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Helminth communities of two species of piscivorous birds, *Ardea alba* (Linnaeus) and *Nyctanassa violacea* (Gmelin) (Ciconiiformes: Ardeidae), in two coastal lagoons from Guerrero state, Mexico

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Abstract The composition and species richness in helminth communities of two species of heron, Ardea alba and Nyctanassa violacea, in two coastal lagoons from Guerrero, Mexico were examined. Nineteen species of helminth (7,804 individuals) were identified in 43 adult birds: 15 digeneans, 1 acanthocephalan, 1 cestode, and 2 nematodes. Eight species co-occurred in herons of both species and lagoons. The prevalence values of seven species and the mean abundance of five species varied significantly between species of birds and between lagoons. The heterophyid, Ascocotyle (Phagicola) longa, was the helminth numerically dominant in the helminth community of A. alba in both lagoons, while the cestode, Parvitaenia cochlearii, dominated the community of N. violacea. At the component community level, species richness varied significantly: 10 species in A. alba from Coyuca to 16 in N. violacea (Tres Palos). All of the birds examined were infected with helminth parasites: three to seven species per host in A. alba from Coyuca, and two to eight species in A. alba and N. violacea from Tres Palos. The results indicate that even

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Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Apartado Postal 1-69, C.P. 42001, Pachuca, Hidalgo, Mexico though species composition was similar between both species of heron, the structure of their communities was not the same. Differences in the feeding behavior of the birds (day/ night habits), as well as local differences in the abundance of species of fish, and infection levels of helminths in each lagoon are suggested as being responsible for the variations registered in the structure of the helminth communities.

Introduction

Piscivorous birds tend to harbor richer and more diverse helminth communities than fish (Kennedy et al. 1986; Poulin 1999). They are also considered important agents of dissemination of helminth parasites, particularly of allogenic species, many of which use aquatic birds as definitive hosts (Esch et al. 1988). Egrets and herons (Ardeidae) are an important group of fish-eating birds that inhabit coastal lagoons temporally or permanently, where they feed on a great variety of prey items such as fish, tadpoles, frogs, snakes, snails, crustaceans, aquatic insects, and small mammals. In Mexico, Ardeidae is represented by 15 species, of which at least 10 inhabit the coastal lagoons of the Mexican state of Guerrero (unpublished data). Two species, Ardea alba (Linnaeus) (great white or common egret, often referred to as a heron) and Nyctanassa violacea (Gmelin) (American night or yellow-crowned night heron), are considered permanent residents because they nest in the margins of local lagoons. However, populations of A. alba in these coastal lagoons are larger than those of N. violacea (unpublished data).

Studies on helminths of piscivorous birds in Mexico are very scarce, and most are taxonomic surveys (LamotheArgumedo and Pérez-Ponce de León 1986; Scholz et al. 2002; Ortega-Olivares et al. 2008), or they only present checklists of helminths (Ramos-Ramos 1995; Barrera-Guzmán and Guillén-Hernández 2008; García-Prieto et al. 2010). To date, only one study described helminth communities of one aquatic bird in both qualitative and quantitative forms (Violante-González et al. 2011).

Studies on the helminth fauna of fishes in Guerrero indicate that at least 14 species of larval helminths parasitize the different species of fish that inhabit these two coastal lagoons (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007). However, only one study of the helminth community of a piscivorous bird (*Phalacrocorax brasilianus*) has been carried out in Guerrero. Therefore, the important role that other species of birds may play in the life cycle of helminths that use fish as intermediary or paratenic hosts in these lagoons has not been assessed. Therefore, the aim of the present study was to determine the species richness and composition in the helminth communities of two species of heron, *A. alba* and *N. violacea*, that differ in abundance and feeding behavior in two coastal lagoons from Guerrero, Mexico.

