

# Metazoan parasite community of blue sea catfish, *Sciades guatemalensis* (Ariidae), from Tres Palos Lagoon, Guerrero, Mexico

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**Abstract** The seasonal dynamic of the metazoan parasite community of the blue sea catfish (*Sciades guatemalensis*) from Tres Palos Lagoon, Guerrero, Mexico, was studied at the component community and infracommunity levels. A total of 382 fish were collected during the regional dry and rainy seasons (a total of seven seasons) between April 2000 and September 2007. Nine helminths were collected: *Neotetraonchus* sp., *Pseudoacanthostomum panamense*, *Austrodiplostomum compactum*, *Clinostomum complanatum*, *Metadena* sp., *Pseudoleptorhynchoides lamothei*, *Neoechinorhynchus* cf. *golvani*, *Hysterothylacium perezii*, and *Contracaecum* sp. The infection dynamics of some dominant helminths was influenced by environmental changes generated by the dry/rainy season cycle. Nested (non-random) species composition was observed in the infracommunities during almost all of the sample period. Variation in the intensity of nestedness was attributed to a sequential colonization process over time by the dominant helminths.

## Introduction

The blue sea catfish (*Sciades guatemalensis*) is found along the Pacific coast of Mesoamerica and Central America from

the Gulf of California to Panama (Castro-Aguirre et al. 1999). Due to constant local demand, it is a major fishery catch in the coastal lagoons of Guerrero state, Mexico. Considered to be a carnivorous secondary consumer, it is a characteristic estuarine species of the Guerrero coastal lagoon system (Yáñez-Arancibia 1978). The species' parasite fauna from two coastal lagoons has been reported previously (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007), but no studies have focused on the stability of its parasite community over time in terms of species composition and abundance.

The majority of research in Mexico on temporal variation in tropical parasite communities has involved freshwater cichlids (Salgado-Maldonado 1993; Pineda-López 1994; Jiménez 2003; Vidal-Martinez and Poulin 2003), although one study was made of the parasite community of an estuarine eleotrid, *Dormitator latifrons*, (Violante-González et al. 2008). Some of these studies have shown high variation in parasite abundance over time in response to alterations generated by the seasonal dry/rain cycles, which presumably affect the parasite species recruitment process (Salgado-Maldonado 1993; Violante-González et al. 2008). Abundance has also been shown to respond to seasonal increases in host feeding and reproductive activity influenced by seasonal water temperature fluctuations (Jiménez 2003; Jiménez-García and Vidal-Martínez 2005; Violante-González et al. 2008). Pineda-López (1994), in contrast, suggested that helminth communities in tropical climates are stable or change very little over time. Therefore, it is still unclear, if tropical estuarine parasite communities experience temporal changes in abundance and species composition over time.

For several years we have been collecting parasite community data from Tres Palos Lagoon, Guerrero, during the two seasons that occur regionally (dry and rainy). The

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objective of this study was to determine if helminth community structure and species composition vary over time in blue sea catfish, *S. guatemalensis*, from Tres Palos Lagoon.

## Materials and methods

Tres Palos Lagoon (16°47' N, 99°39' W; Fig. 1) is located on the Pacific coast of Mexico, 25 km east of Acapulco. It covers 55 km<sup>2</sup> (5,500 ha) and ranges in depth from 0.5–8 m. Continuous discharge of urban waste into the lagoon via the Sabana River have made it eutrophic (Violante-González 2006) and consequently primary productivity is very high (80 to 106 µg L<sup>-1</sup> chlorophyll-*a* concentration), particularly during the rainy season (Violante-González et al. 2008). Water in the lagoon is brackish with salinity that ranges from 3 to 5 ppm year round.

The region experiences two distinct seasons during the year; a rainy season from June to November and a dry season from December to May (Violante-González 2006). For this study, temperature and precipitation data for the area were obtained from the local meteorological station. Differences in environmental parameters between seasons were determined with a one-way analysis of variance (ANOVA) and a Student's *t*-test.

