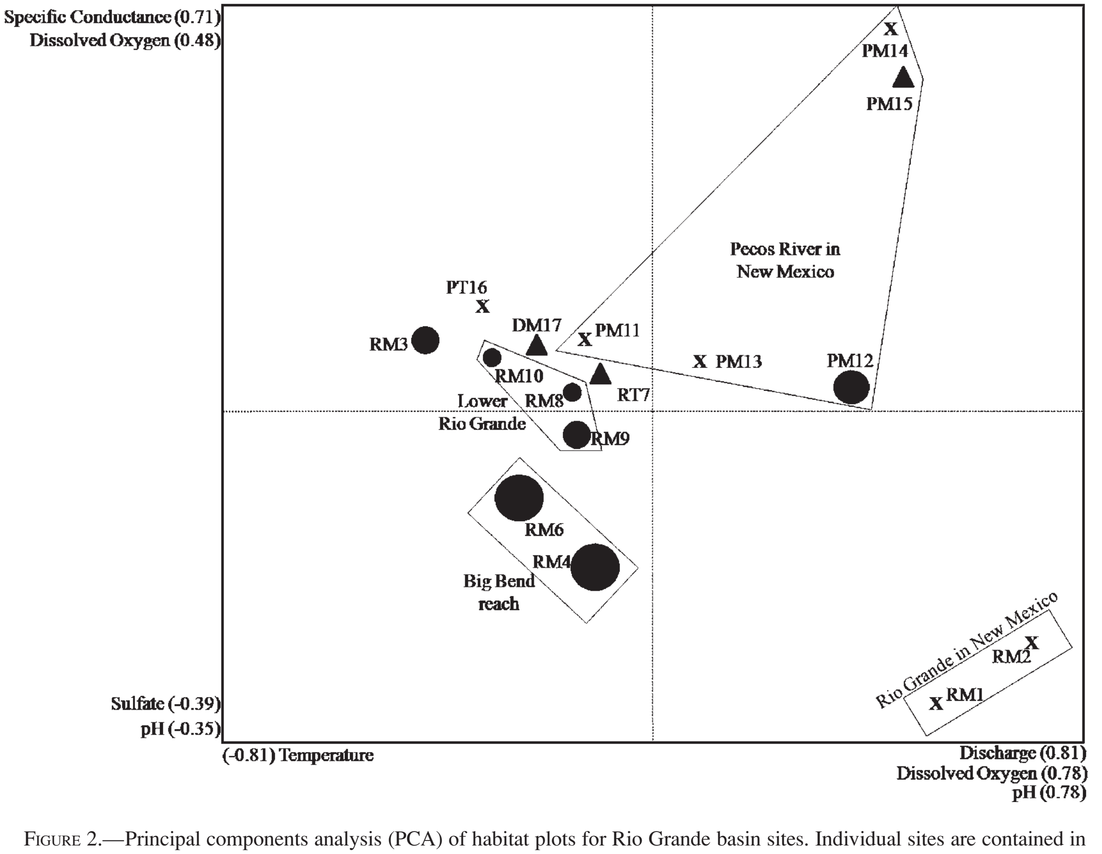

FIGURE 2.—Principal components analysis (PCA) of habitat plots for Rio Grande basin sites. Individual sites are contained in ordination space, and the strongest habitat loadings are located in the margins. Asian fish tapeworms were not detected at sites marked with an X. Triangles indicate sites with confirmed Asian fish tapeworm occurrence (prevalence was not calculated), and circles are scaled to visually represent prevalence at sites for which prevalence was calculated (scaled to the highest observed prevalence at the site, 2–27%).