Materials and methods

Forty-three adults of *A. alba* (Linnaeus) and *N. violacea* (Gmelin) were collected between May and December 2008 from two coastal lagoons: Coyuca ($16^{\circ}57'$ N; $100^{\circ}02'$ W, only *A. alba*, n=14) and Tres Palos ($16^{\circ}48'$ N; $99^{\circ}47'$ W, *A. alba*, n=16, *N. violacea*, n=13) (Scientific Collector's Permit FAUT-217, Direction of Wild Life, SEMARNAT, México, issued to SM). All birds were necropsied and helminths were collected from internal organs (trachea, esophagus, heart, lung, kidney, liver, pancreas, spleen, intestine, and cloaca) and counted.

Helminths collected were processed according to Violante-González et al. (2011). Platyhelminths were put in alcohol–formalin–acetic acid per 24 h and then fixed in 70% ethanol, and acanthocephalans were placed in distilled water and refrigerated overnight (6–12 h) in order to evert the proboscis, and fixed in 70% ethanol. Helminths were stained with carmine or Gomori's trichrome, dehydrated using a graded alcohol series, cleared in methyl salicylate, and mounted whole on slides. Nematodes were cleared with glycerin for examination using light microscopy and then stored in 70% ethanol. Voucher specimens of all taxa of helminths were deposited in the Colección Nacional de Helmintos (CNHE), Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

Helminth community composition was described using prevalence (percent of infected host), mean abundance (mean number of helminths per examined host±standard

deviation), and intensity for each species of helminth per host (Bush et al. 1997). Possible differences in infection parameters for species recorded in the two species and between lagoons were evaluated using *G* tests (Sokal and Rohlf 1998) for prevalence and a χ^2 test for abundance. Significance for all the statistical analyses was established at *P*=0.05, unless stated otherwise.

Analyses were made at the levels of component community (i.e., total helminths in the sample of heron collected) and infracommunity (i.e., total helminths in each individual heron) (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 as a measure of numerical dominance (Magurran 2004). Component community predictability was determined by the Jaccard Similarity Index.

Infracommunities were described in terms of mean number of species per host, mean number of individual helminths, and the mean Brillouin Diversity Index (H') value per host. A oneway ANOVA was applied to determine significant differences in infracommunity parameters between heron species and lagoons. Normality was evaluated using the Kolmogorov– Smirnov test following Lilliefors approach (Sokal and Rohlf 1998), and when significant deviations from normality were found, the data were $log(_{x+1})$ transformed. 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 in order to determine the degree of contribution of each species of helminth to the structure of the infracommunity in each species of bird and each lagoon (for *A. alba*).

Results

Nineteen species of adult helminths were collected from the two species of herons: 15 digeneans, 1 acanthocephalan, 1 cestode, and 2 nematodes (Table 1). Eight species cooccurred in birds of both species and lagoons (Table 1). The frequency distributions of prevalence values for helminths from birds of each species and lagoon indicate that the parasite communities were formed by two species groups: common species, with a prevalence greater than 20% and mean abundance >2 helminths per host, and rare species, with a prevalence less than 20% and mean abundance <1 (Fig. 1). In *A. alba* from Coyuca and *N. violacea*, the number of species considered as common was similar to that of rare ones; in *A. alba* from Tres Palos, the number of common species was higher (Fig. 1).

Some species of helminths that were considered common in one species of host were not in the other species; this

Table 1 Infection parameters for the helminths of A. alba and N. violacea (Ardeidae) from two coastal lagoons, Coyuca and Tres Palos, in Guerrero, Mexico