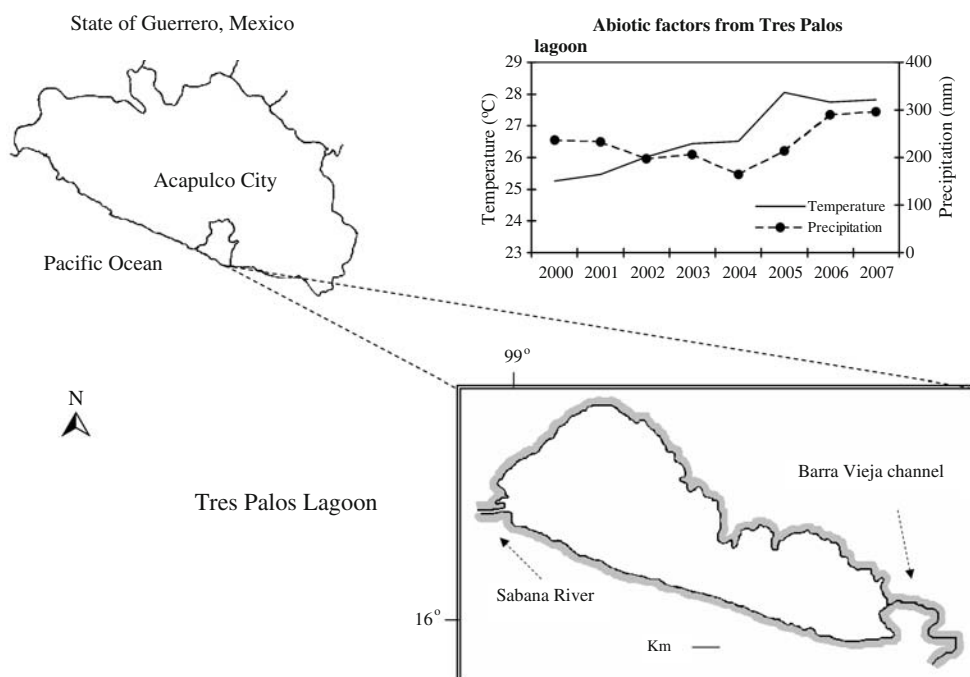
A total of 382 adult specimens of *S. guatemalensis* (total length=23.4±2.2 cm to 26.4±4.3 cm) were collected using gill nets between April 2000 and September 2007. The number of specimens examined per season each year ranged from 45 to 87 (Table 1). A complete necropsy was

made for all fish and helminths were collected from internal and external organs according to Lamothe-Argumedo (1997) and Vidal-Martínez et al. (2001). Voucher specimens of most taxa were deposited in the National Helminth Collection, Institute of Biology, National Autonomous University of Mexico, Mexico City (CNHE).

Autogenic species of parasite were defined as those which reach maturity in aquatic hosts and thus have a limited ability to colonize new locations. Allogenic species were those with birds or mammals as definitive hosts and whose natural migrations favor helminth dispersion, providing them a wide geographic distribution (Esch et al. 1988). Active transmission was defined as movement of a parasite to a host by its own means, whereas passive transmission was defined as movement of a parasite from one host to another without energy expenditure by the parasite (Bush et al. 2003). The host range concept (Rohde 2005) was used to classify the species of parasite as specialists or generalists. According to this concept, a specialist parasite is one that has a marked affinity for a specific host family, genus, or species, while a generalist is one that parasitizes a number of families. Based on their prevalence and abundance, the species of parasite also were classified as dominant (abundant and frequent, prevalence >40% and mean abundance=6–7.43 parasites per fish), common (low abundance but frequent, prevalence 20–40% and mean abundance=1–6), or rare (low abundance and low frequency, prevalence <20 % and mean abundance <1 per fish).

