Richness and Species Composition of Helminth Communities in Yellowfin Snook (*Centropomus robalito*) (Centropomidae) from Coastal Lagoons in Guerrero, Mexico

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ABSTRACT: Adult yellowfin snook (*Centropomus robalito*) were collected between January and May 2008 (dry season), to assess the consistency (repeatability) of the species composition and richness of their helminth communities in 4 coastal lagoons from Guerrero, Mexico. Fifteen species of helminth were identified: 4 Monogenea, 6 Digenea, 1 Acanthocephala, and 4 Nematoda. The helminth communities in the 4 lagoons consisted mainly of marine autogenic species, were poor in richness and diversity, and exhibited low qualitative similarity at the component level (29.5% to 62.1%) and the infracommunity level (0.48 ± 0.30 to 0.69 ± 0.19), indicating that species composition and richness of the helminth communities of *C. robalito* are not predictable at a spatial scale. Significant nestedness occurred in the infracommunities of all lagoons, as well as among 2 sampling periods in Tres Palos Lagoon, suggesting a certain degree of structure in species composition in infracommunities in space and time.

KEY WORDS: *Centropomus robalito*, helminth community, coastal lagoon, Guerrero, Mexico.

Studies of richness and species composition are central themes in helminth community ecology because they help us to understand the factors that determine the structure of communities (Violante-González et al., 2010). However, it also is important to know how consistent richness and species composition of parasite communities are in space in time. Spatial or temporal variation in community structure may indicate how important local factors (abiotic and biotic conditions) are in structuring the helminth community, particularly when disparities are found between different species of host (Machado et al., 1995; Salgado-Maldonado and Kennedy, 1997; Vidal-Martínez and Poulin, 2003; Aguirre-Macedo et al., 2007; Mwita and Nkwengulila, 2008; Tavares and Luque, 2008). Despite this, few studies have identified factors that determine species composition and richness in the parasite communities of fish from tropical environments in Mexico. Available data mainly covers brackish environments in southeastern Mexico (Salgado-Maldonado and Kennedy, 1997; Vidal-Martínez and Poulin, 2003; Aguirre-Macedo et al., 2007; Rodríguez-González and Vidal-Martínez, 2008; Pech et al., 2009), and only 3 studies have focused on the southern Pacific Coast of Mexico (Violante-González et al., 2008, 2009, 2010).

Tropical coastal lagoons generally are brackish environments with specific characteristics that are determined by environmental dynamics such as the dry/rainy season cycle and the extent and frequency of the connection to the ocean (Yáñez-Arancibia, 1978; Violante-González et al., 2009). *Centropomus robalito* Jordan y Gilbert, 1882, the yellowfin snook, is one of the most commercially important fish species occurring in the coastal lagoons of Guerrero State, México (Díaz-Jaimes et al., 2007). Adults of the species inhabit demersal marine waters along the Pacific coast of México, but juvenile fish also routinely enter coastal lagoons in search of refuge and food, and then remain inside the lagoons until reaching sexual maturity (up to 17 cm total length). Mature fish return to marine waters to reproduce, after which they remain near the coast (Yáñez-Arancibia, 1978; Bussing, 1995). Taxonomic records exist for the helminths of *C. robalito* from 1 coastal lagoon in Guerrero, México (Violante-González et al., 2007), but there are no studies of the species from any other lagoon in the region. The objective of the present study was to assess the spatial and temporal consistency (repeatability) of species composition and richness in the helminth communities of *C. robalito* collected from 4 coastal lagoons in Guerrero, México.

MATERIALS AND METHODS

Specimens of *C. robalito* (230 adults) were collected with the use of gill nets between January and May 2008 (dry

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Figure 1.   Coastal lagoon study sites, State of Guerrero, Mexico.

season). Fish were collected from 4 coastal lagoons in Guerrero State, Mexico: Chautengo (16°36′N, 99°09′W, *n* = 62); Coyuca (16°57′N, 100°02′W, *n* = 49); Tecomate (16°41′N, 99°19′W, *n* = 54); and Tres Palos (16°48′N; 99°47′W, *n* = 65) (Fig. 1). Additional fish (*C. robalito*; *n* = 47) collected from Tres Palos Lagoon in 2004 were included for comparative temporal analysis. All fish were necropsied and helminths were collected from internal and external organs according to Vidal-Martinez et al. (2001). All helminths recovered from each fish were counted. Monogeneans were mounted unstained in Gray and Wess medium for study of sclerotized structures; other specimens were stained with Gomori's trichrome or Genacher borax carmine and mounted in Canada balsam for observing internal anatomy. Digeneans (adults and metacercariae), were fixed in formalin-ethanol-acetic acid (AFA). Acanthocephalans were placed in distilled water and refrigerated overnight (6– 12 hr) to evert the proboscis, then fixed in 70% ethanol. Digeneans and acanthocephalans were stained with carmine or Gomori's trichrome, dehydrated with the use of a graded alcohol series, cleared in methyl salicylate, and mounted whole on slides. Nematodes were cleared with glycerin for light microscopy and stored in 70% ethanol.