Parasite (+ abbreviations)	CNHE (Coll. No.)	NI/host/ lagoon	P (%)	Total	Mean abundance	Range of intensity	ICI
Digenea (adult)							
Apharyngostrigea cornu Zeder, 1800 (intestine) Aph	8010	10/Aa Co	71.4	150	10.7 ± 15.1	2-39	0.16
	8011	14/Aa TP	87.5	194	12.1 ± 15.4	2-49	0.18
	8012	5/Nv TP	36.5	15	1.15 ± 1.41	1-4	0.06
Ascocotyle (Phagicola) longa Ransom, 1920	8013	9/Aa Co	64.3	2214	158.1 ± 244.1	2-700	0.14
(intestine) Alo	8014	16/Aa TP	100	1938	121.1 ± 153.5	3-415	0.21
	8015	2/Nv TP	15.4	15	1.1 ± 6.4	3-12	0.03
Ascocotyle (Phagicola) sp. (intestine) Asc	8016	2/Nv TP	15.4	5	$0.4\ \pm 0.7$	2-3	0.03
Centrocestus formosanus Nishigori, 1924 (intestine) Cen	8017	7/Aa Co	50	255	$18.2~{\pm}39.0$	4-120	0.11
	8018	6/Aa TP	37.5	480	30 ± 41.4	37-129	0.08
Clinostomum complanatum Rudolohi, 1814 (esophagus) Cli	8019	4/Aa Co	28.6	7	0.5 ± 1.0	1-3	0.06
	8020	2/Aa TP	12.5	26	1.6 ± 11.3	5-21	0.03
	8021	2/Nv TP	15.4	60	4.6 ± 41.0	1-59	0.03
Cloacitrema ovatum Yamaguti, 1935 (cloaca) Clo	8022	1/Nv TP	7.7	2	0.1	2	0.01
Diplostomum (Austrodiplostomum) compactum Lutz, 1928 (stomach) Dip	8023	1/Nv TP	7.7	2	0.1	2	0.01
Echinochasmus leopoldinae Scholz, Ditrich & Vargas-Vázquez, 1996 (intestine) Ech	8024	4/Aa TP	25	978	61.1 ± 280	2-487	0.05
	8025	3/Nv TP	23.1	36	2.8 ± 12.1	1-25	0.04
Haplorchis pumilio Looss, 1896 (intestine) Hap	8029	4/Nv TP	30.8	233	$1.9~\pm70.3$	5-160	0.05
Mehrastomum minutum Saksena, 1959 (cloaca) Meh	8026	3/Aa Co	21.4	3	0.2	1	0.05
	8027	2/Aa TP	12.5	2	0.1	1	0.03
	8028	2/Nv TP	15.4	25	1.92 ± 16.26	1-24	
Microparyphium facetum Dietz, 1909 (cloaca) Mic	8030	2/Nv TP	15.4	3	$0.2\ \pm 0.7$	1-4	0.03
Odhneria raminellae Travassos, 1921 (stomach) Odh	8031	1/Aa Co	7.1	69	4.9	69	0.02
Posthodiplostomum minimum MacCallum, 1921	8035	2/Aa TP	12.5	6	0.4 ± 1.4	2-4	0.03
(intestine) Pos	8036	10/Nv TP	76.9	127	9.8 ± 10.5	2-32	0.13
Riberoia ondatrae Price, 1942 (intestine, stomach) Rib	8032	3/Aa Co	21.43	5	0.36 ± 0.58	1-2	0.05
	8033	10/Aa TP	62.5	60	3.7 ± 7.1	1-19	0.13
	8034	6/Nv TP	46.1	04	7.2 ± 25.3	1-66	0.08
<i>Tylodelphys</i> sp. (intestine) Tyl Acanthocephala	8037	1/Aa TP	6.2	3	0.2	3	0.01
Southwellina hispida (Van Cleave, 1925)	8046	9/Aa Co	64.3	29	2.1 ± 1.7	1-6	0.14
Witenberg, 1932 (intestine) Sou	8044	10/Aa TP	62.5	16	$1.0\ \pm 0.8$	1-3	0.13
	8045	12/Nv TP	92.3	45	3.5 ± 2.1	1-8	0.16
Cestoda							
Parvitaenia cochlearii Coil, 1955 (intestine) Par	8038	3/Aa Co	21.4	6	0.4 ± 1.7	1-4	0.05
	8039	2/Aa TP	12.5	10	0.6 ± 1.4	4-6	0.03
	8040	12/Nv TP	92.3	444	34.1 ±38.3	3-91	0.16
Nematoda							
Capillaria sp. (intestine) Cap		2/Nv TP	15.4	5	0.4 ± 2.1	1-4	0.03
Contracaecum multipapillatum Drasche, 1882	8041	14/Aa Co	100	40	2.9 ± 2.7	1-9	0.22
(stomach, intestine) Con	8042	8/Aa TP	50	42	2.6 ± 4.1	1-10	0.10
	8043	11/Nv TP	84.6	160	12.3 ± 10.8	2-34	01.4