Variation in species composition over time was described using prevalence (percent infected hosts) and mean

**Fig. 1** Location of Tres Palos Lagoon in the state of Guerrero, Mexico. (Inserts temperature and precipitation recorded during 8 years)



**Table 1** Infection parameters of helminths of *Sciades guatemalensis* (blue sea catfish) from Tres Palos Lagoon, Guerrero, Mexico

Parasite	Site	CHNE	N/season	P(%)	Total	Abundance	Range of intensity
<b>Monogenea</b>							
<i>Neotetraonchus</i> sp. <sup>(Au, Ac)</sup>	Gills	6264	44/D00	29.17	10	0.42±0.8	1–3
			87R00	18.39	66	0.76±4.3	1–19
			48/D01	18.75	19	0.40±0.8	1–3
			48/D02	47.92	88	1.83±4.3	1–16
			46/R02	30.77	28	1.08±1.9	1–6
			45/D03	52.00	73	2.92±3.1	1–12
			64/R07	<b>96.88</b>	483	<b>7.55±7.5</b>	1–37
<b>Digenea (adult)</b>							
<i>Pseudoacanthostomum panamense</i> <sup>(Au, Ac)</sup> Caballero, Bravo-Hollis and Grocott, 1953	Intestine	6261	44/D00	16.67	17	0.71±2.6	2–7
			87R00	11.49	69	0.79±10.8	2–37
			48/D01	12.50	18	0.38±1.8	1–6
			48/D02	27.08	181	3.77±15.7	2–59
			46/R02	23.08	20	0.77±2.9	1–7
			45/D03	12.00	11	0.44±2.9	2–7
			64/R07	<b>62.50</b>	1,638	<b>25.59±115.9</b>	1–709
<b>Digenea (larval)</b>							
<i>Austrodiplostomum compactum</i> <sup>(Al, Ac)</sup> Lutz, 1928	Eyes	6094	44/D00	12.5	5	0.21±0.6	1–2
			87R00	11.49	16	0.18±0.8	1–3
			48/D01	22.92	30	0.63±1.7	1–6
			48/D02	12.50	20	0.42±3.9	1–11
			46/R02	46.15	90	3.46±9.8	1–28
			45/D03	44.00	91	3.6±5.4	1–17
			64/R07	14.06	50	0.78±5.7	1–16
<i>Clinostomum complanatum</i> <sup>(Al, Ac)</sup> Rudolphi, 1814	Muscle	6251	44/D00	4.17	2	0.08	2–2
			87R00	3.45	6	0.07±1.7	1–4
			48/D01	2.08	2	0.04	2–2
			48/D02	8.33	6	0.13±0.6	1–2
			46/R02	15.38	10	0.38±1.7	1–4
			45/D03	4.00	1	0.04	1–1
			64/R07	14.06	50	0.78±5.7	1–16
<i>Metadena</i> sp. <sup>(Al, Ac)</sup>	Intestine	6260	44/D00	8.33	4	0.17±1.4	1–3
			48/D01	4.17	8	0.17±2.8	2–6
			48/D02	6.25	22	0.46±4.2	4–12
			46/R02	15.38	30	1.15±5.2	3–12
			45/D03	4.00	7	0.28	7–7
<b>Nematoda (adult)</b>							
<i>Hysterothylacium perezii</i> <sup>(Au, Pa)</sup> Gopar-Merino et al. 2005	Intestine	6227	44/D00	45.83	22	0.92±1.4	1–5
			87R00	44.83	309	3.55±8.4	1–41
			48/D01	22.92	62	1.29±8.6	1–28
			48/D02	<b>72.92</b>	755	<b>15.73±47.3</b>	1–233
			46/R02	<b>84.62</b>	216	<b>8.31±8.9</b>	1–31
			45/D03	64.00	58	2.32±2.6	1–9
64/R07	<b>70.31</b>	628	<b>9.81±14.7</b>	1–79			
<b>Nematoda (larval)</b>							
<i>Contracaecum</i> sp. <sup>(Al, Pa)</sup>	Mesentery	6226	87R00	5.75	10	0.11±1.0	1–3
			48/D01	2.08	2	0.04	2–2
			48/D02	8.33	16	0.33±2.5	1–6
			46/R02	11.54	6	0.23±1.0	1–3