Voucher specimens of most helminth taxa were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico. Acanthocephalans from this region previously had been reported as *Neoechinorhynchus golvani* or *N*. cf. *golvani* (Violante-González and Aguirre-Macedo, 2007; Violante-González et al., 2007, 2008, 2009). Based on Martínez-Aquino et al. (2009) and Monks et al. (2011) the specimens collected as part of the current study have been assigned to *Neoechinorhynchus brentnickoli* Monks, Pulido-Flores, and Violante-González, 2011.

Autogenic species were defined as those helminths that reach maturity in aquatic hosts and thus have a limited

ability to colonize new locations. Allogenic species were those that use birds or mammals as definitive hosts, the natural migration patterns of which favor parasite dispersion, and thus produce a wider geographic distribution of their parasites (Esch et al., 1988). A conservative approach to species distribution of helminths based on the life cycle and hosts was applied with the use of the general categories of freshwater, brackish water, and marine habitats (Violante-González et al., 2010).

Interlagoon and sampling period differences in helminth community composition were described with the use of prevalence (percent of infected fish), mean abundance (mean number of helminths per fish), and intensity for each species of helminth per lagoon (Bush et al., 1997). Possible differences in infection parameters for species recorded in all or most of the lagoons were evaluated with the use of *G*-tests (Sokal and Rohlf, 1998) for prevalence, and a χ^2 test for abundance.

Analyses were made at the levels of component community (i.e., total helminths in the total sample of fish collected per lagoon) and infracommunity (i.e., total helminths in each individual fish) (Holmes and Price, 1986). Component community parameters included the total number of species of helminth, total number of individual helminths, 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, 2004). The qualitative Jaccard similarity index was used to evaluate similarity or difference in the species composition of the helminth community between lagoons and sampling periods. A Student's *t*-test was applied to identify differences between component community parameters, and correlations were calculated with the use of the Spearman range coefficient (r_s) (Krebs, 1999).

Infracommunities were described in terms of mean number of species per host, mean number of individual

Table 1. Infection parameters for helminths of yellowfin snook (*Centropomus robalito*) from 4 coastal lagoons in Guerrero, Mexico. Significantly different measurements of prevalence (*G*-test) and abundance (χ^2-test) are in bold (*P* < 0.05).