Discussion

Spatial differences in prevalence of the Asian fish tapeworm were found among reaches of the Rio Grande drainage, with higher prevalence being observed in the Big Bend National Park reach than in the lower Rio Grande and upper Pecos River. Differences among reaches might be attributable to interactions with biotic and abiotic factors, including temporal variations in the intermediate host populations and sensitivity of the Asian fish tapeworm life cycle stages to abiotic parameters (Liao and Shih 1956). The PCA indicates that water temperature is related to Asian fish tapeworm prevalence when comparing position of site scores on PC-I and PC-II and prevalence levels observed at each site. Temperature is an important abiotic parameter affecting survival and development of all life stages of the Asian fish tapeworm (Liao and Shih 1956), and spatial patterns of Asian fish tapeworm prevalence suggest that temperature might be an important factor controlling the species' distribution in the Rio Grande. Sites with higher mean annual temperatures were associated with the presence of the Asian fish tapeworm, while the parasite was not collected at sites with lower mean annual temperatures. Greater river discharge, pH, and specific conductance also were associated with sites where the Asian fish tapeworm was not detected. Lower prevalence within the lower reach of the Rio Grande as compared with the Big Bend National Park reach might result from the effects of hypolimnetic-release reservoirs on environmental factors, including decreased downstream temperatures, decreased availability of nutrients, and altered water chemistry (Edwards 1978).

Annual decreases in streamflow for the Big Bend National Park tributary site (RT5) reduce the stream to a series of pools that are disconnected from the main stem. Slow velocities and lentic habitats can promote the retention and consumption of infected copepods, resulting in an increase in Asian fish tapeworm prevalence and abundance (summarized by Marcogliese 2001). One month after RT5 became lentic, prevalence increased from 8% to 28% and abundance increased from 0.10 to 0.73. The concentration of infected fish and copepods in these isolated pools might also serve as a continuous source of infected hosts to the main stem when a hydrologic connection is reestablished by increased streamflow, which has been suggested in other systems (Choudhury et al. 2004).

Patterns of Asian fish tapeworm occurrence within the drainage and PCA indicate two points of introduction in the drainage. Greater prevalence in the Big Bend National Park region, lower prevalence downstream, and the lack of Asian fish tapeworm collections at Rio Grande sites in New Mexico suggest that the Río Conchos is one likely point of introduction within the system. The Río Conchos is a probable point of introduction because the occurrence of this tapeworm has been confirmed in many Mexican systems (Salgado-Maldonado et al. 2001a, 2001b). Asian fish tapeworm occurrence at lower Pecos River sites in New Mexico and its absence downstream from site PM15 near the Malaga Bend salt springs suggest that salinity is inhibiting Asian fish tapeworm dispersal downstream, as salinity can decrease survival of coracidia (Pietrock and Marcogliese 2003). Dispersal upstream into the upper Pecos River sites is likely inhibited by the lower water temperatures that are characteristic of snowmelt systems. This isolated section of Asian fish tapeworm occurrence is suggestive of a second point of introduction, possibly from a hatchery in the area where the Asian fish tapeworm is documented to occur (Choudhury et al. 2006).

Occurrence and pathological effects of the Asian fish tapeworm are a concern for management of ichthyofauna in the Rio Grande and nearby watersheds. Over 50% of the Rio Grande ichthyofauna in Texas are considered imperiled (Hubbs et al. 2008), and possible short- and long-term pathological impacts on these taxa include intestinal blockage and perforation, distended abdomen, necrosis, inflammation, hemorrhaging, loss of intestinal microvilli, and loss of enterocytes, which can reduce growth and decrease survivorship (Scott and Grizzle 1979; Hoffman 1980; Hoole and Nisan 1994; Hansen et al. 2006; Bean and Bonner 2009). Collectively, these pathogenic effects add additional stress to an assemblage that is already affected by reduced water quantity, reduced water quality, and increased habitat fragmentation (Edwards and Contreras-Balderas 1991). Pathogenic effects and degraded habitat also could hinder efforts to reintroduce the Rio Grande silvery minnow *Hybognathus amarus* into the Big Bend National Park reach as copepods make up at least 10% of this fish's diet (Watson et al. 2009). Furthermore, occurrence of the Asian fish tapeworm within the Rio Grande basin serves as a source of dispersal into nearby watersheds, potentially affecting a large pool of endemic fish species as well as recreational and commercial fisheries east of the Rio Grande in Texas.

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