**Table 1** (continued)

Parasite	Site	CHNE	N/season	P(%)	Total	Abundance	Range of intensity
			45/D03	8.00	4	0.16	2–2
			64/R07	21.88	16	0.25±0.4	1–2
Acanthocephala (adult)							
<i>Pseudoleptorhynchoides lamothei</i> . (Au, Pa) Salgado-Maldonado 1976	Intestine	6263	44/D00	20.83	24	1.00±4.2	2–12
			87R00	45.98	591	6.79±22.0	1–94
			48/D01	47.92	215	4.48±13.9	1–54
			48/D02	<b>91.67</b>	887	<b>18.48±36.5</b>	1–179
			46/R02	46.15	146	5.84±11.0	2–34
			45/D03	<b>52.00</b>	464	<b>17.85±81.5</b>	2–212
<i>Neoechinorhynchus cf. golvani</i> (Au, Pa) Salgado-Maldonado, 1978	Intestine	6262	48/D02	4.17	7	0.15±0.7	3–4
			64/R07	20.31	66	1.03±6.1	1–79
			64/R07	3.13	4	0.06±1.4	1–3

Higher significance values of prevalence ( $G$  test), and abundance ( $\chi^2$  test), are in bold ( $P<0.05$ )

Colonization strategy: *Au* autogenic species, *Al* allogenic species; transmission form: *Ac* active transmission, *Pa* passive transmission; *CNHE* National Helminth Collection; *N* number of fish examined; Seasons: *D* dry (December–May), *R* rainy (June–November); *P*(%) prevalence of infection (% infected); *Total* total number of individual parasites; *Abundance* number of parasites per examined fish±standard deviation; *Intensity* range (i.e., min–max)

abundance (mean number of parasites per examined fish), calculated and applied according to Bush et al. (1997), for each species of helminth per season. Possible differences in infection parameters between seasons were evaluated using  $G$ -tests (Sokal and Rohlf 1998) for prevalence and a  $\chi^2$  test for abundance. Significance for all the statistical analyses was established at  $P=0.05$ , unless stated otherwise.

Analyses were made at the component community (all helminth parasites in all hosts collected per season) and infracommunity (all helminth parasites in each individual host) levels (Holmes and Price 1986). Component community parameters included total number of parasite species, total number of individual parasites, the Shannon–Wiener Index ( $H$ ) as a measure of diversity, species evenness (equitability) (Krebs 1999), and the Berger–Parker Index (BPI) as a measure of numerical dominance (Magurran 1991). A  $\chi^2$  test was used to determine differences in component community parameters between seasons and correlations were made using the Spearman range coefficient ( $r_s$ ; Krebs 1999). Infracommunities were described in terms of mean number of helminth species per fish host, mean number of parasite individuals, and mean value of the Brillouin Diversity Index ( $H'$ ) per fish. A one-way analysis of covariance (ANCOVA) was used to determine differences in infracommunity parameters between seasons.

The presence of nestedness in species composition between seasons was determined with the nestedness temperature calculator (Atmar and Patterson 1995), which

employs a randomness matrix based on disorder, or entropy. The relationship between entropy and heat is used to quantify the randomness matrix in terms of temperature, with 0°C representing minimum entropy (perfect nestedness) and 100°C representing maximum entropy (randomness). This is done by building a presence–absence matrix of parasite species in each infracommunity for each sample. The nestedness temperature calculator packs the observed data into the matrix in such a way that presences are concentrated in the upper left-hand corner as much as possible, while primary information (species-per-site data) is maintained within the matrix. The packed matrix is then compared with a maximum nestedness equivalent to identify unexpected presences and absences. For each observed matrix a  $T^\circ$  value is calculated where 0°C represents a perfectly nested matrix and 100°C a completely random matrix. The significance of a derived  $T^\circ$  was estimated with a  $t$  test, using a normal distribution of 500 Monte Carlo simulated  $T^\circ$  values. As a complement to this analysis, the infracommunity index (ICI) (Zander 2004), which describes the frequency of double and multiple infections by a single parasite species in a distinct host, was calculated:

$$ICI = (M_{ij}/N_j) \times I_j,$$

where  $I_j$  = mean number of parasite species in host  $j$  (= mean infracommunity);  $M_{ij}$  = the ratio (numbers) of multiple-infected host  $j$  with parasite  $i$  and other parasites;  $N_j$  = the ratio (numbers) of infected host  $j$ .