Parasite*	Site	Cs†	CNHE‡	N/lagoon§	P%‖	Total¶	Abundance#	Intensity**
Monogenea								
Cornutohaptor nigrescensi Mendoza-Franco, Violante-González, and Vidal-Martínez, 2006 (Ma)	Gills	Auto	7134	49/Co	2	1	0.02	1
Rhabdosynochus lituparvus Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008 (Ma)	Gills	Auto		62/Ch	**38.7**	93	1.5 ± 3.0	1–11
				49/Co	**26.5**	59	1.2 ± 4.3	1–12
				54/Te	13	9	0.2 ± 0.5	1–2
				47/TP04	8.5	8	0.2 ± 0.8	1–3
				65/TP	13.9	5	1.1 ± 0.7	2–3
Rhabdosynochus siliquaus Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008 (Ma)	Gills	Auto		62/Ch	**77.4**	254	4.1 ± 5.1	1–24
				49/Co	**46.9**	83	1.7 ± 4.2	1–16
				54/Te	29.6	56	1.0 ± 1.8	1–8
				47/TP04	14.9	38	0.8 ± 2.5	2–9
				65/TP	24.6	31	0.5 ± 1.8	2–7
Rhabdosynochus volucrisi Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008 (Ma)	Gills	Auto		62/Ch	**98.4**	532	8.6 ± 9.5	1–45
				49/Co	**77.8**	226	4.6 ± 6.8	1–30
				54/Te	**59.3**	153	2.8 ± 2.2	2–10
				47/TP04	**44.7**	105	2.2 ± 4.6	1–20
				65/TP	**24.62**	77	1.18 ± 4.6	1–16
Digenea (adult)								
Paracryptogonimus yamagutii Lamothe-Argumedo, 1969 (Ma)	Intestine	Auto	7147	62/Ch	**53.2**	575	9.3 ± 39.9	1–194
			7145	49/Co	**81.6**	762	15.6 ± 26.6	1–133
			7148	54/Te	**70.4**	1224	22.7 ± 50.4	1–226
			7146	47/TP04	**55.3**	302	6.4 ± 20.8	1–86
				65/TP	**53.9**	141	2.2 ± 4.3	1–18
Paropecoelus parupenei Yamaguti, 1970 (Mw)	Intestine	Auto	7144	54/Te	**3.7**	9	0.2 ± 2.1	3–6
Stephanostomum baccatum (Nicoll, 1907) Manter, 1934 (Ma)	Intestine	Auto	7115	54/Te	**5.6**	9	0.2 ± 1.0	
Digenea (larvae)								2–4
Ascocotye (Phagicola) longa Ransom, 1920 (Bw)	Heart, mesentery, liver	Allo		49/Co	**2**	3	0.1	
				47/TP04	**2.1**	6	0.1	
Diplostomum (Austrodiplostomum) compactum Lutz, 1928 (Fw)	Eyes	Allo	7138	62/Ch	**22.6**	38	0.6 ± 1.7	3
			7136	49/Co	**40.8**	52	1.1 ± 1.5	6
			7137	54/Te	**3.7**	6	0.1	1–7
			7135	47/TP04	**4.3**	7	0.2 ± 2.1	1–6
				65/TP	**12.3**	13	0.2 ± 1.2	3
Pseudoacanthostomum panamense Caballero y Caballero, Bravo-Hollis, and Grocott, 1952 (Bw)	Mesentery, inside intestinal wall	Auto	7143	49/Co	**4.1**	10	0.2 ± 2.8	2–5
			7151	47/TP04	**6.4**	7	0.2 ± 2.3	1–4
				65/TP	**1.5**	5	0.1	3–7
Acanthocephala (juvenile)								1–5
Neoechinorhynchus brentnickoli (Fw)	Intestine	Auto	7141	62/Ch	**1.6**	1	0.02	5
			7142	54/Te	**29.6**	134	2.5 ± 8.7	
			7139	47/TP04	**42.6**	140	3.0 ± 10.3	1
			7140	65/TP	**52.3**	148	2.3 ± 3.0	1–29
Nematoda (adult)								1–47
Cucullanus sp. (Ma)	Intestine	Auto	7158	54/Te	**3.7**	5	0.1 ± 0.7	1–11
Hysterothylacium perezi Gopar-Merino, Osorio-Sarabia, and García-Prieto, 2005 (Bw)	Intestine	Auto	7161	65/TP	**3.1**	49	0.8 ± 2.1	2–3

Table 1. Continued.

Parasite*	Site	Cs†	CNHE‡	N/lagoon§	P%‖	Total¶	Abundance#	Intensity**
Philometra centropomi	Skin	Auto	7164	62/Ch	**19.4**	48	0.8 ± 3.4	23–26
Caballero y Rodríguez,			7167	49/Co	**85.7**	593	12.1 ± 12.4	
1974 (Ma)			7165	54/Te	**22.2**	48	0.9 ± 4.7	1–11
				47/TP04	**70.2**	241	5.1 ± 7.0	1–52
				65/TP	**67.7**	204	3.1 ± 5.3	2–14
Nematoda (larvae)								1–35
Contracaecum sp. (Fw)	Mesentery,	Allo	7162	62/Ch	11.3	17	0.3 ± 2.0	1–27
	intestine		7163	49/Co	**18.4**	14	0.3 ± 0.9	
				54/Te	11.1	10	0.2 ± 1.0	1–6
				47/TP04	**31.9**	48	1.0 ± 4.3	1–3
				65/TP	13.9	27	0.4 ± 2.1	1–3

* Distribution of helminths: Fw, fresh water; Bw, brackish water; Ma, marine.

† Colonization strategy (Cs): Auto, autogenic species; Allo, allogenic species.

‡ CNHE, accession number, Colección Nacional de Helmintos, Instituto de Biología, Universidad Nacional Autónoma de México.

§ Lagoon: *N*, number of fish examined; Ch, Chautengo; Co, Coyuca; Te, Tecomate; TP, Tres Palos, 2007–2008 collections; TP04, Tres Palos, 2004 collection.

‖ Prevalence.

¶ Total = total number of individual helminths collected.

Abundance = mean number of parasites per examined fish ± standard deviation.

** Intensity = range (i.e., minimum–maximum number of helminths present).

helminthes, and the mean Brillouin diversity index (H′) (Krebs, 1999) value per host. To identify differences in infracommunity parameters between lagoons, a 1-way ANCOVA with total length as a covariate to control for the influence of host size was used. Normality was evaluated with the use of the Kolmogorov–Smirnov test following Lilliefors' approach (Sokal and Rohlf, 1998) and data were log-transformed when significant deviations from normality were identified.