## Results

### Abiotic factors

During the 8-year study period, temperature varied significantly ( $P<0.001$ ):  $25.2\pm 1.0^{\circ}\text{C}$  (2000) to  $28.8\pm 0.8^{\circ}\text{C}$  (2007; one-way ANOVA  $F=15.11$ ). Precipitation also varied significantly ( $P<0.001$ ):  $165.10\pm 76.5$  mm (2004) to  $295.6\pm 255.2$  mm (2007;  $t=14.4$ , Fig. 1).

### Species composition

Nine species of helminth were identified in 382 specimens of *S. guatemalensis* collected during seven individual seasons (April 2000 to September 2007): one monogenean, four digeneans, two acanthocephalans, and two nematodes (Table 1). Four of the species recovered as larval stages were classified as allogenic since they mature in ichthyophagous aquatic birds living around the lagoon. The autogenic species were *Neotetraonchus* sp. (Monogenea), *Pseudoacanthostomum panamense* (Digenea), *Pseudoleptorhynchoides lamothei*, and *Neoechinorhynchus* cf. *golvani* (Acanthocephala), and *Hysterothylacium perezii* (Nematoda) (Table 1). All nine were classified as generalists because they have been recorded in other hosts from different families living in the same lagoon (Violante-González et al. 2007).

The frequency distribution of prevalence values for each species in all seasons produced three separate groups: dominant species (prevalence  $>40\%$ ), *H. perezii* and *P. lamothei*; common species (20–40%), *Neotetraonchus* sp., *P. panamense*, and *Austrodiplostomum compactum*; and rare species (prevalence  $<20\%$ ). Considering all sampling periods, prevalence and abundance differed significantly between seasons and years in four species (Table 1). Relatively high percentages of infection were observed for *H. perezii* in the 2002 dry season and the 2002 and 2007

rainy seasons ( $G=46.11$ ,  $P<0.05$ ); for *P. lamothei* in the 2002 and 2003 dry seasons ( $G=73.63$ ,  $P<0.05$ ); and for *P. panamense* and *Neotetraonchus* sp. in the 2007 rainy season ( $G=87.75$ ,  $P<0.05$  and  $G=108.04$ ,  $P<0.05$ , respectively). The highest mean abundance values for these same species were recorded in these same sampling periods ( $\chi^2$  test,  $P<0.05$ ; Table 1), indicating a positive correlation between prevalence and average abundance values in each case ( $P<0.05$ ).

### Component community

Species collected by season varied from seven to nine, although the number did not vary significantly between any seasons ( $\chi^2=0.44$ ,  $P>0.05$ ; Table 2). Total number of individual parasites ranged from 84 (2000 dry) to 2,885 (2007 rainy), and varied significantly between seasons and years ( $\chi^2=520.50$ ,  $P<0.05$ ; Table 2). *P. lamothei* was numerically dominant during six consecutive seasons, while *H. perezii* was numerically dominant only during the 2007 rainy season (Table 2). Shannon–Wiener diversity index values ranged from 1.65 to 2.43, although these did not differ between seasons and years ( $\chi^2=0.26$ ,  $P>0.05$ ). Evenness was positively correlated with diversity values during all the seasons sampled ( $r_s=0.89$ ,  $P<0.01$ ).

### Infracommunities

All fish collected were adults, though body size differed significantly between sampling periods (one-way ANOVA;  $F=4.47$ ,  $P<0.05$ ). The largest fish ( $26.6\pm 4.2$ ) were collected in the 2000 rainy season, and the smallest ( $23.4\pm 2.2$ ) in the 2003 dry season. Length of fish was positively correlated to mean number of individual parasites ( $r_s=0.300$ ,  $P<0.05$ ,  $n=307$ ).

The mean number of species of helminth ranged from  $1.52\pm 0.63$  (dry-2001) to  $2.89\pm 1.1$  (rainy-2007), and the

**Table 2** Characteristics of the helminth parasite component communities and infracommunities of *Sciades guatemalensis* (blue sea catfish) from Tres Palos Lagoon, Guerrero, Mexico, during seven climatic seasons

Season	Component communities							Infracommunities		
	No. of host	No. of species	No. of parasites	BPI	Dominant species	H	Evenness	Mean number of species	Mean number of individuals	Mean value of Brillouin Index
Dry 00	44	7	84	0.28	Pseu	2.43	0.87	$1.57\pm 0.7$	$4.0\pm 2.7$	$0.28\pm 0.35$
Rainy 00	87	7	1,067	0.55	Pseu	1.69	0.60	$1.52\pm 0.7$	$13.17\pm 18.5$	$0.25\pm 0.34$
Dry 01	48	8	356	0.60	Pseu	1.83	0.61	$1.52\pm 0.6$	$8.48\pm 11.6$	$0.27\pm 0.34$
Dry 02	48	9	1,982	0.45	Pseu	1.81	0.57	$2.79\pm 0.9$	$41.29\pm 58.3$	$0.77\pm 0.4$
Rainy 02	46	8	864	0.54	Pseu	1.9	0.63	$2.73\pm 1.2$	$33.23\pm 64.0$	$0.70\pm 0.45$
Dry 03	45	8	391	0.37	Pseu	2.22	0.74	$2.40\pm 1.0$	$15.64\pm 12.3$	$0.70\pm 0.43$
Rainy 07	64	7	2,885	0.22	Hyst	1.65	0.59	$2.89\pm 1.1$	$45.08\pm 97.5$	$0.81\pm 0.45$

BPI Berger–Parker Index, H Shannon–Wiener diversity index, Pseu *Pseudoleptorhynchoides lamothei*, Hyst *Hysterothylacium perezii*

mean number of individual parasites from  $4.0 \pm 2.7$  (dry-2000) to  $45.08 \pm 97.51$  (rainy-2007; Table 2). The Brillouin diversity index values varied from  $0.25 \pm 0.35$  (rainy-2000) to  $0.81 \pm 0.45$  (rainy-2007). The mean number of species of helminth was highest in the 2002 dry season and 2007 rainy season (one-way ANCOVA  $F=28.41$ ,  $P<0.001$ ), as was mean number of individuals (one-way ANCOVA  $F=4.25$ ,  $P<0.001$ ) and mean diversity (one-way ANCOVA  $F=5.96$ ,  $P<0.001$ ).

#### Nestedness

Nestedness occurred during six of the sampling periods, the exception being the 2000 dry season (Table 3). Nestedness intensity (lowest value  $T^\circ$ ) was highest in the 2007 rainy season ( $T^\circ=11.45^\circ$ ). Species composition remained almost unchanged, although the rank assigned to each species within the packed component community matrix varied between seasons and years (Table 3). *H. perezi* and *P. lamothei* were top-ranked in the highest number of seasons (three each) (Table 3).

The infracommunity index values (ICI) indicated that *H. perezi*, *P. lamothei*, and *Neotetraonchus* sp. had the highest number of double or multiple co-occurrences with other species of helminth (ICI > 0.20) in two or more seasons. Nestedness intensity depended on the higher number of double or multiple co-occurrences between these three species and the remaining six species in the *S. guatemalensis* parasite community.

#### Discussion

The results indicate that although species composition and species richness of helminths varied little during the seven-season study period, some species exhibited seasonal changes in their infection dynamic. Two biotic factors may have influenced these seasonal variations. Environmental variations caused by the seasonal dry/rainy cycle influence intermediate host availability and can lead to consequent alterations in the recruitment processes of some allogenic species. Changes in the feeding and reproductive behavior of *S. guatemalensis* may also influence the recruitment of intestinal species.