Nestedness analyses were used to assess the predictability (consistency of species composition) of the community structure of helminths in both space (among lagoons) and time (among sampling periods in Tres Palos 2004–2008). The presence of nestedness in species composition 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). The significance of $T°$ values was estimated with the use of a Student's *t*-test with a normal distribution of 500 Monte Carlo simulated $T°$ 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 species of parasite in a distinct host, was calculated.

RESULTS

Species composition

Fifteen species of helminth were identified in the 277 fish collected: 4 monogeneans, 6 digeneans (3 adult and 3 larval forms), 1 acanthocephalan, and 4 nematodes (3 adult and 1 larval form) (Table 1). Of these, 12 species were classified as autogenic and 3 as allogenic. Based on geographic distribution of the species, 9 were of marine origin, 3 of freshwater, and 3 of brackish water origin (Table 1). The number of species of marine origin ranged from 5 (Chautengo and Tres Palos) to 8 (Tecomate) and the number of freshwater species from 2 to 3 (Fig. 2) although no significant difference was detected in the proportion of species from a particular habitat between lagoons ($P > 0.05$).

Seven species (*Rhabdosynochus lituparvus* Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008; *Rhabdosynochus siliquaus* Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008; *Rhabdosynochus volucrisi* Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008; *Diplostomum* (*Austrodiplostomum*) *compactum* Lutz, 1928; *Paracryptogonimus yamagutii* Lamothe-Argumedo, 1969; *Contracaecum* sp., and *Philometra centropomi* Caballero y Rodríguez, 1974) were widely distributed and occurred in the helminth communities of all 4 lagoons. The prevalence of these widespread species varied significantly between specific lagoons (*R. lituparvus*, $G = 30.43$, $P < 0.05$; *R. siliquaus*, $G = 62.39$, $P < 0.05$; *R. volucrisi*, $G = 53.68$, $P < 0.05$; *D. (A.) compactum*, $G = 57.34$, $P < 0.05$; *P. yamagutii*, $G = 10.17$, $P < 0.05$; *Contracaecum* sp., $G = 17.39$, $P < 0.05$; *Ph.*
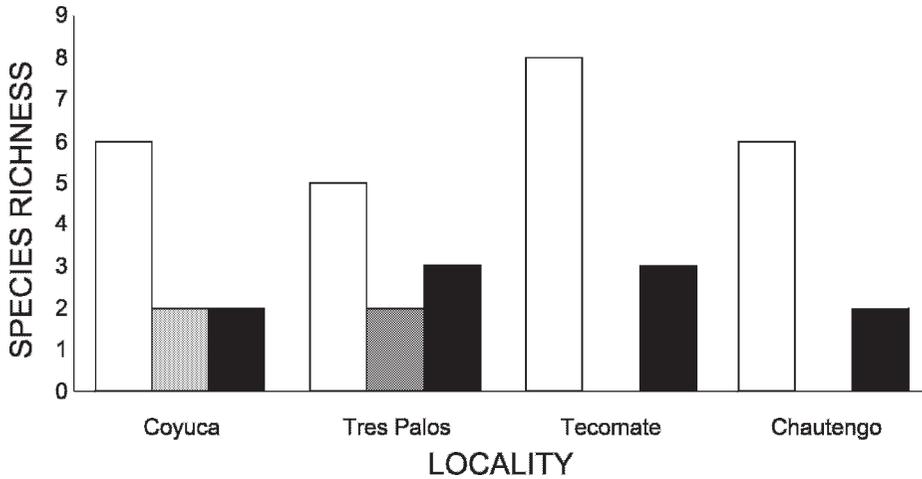
Figure 2. Species richness of helminths in yellowfin snook, *Centropomus robalito* from marine (open bars), brackish water (shaded bars), and freshwater environments (closed bars) in 4 coastal lagoons, Guerrero, Mexico.

centropomi, $G = 69.04$, $P < 0.05$). In contrast, the difference in abundance between lagoons was significant only for *P. yamagutii* ($\chi^2 = 23.04$, $P < 0.05$), and *Ph. centropomi* ($\chi^2 = 19.71$, $P < 0.05$) (Table 1). Overall, prevalence correlated positively with abundance in all communities, indicating that the most prevalent species also were the most abundant ($P < 0.05$).

Component community

The number of species collected by lagoon ranged from 8 (Chautengo) to 11 (Tecomate), with significant differences between lagoons ($t = 20.04$, $P < 0.05$). The total number of individual helminths ranged from 700 (Tres Palos, 2008) to 1,803 (Coyuca) and varied significantly between lagoons

($t = 6.02$, $P < 0.05$) (Table 2). *Paracryptogonimus yamagutii* was numerically dominant in 4 component communities. The Shannon–Wiener diversity index values ranged from 1.43 (Tecomate) to 2.67 (Tres Palos, 2008) and also varied between lagoons ($t = 10.14$, $P < 0.05$). Evenness was positively correlated with diversity values in all communities ($r_s = 0.98$, $P < 0.05$), indicating that the most diverse communities were those that presented a higher uniformity in species abundance. Qualitative similarity between the component communities of different lagoons ranged from 29.5% (Chautengo–Tres Palos, 2008) to 62.1% (Chautengo–Coyuca) (Fig. 3), and varied significantly between pairs of communities ($t = 8.68$, $P < 0.05$). The highest similarity (79.5%) was between the samples taken in 2004 and 2008 from Tres Palos Lagoon (Fig. 3). No correlation was found between

Table 2. Characteristics of the helminth component communities and infracommunities in yellowfin snook (*Centropomus robalito*) from 4 coastal lagoons. Significantly different measurements are in bold ($P < 0.05$).*

								Infracommunities		
	Component communities								Mean	Mean value of
Lagoon, sampling date	No. of hosts	No. of species	No. of parasites	BPI	Dominant species	H	Evenness	Mean no. of species	no. of individuals	Brillouin index
Chautengo, January 2008	62	8	1,558	0.37	Para	2.09	0.69	3.2 ± 1.34	25.1 ± 36.6	1.15 ± 0.40
Coyuca, February, 2008	49	10	**1,803**	0.42	Para	2.06	0.62	**3.9 ± 1.4**	**36.8 ± 35.2**	**1.20 ± 0.49**
Tecomate, May 2008	54	11	**1,663**	0.74	Para	1.43	0.43	2.5 ± 1.4	30.8 ± 49.4	0.83 ± 0.32
Tres Palos, January 2004	47	10	902	0.33	Para	2.45	0.74	2.8 ± 1.6	19.2 ± 22.4	0.97 ± 0.41
Tres Palos, April 2008	65	10	700	0.29	Phi	**2.67**	0.82	2.5 ± 1.4	10.8 ± 10.1	0.92 ± 0.40

*BPI, Berger-Parker index; H, Shannon–Wiener diversity index; Para, *Paracryptogonimus yamagutii* Lamothe-Argumedo, 1969, Phi, *Philometra centropomi* Caballero y Rodríguez, 1974.
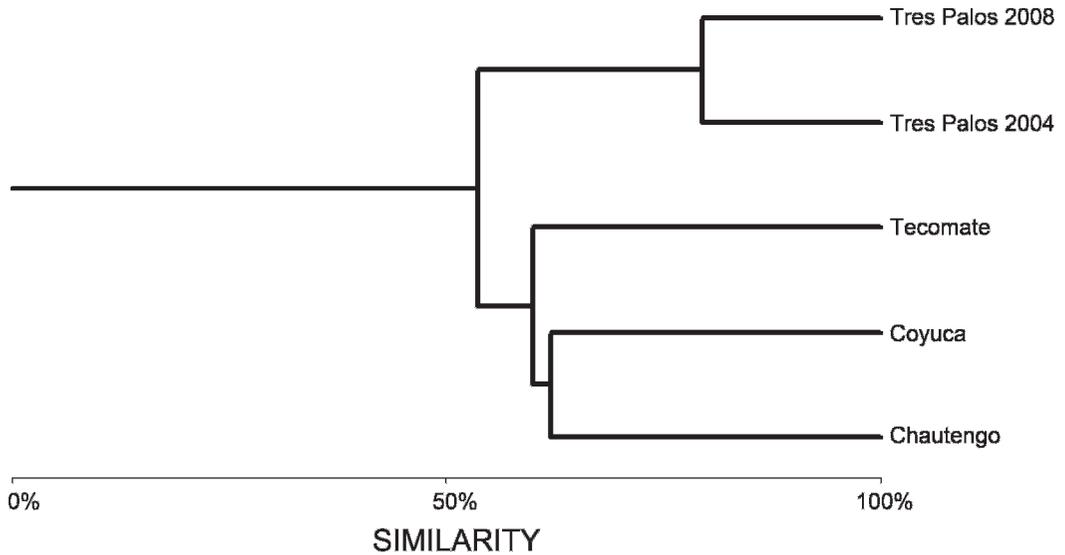
Figure 3.   Jaccard index of similarity for helminth component communities in yellowfin snook, *Centropomus robalito*, from 4 coastal lagoons, Guerrero, Mexico. (Tres Palos samples for both 2004 and 2008 are included for temporal comparison.)

the distance between lagoons and the similarity of communities ($r_s = 0.600$, $P > 0.05$).