Five members of the parasite community of *S. guatemalensis* were autogenic species: *Neotetraonchus* sp., *P. panamense*, *P. lamothei*, *N. cf. golvani*, and *H. perezi*. The remaining four species were classified as allogenic because they mature in the aquatic birds, *Casmerodius albus egretta* (great egret) and *Phalacrocorax olivaceus* (Neotropic cormorant), which inhabit Tres Palos Lagoon (Violante-González 2006; Table 1). All five of the autogenic species are considered to be generalists because

**Table 3** Composition and rank (position within packed component community matrices) of species according to the climatic season

Helminth	Dry 00		Rainy 00		Dry 01		Rainy 01		Dry 02		Rainy 02		Dry 03		Rainy 07	
	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI
<i>H. perezi</i>	1	<b>0.292</b>	2	<b>0.295</b>	3	0.151	2	<b>0.570</b>	1	<b>0.310</b>	1	<b>0.310</b>	1	<b>0.267</b>	2	<b>0.243</b>
<i>Neotetraonchus</i> sp.	2	0.186	3	0.121	4	0.123	3	<b>0.375</b>	4	0.113	2	0.113	2	<b>0.217</b>	1	<b>0.335</b>
<i>P. lamothei</i>	3	0.133	1	<b>0.302</b>	1	<b>0.315</b>	1	<b>0.717</b>	3	0.169	3	0.169	3	<b>0.217</b>	5	0.070
<i>P. panamense</i>	4	0.106	5	0.076	5	0.082	4	0.212	5	0.085	5	0.085	5	0.050	3	<b>0.216</b>
<i>A. compactum</i>	5	0.080	4	0.076	2	0.151	5	0.098	2	0.169	2	0.169	4	0.183	6	0.049
<i>Metaena</i> sp.	6	0.053			6	0.027	8	0.049	7	0.056	7	0.056	8	0.017		
<i>C. complanatum</i>	7	0.027	7	0.023	7	0.014	6	0.065	6	0.056	6	0.056	7	0.017		
<i>Contracaecum</i> sp.			6	0.038	8	0.014	7	0.065	8	0.042	8	0.042	6	0.033	4	0.076
<i>N. cf. golvani</i>							9	0.033							7	0.011
Number of host	44		87		48		48		46		46		45		64	
Number of species	7		7		8		9		8		8		8		7	
$T^\circ$	34.61°		<b>27.04°</b>		<b>24.09°</b>		<b>20.33°</b>		<b>23.36°</b>		<b>28.04°</b>		<b>28.04°</b>		<b>11.45°</b>	
<i>P</i>	0.444		0.0018		0.0193		0.00001		0.00039		0.0094		0.00001		0.00001	

Higher values of infracommunity-index (ICI>0.20) and significant values of the nestedness temperature index ( $T^\circ$ ) are in bold

they have been reported in other hosts from the same lagoon (Violante-González 2006; Violante-González et al. 2007), although at least *P. panamense*, *P. lamothei*, and *H. perezii* mature only in *S. guatemalensis*, indicating that this species is their preferential host (Holmes 1976).

The seasonal variations observed in the infection parameters of the four most frequent and abundant species of helminth suggest that the transmission process of some parasites can experience interseasonal or interannual fluctuations that may be due to variations in intermediate host availability (Moravec et al. 2002; Violante-González 2006; Violante-González et al. 2008). During the dry season (December–May), the environment of Tres Palos Lagoon is relatively stable (Violante-González 2006). This could favor transmission of some parasites (both active and passive transmission forms) through higher availability of intermediate hosts (snails or crustaceans). The feeding activity of *S. guatemalensis* is also higher during the dry season than in the rainy season, when it reproduces (Violante-González 2006). This favors acquisition of parasites during the dry seasons by passive transmission. Two species, *P. lamothei* and *H. perezii*, that use passive transmission had higher infection levels during some dry seasons (Table 1). In previous studies, temporal variation in the infection levels of the acanthocephalans *Neoechinorhynchus agilis* and *N. cf. golvani* were found to be linked to reproductive aspects of its hosts *Liza abu* (Mhaisen et al. 1988) and *D. latifrons* (Violante-González et al. 2008). Indeed, many studies have shown that seasonal variation in the diet and amount of food ingested by hosts is clearly related to the population dynamics and community structure of parasites (Esch et al. 1988; Zander and Kesting 1998; Fiorillo and Font 1999; Zander et al. 2002; Klimpel et al. 2003; Fellis and Esch 2004; Zander 2003, 2004, 2005).