Infracommunities

All of the fish examined were adult, with a mean total length of 18.7 ± 1.5 cm (Tres Palos, 2008) to 22.0 ± 2.1 cm (Coyuca); mean total length varied significantly between lagoons (ANOVA $F = 43.57$, $P < 0.0001$), but not among sampling periods (Tres Palos, ANOVA $F = 3.43$, $P > 0.05$). Of the fish examined, 96% were infected with 1–7 species of helminth and 46% were infected with 3 or 4 different species. Overall, body size (total length) was positively correlated with 2 infracommunity parameters, the mean number of parasites ($r_s = 0.227$, $P < 0.01$), and mean richness ($r_s = 0.248$, $P < 0.01$).

Mean number of species ranged from 2.46 ± 1.4 (Tres Palos 08) to 3.86 ± 1.4 (Coyuca), and mean number of parasites from 10.77 ± 10.1 to 36.80 ± 35.2 (Table 2). Brillouin diversity index values varied from 0.92 ± 0.40 to 1.20 ± 0.49. Mean number of species and mean diversity were highest in Coyuca lagoon (1-way ANCOVA, $F = 5.81$; $F = 9.27$, $P < 0.001$, respectively); whereas the difference in mean number of parasites between lagoons was not significant (1-way ANCOVA, $F = 2.13$, $P > 0.05$). Similarity between infracommunities (Fig. 4) ranged from 48% (Tres Palos, 2008) to 69%

(Chautengo), and varied significantly between lagoons ($t = 15.8$, $P < 0.05$).

Nestedness

Nestedness was significant in the infracommunities of all lagoons, as well as among sampling periods (Tres Palos, 2004–2008) (Table 3), indicating that common species were found in infracommunities of varying richness, but rare species mainly occur in more diverse infracommunities. Nestedness was most intense (lowest value T°) in Chautengo ($T^\circ = 7.37^\circ$) but the rank assigned to each species within the packed component community matrix varied between lagoons and sampling periods (Table 3). *Philometra centropomi* was the highest ranked species in the greatest number of communities (Table 3). The infracommunity index values (ICI) indicated that *R. volucrisi*, *P. yamagutii*, and *Ph. centropomi* had the highest number of double or multiple co-occurrences with other species of helminth (ICI > 0.20) in up to 3 communities. Intensity of nestedness depended on the high number of double or multiple co-occurrences between these 3 species and the remaining species in each component community.

DISCUSSION

The results indicate that even though helminth communities of *Centropomus robalito* were similar in
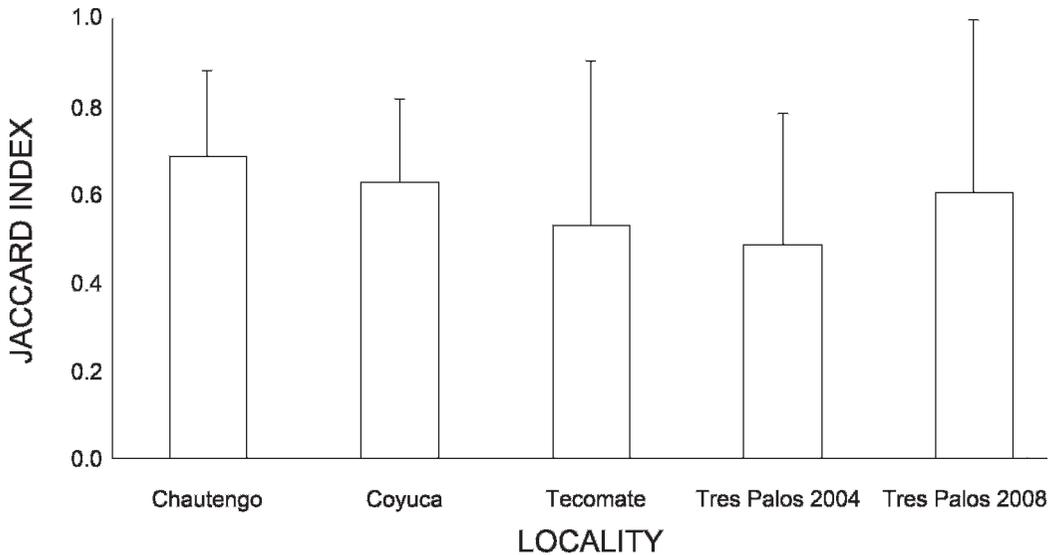
Figure 4. Similarity values (Jaccard index) for helminth infracommunities in yellowfin snook, *Centropomus robalito*, from 4 coastal lagoons, Guerrero, Mexico. (2004 and 2008 samples from Tres Palos are included for temporal comparison.)

species composition and richness in the 4 lagoons, they were not identical. This suggests that local conditions (environmental and biological) have an important effect on the parasite community structure. Feeding habits and body size were the main factors determining species richness and diversity in the parasite infracommunities of *C. robalito*.