The stable environmental conditions in the lagoon during the dry season become unstable during the rainy season (July to November) in response to high input of organic matter from the contiguous Sabana River and other tributaries. This influx causes high mortality among benthonic invertebrates, such as snails, which are buried by silt (Violante-González 2006). However, rainfall can vary widely from 1 year to the next (Fig. 1), producing an inherent annual instability in addition to the interannual variations, possibly explaining the lack of any clear pattern in seasonal variation in the community structure of the parasites of this fish.

At both the component and infracommunity levels, low species abundance and diversity of helminths were found in *S. guatemalensis* (Table 2). Richness (nine species of helminth) was lower than the 14 species reported for the catfish *Ariopsis assimilis* (Vidal-Martínez et al. 2003), but similar to that reported in *Cathorops seemani* (nine species; Pérez-Ponce et al. 1999).

The low complexity food web structure in Tres Palos Lagoon may explain the low species richness in the parasite community of *S. guatemalensis* since food web structure is known to affect species richness and diversity of parasites in many freshwater systems (Carney and Dick 2000; Marcogliese 2001). The community of zooplankton is not very diverse, and the macrobenthic community, including molluscs, is represented by only six species (Stuardo and Villaruel 1976). This low level of biodiversity clearly restricts intermediate host availability in the food web, reducing opportunities for parasite transmission (Carney and Dick 2000; Marcogliese 2001).

At the component community level, both community composition and number of helminth species were similar across the sampling periods. Parasite load (i.e., total number of parasite individuals), however, was significantly higher in the 2002 dry season and 2007 rainy season (Table 2). This seasonal variation is probably related to the higher abundance of *P. lamothei* and *H. perezii* in each of these seasons.

The main factors structuring the parasite infracommunities (Holmes 1990; Zander 2004) in *S. guatemalensis* were the same ones structuring the component communities; that is, feeding behavior and seasonal variation in the availability of infective stages (cercariae or oncomiracidia), both influenced in turn by the seasonal dry/rainy cycle. These two biotic factors structure infracommunities primarily through accumulation of temporarily free living cercariae (*P. panamense*, *A. compactum*, and *C. complanatum*) or ingestion of infected crustaceans (*P. lamothei* and *H. perezii*). Acquisition of some rare species completes the structure.

The presence of nestedness in almost all the seasons that were studied suggests a certain degree of structure in infracommunity species composition over time (Poulin and Valtonen 2001), in other words, species composition exhibited a certain degree of order. Some species of helminth were prevalent at high levels in all infracommunity classes (rich and poor), whereas rare species occurred mainly in species-rich infracommunities.

Nestedness within infracommunities can be generated by several processes, including passive sampling and sequential colonization of parasite species (Carney and Dick 2000; Timi and Poulin 2003). The passive sampling hypothesis is based on probability and predicts that common species will occur in many hosts and rare species in fewer hosts, therefore producing a nested pattern. The nestedness observed in the current study may have been caused by stability in species composition over time. However, some of the dominant species occurred in a higher number of double or multiple co-occurrences with other species (ICI > 0.20, Table 3) and were more abundant in different seasons, suggesting that a sequential colonization process may better explain the variation in intensity of nestedness observed here.

Thus, nestedness can be considered a feature of the parasite infracommunity composition in *S. guatemalensis* in Tres Palos Lagoon. Nestedness has been reported in the parasite communities of fish from other locations (Carney and Dick 2000; Poulin and Valtonen 2001; Valtonen et al. 2001; Timi and Poulin 2003; Vidal-Martinez and Poulin 2003; Norton et al. 2004), including one eleotrid from this same lagoon (Violante-González et al. 2008).

Overall, the results indicate that even though species composition and richness of helminths remained relatively constant over time, the infection dynamics of some dominant helminths were influenced by regional environmental conditions. Environmental factors (dry/rainy cycles) influence intermediate host availability in Tres Palos lagoon and generate alterations in the recruitment processes of some autogenic parasite species. Environmental variations also cause changes in the feeding and reproductive behavior of *S. guatemalensis*, which in turn influences recruitment of intestinal helminth species.

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