The helminth communities of *C. robalito* in the 4 lagoons were comprised mainly of autogenic parasites of marine origin. However, the number of these species varied significantly between the lagoons. This could be a result of the different environmental conditions that exist in each lagoon, in this case in relation to marine influence (Violante-González et al., 2010). For example, Tecomate has a great marine influence (salinity > 15 ppt) because its inlet channel is relatively short, providing ready communication with the ocean. The ichthyofauna of this lagoon includes over 80% marine species (Yáñez-Arancibia, 1978), and therefore it is probable that the helminths in the fish in the lagoon are exchanged between visiting species of fish that are mainly of marine origin.

Seven species of helminths were recovered from the intestine of the fish (Table 1), indicating that diet is an important factor in structuring the parasite community in this species of fish (Choudhury and Dick, 2000; Tavares and Luque, 2004; Mwita and Nkwengulila, 2008; Violante-González et al., 2010). Yellowfin snook are considered a tertiary predator

because it feeds on several species of fish in juvenile stages as well as crustaceans, such as shrimp and crab, insect larvae, and molluscs (Yáñez-Arancibia, 1978; Bussing, 1995). This predatory behavior exposes the fish to the infective stages of a large variety of trophically transmitted parasites. The diet of this fish varies temporally (dry and rainy) as well as among the different lagoons (Yáñez-Arancibia, 1978), which might explain the observed differences in the prevalence or abundance of some trophically transmitted parasite species (i.e., *N. brentnickoli* and *Contracaecum* sp.).

The component communities of the helminths of *C. robalito* were composed of a low number of species and low diversity, and they were dominated by a single species (*P. yamagutii*) (see Table 2). The parasite richness registered at the component level (8–11 species) was similar to that observed for other component communities of tropical freshwater species of fish (Choudhury and Dick, 2000), and other species of fish in Coyuca and Tres Palos lagoons (7–13 species: Violante-González and Aguirre-Macedo, 2007; Violante-González et al., 2007). A possible explanation for the low richness of parasite species in this host may be related to the low complexity of food-web structure in these lagoons, which is known to affect species richness and diversity of helminths in many freshwater systems (Carney and Dick, 2000; Marcogliese, 2001). Zooplankton is not very diverse, and organisms of the macrobenthos, including

Table 3.   Composition and rank (position within packed component community matrices) of species among lagoon and sampling periods. Higher values of the infracommunity index (ICI > 0.20) and significant values of the nestedness temperature index ($T°$) are in bold.

Helminth	Chautengo		Coyuca		Tecomate		Tres Palos, 2004		Tres Palos, 2008	
	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI	Ranked	ICI
Rhabdosynochus volucrisi Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008	1	**0.305**	3	**0.201**	2	**0.218**	3	0.149	4	0.092
Rhabdosynochus siliquaus Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008	2	**0.240**	4	0.122	3	0.109	6	0.050	5	0.052
Paracryptogonimus yamagutii Lamothe-Argumedo, 1969	3	0.165	2	**0.211**	1	**0.259**	2	0.184	2	**0.202**
Rhabdosynochus lituparvus Mendoza-Franco, Violante-González, and Vidal-Martínez, 2008	4	0.120	6	0.069	6	0.048	7	0.028	8	0.012
Diplostomum (Austrodiplostomum) compactum Lutz, 1928	5	0.070	5	0.106	9	0.014	9	0.014	7	0.046
Philometra centropomi Caballero y Rodríguez, 1974	6	0.060	1	**0.222**	5	0.082	1	**0.234**	1	**0.250**
Contracaecum sp.	7	0.035	7	0.048	7	0.041	5	0.106	6	0.052
Neoechinorhynchus brentnickoli	8	0.005		0.038	4	0.1094	4	0.142	3	0.196
Pseudoacanthostomum panamense Caballero y Caballero, Bravo-Hollis, and Grocott, 1952			8	0.011			8	0.021	10	0.006
Ascocotye (Phagicola) longa Ransom, 1920			9	0.005			10	0.007		
Cornutohaptor nigrescensi Mendoza-Franco, Violante-González, and Vidal-Martínez, 2006			10	0.005						
Stephanostomum baccatum (Nicoll, 1907) Manter, 1934					8	0.020				
Paropecoelus parupenei Yamaguti, 1970					10	0.014				
Cucullanus sp.					11	0.014				
Hysterothylacium perezi Gopar-Merino, Osorio-Sarabia, and García-Prieto, 2005									9	0.012
$T°$	**9.37°**		**14.14°**		**15.25°**		**18.87°**		**15.71°**	
P	0.00001		0.00001		0.00001		0.00001		0.00001	

molluscs, are scarce, being represented by just 6 species (Stuardo and Villarroel, 1976). The impoverishment of biodiversity in these lagoons clearly restricts intermediate host availability in the food web, reducing the opportunity for transmission of higher numbers of individual helminths and limiting the overall number of species (Carney and Dick, 2000; Marcogliese, 2001).

Although the total number of species was similar among the component communities, the values of qualitative similarity among pairs of communities were low in most of the cases (Fig. 3), indicating that the communities are not predictable in terms of species composition. Some studies have indicated that the distance between sampling localities is one of the best predictors of the similarity among helminth

communities (Poulin and Morand, 1999; Poulin, 2003). This is because hosts in locations closer to each other are exposed to regional pools of parasites that are more similar than those in locations further away (Vidal-Martínez and Poulin, 2003). However, other studies suggest that the parasite communities of the same species of host can be affected more strongly by local environmental conditions that would restrict or favor a particular species composition (Machado et al., 1995; Salgado-Maldonado and Kennedy, 1997; Valtonen et al., 2001; Vidal-Martínez and Poulin, 2003; Aguirre-Macedo et al., 2006; Mwita and Nkwengulila, 2008).

Our results support the second of the 2 hypotheses because there was no observed relation between the percentages of similarity of communities from different lagoons and the distance of separation between lagoons. Lagoons located at a greater distance (for example, Chautengo and Coyuca; separated by a distance of 114 km) had a high similarity in species composition (62.1%), whereas pairs located more closely (Chautengo and Tres Palos; separation 55 km) were much less similar (29.5%) (Fig. 3).

On the other hand, the high similarity registered at the temporal level (i.e., Tres Palos, 2004 compared to 2008, Fig. 3), suggests that the species composition of the helminth community of *C. robalito* it can be constant over time at least within a particular locality.

The helminth infracommunities of *C. robalito* exhibited the same pattern observed at the component level, i.e., a low number of species and low diversity (Table 2) and similarity (Fig. 4). It has been suggested that component communities that are poor in species richness also generally have infracommunities poor in number of species (Choudhury and Dick, 2000). According to Kennedy (1990), the number of species in an infracommunity reflects the availability of species in the locality, the opportunity of transmission and infection, and, thus, the probability of host infection. These factors also translate into the pattern exhibited by the component community, producing a similar structure.

The variation found in the mean species richness between lagoons, can also be attributed to differences in the host's body size, because this host's trait correlated positively with the mean number of species and the mean diversity. For example, all the infracommunity parameters were higher in the Coyuca lagoon (Table 2), in which the fish were significantly larger, indicating that larger hosts harbored more individual helminths and more species of parasite than smaller ones (Table 2). This can be

attributed to the fact that larger fish ingest larger quantities of food and have had more time to accumulate parasites than smaller fish (Bush et al., 2003; Zander, 2004). The variation of feeding habits of this host in the studied lagoons (Yáñez-Aracibia, 1978) probably also may have influenced the species composition of the infracommunities.

Nestedness was observed in the infracommunities of all lagoons as well as among sampling periods (Table 3), suggesting a certain degree of structure in the species composition of these infracommunities in space and time (Poulin and Valtonen, 2001), i.e. species composition exhibited a certain degree of order, because the common species were found in infracommunities of varying richness, but rare species mainly occur in more diverse infracommunities. Nestedness within infracommunities has been attributed to several processes, including variation in host size and sequential colonization of parasite species (Carney and Dick, 2000; Timi and Poulin, 2003; Vidal-Martínez and Poulin, 2003; Violante-González et al., 2008, 2009). However, the spatial and temporal nestedness observed in this study may have been caused by the stability in species composition, due to the persistence of some marine species. The dominant marine helminths (*R. volucrisi*, *P. yamagutii*, and *Ph. centropomi*) occurred in a significant number of double or multiple co-occurrences with other species (ICI > 0.20, Table 3) in the majority of the infracommunities, indicating that those species were those that contributed to a great extent to degree to the nestedness inside those infracommunities.

The component communities and infracommunities of *C. robalito* in the 4 lagoons of Guerrero that were studied are complex, and long-term studies are necessary in order to determine if the results presented herein are consistent over time or if they can be or are variable in accord with yearly differences in biotic and environmental factors, particularly rainfall, marine currents, and temperature, all factors that are important in costal lagoons of the region. It must be determined whether the results obtained for a species with a strong marine connection are characteristic of all marine fish or if they apply only to those species that exhibit the same migratory behavior and enter lagoons to reproduce. Finally, there are populations of *C. robalito* located all along the Pacific coast of México so it is important to determine if the same or different patterns occur in other regions or if this one is characteristic only of fish in the coastal lagoons of Guerrero.

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