Higher significance values of prevalence (G test), abundance (χ^2 -test), and infracommunity index (ICI >0.10) are in bold (P<0.05)

CNHE National Helminth Collection, NI number of infected. Aa Ardea alba, Nv Nyctanassa violacea. Co Coyuca, TP Tres Palos, P (%) prevalence of infection (percentage infected), total total number of individual parasites, mean abundance mean number of parasites per examined fish \pm standard deviation, intensity range (i.e., min-max)

Fig. 1 Prevalence (columns) and mean abundance (black dots) of helminths infecting A. alba and N. violacea (Ardeidae) from two coastal lagoons, Coyuca and Tres Palos, in Guerrero, Mexico: A. alba in Coyuca (a) and Tres Palos (b), and N. violacea in Tres Palos lagoon (c). Codes of species in Table 1



pattern was the same when only the common species of *A*. *alba* were compared between lagoons. The nematode *Contracaecum multipapillatum*, the digenean *Apharyngostrigea cornu*, and the acanthocephalan *Southwellina hispida* were the only helminths considered to be common species in both species of host and lagoons (Fig. 1).

The prevalence of seven species of helminths varied significantly between species of heron and lagoons: three species were more prevalent in *A. alba* from Tres Palos (*A. cornu*, *G*= 20.9, *P*<0.05; *Ascocotyle* (*Phagicola*) *longa*, *G*=60.3, *P*< 0.05; *Riberoia ondatrae*, *G*=19.7, *P*<0.05), 2 in *A. alba* from Coyuca (*Clinostomum complanatum G*=7.8, *P*<0.05; *C.* multipapillatum G=16.77, P<0.05), and two in N. violacea (Parvitaenia cochlearii, G=90.9, P<0.05; S. hispida, G=7.7, P<0.05). In contrast, mean abundance only varied significantly for five species: C. multipapillatum (χ^2 =10.3, P<0.05), P. cochlearii (χ^2 =64.2, P<0.05), and R. ondatrae (χ^2 =6.2, P< 0.05) were more abundant in N. violacea, and A. cornu (χ^2 = 8.9, P<0.05) and A. (P.) longa (χ^2 =144.1, P<0.05) were more abundant in A. alba from Tres Palos and Coyuca, respectively. Finally, prevalence values correlated positively with abundance in both species of heron and between lagoons, indicating that the most prevalent species were also the most abundant (A. alba in Coyuca, r_s =0.649, P<0.05; Tres Palos, r_s =0.709, P<0.05; N. violacea, r_s =0.816, P<0.05).

The analysis of the component communities indicated that the total number of species of helminth registered in each species of host was significantly different: 10 (A. alba from Coyuca) and 16 (N. violacea) ($\chi^2 = 7.2$, P<0.05). The total number of helminths ranged from 1,271 (N. violacea) to 3,755 (A. alba from Tres Palos) and also varied significantly ($\chi^2 =$ 1,203.8, P<0.05; Table 2). Values of the Shannon-Wiener diversity index ranged from 3.03 to 3.55 and evenness from 0.88 to 0.91, although none of the two parameters varied significantly between species of host or lagoons (P > 0.05). The Berger-Parker Index values ranged from 0.35 in N. violacea to 0.80 in A. alba from Coyuca, and were significantly different. Ascocotyle (P.) longa was the helminth numerically dominant in A. alba of both lagoons, and P. cochleari in N. violacea. The qualitative similarity values between the communities ranged between 61% (N. violacea-A. alba from Covuca) and 81% (A. alba Tres Palos-Covuca) and varied significantly ($\chi^2 = 12.2, P < 0.05$).

All the birds examined were infected with helminths: three to seven species per bird in *A. alba* from Coyuca,

two to eight species in *A. alba* from Tres Palos, and two to eight in *N. violacea* (Fig. 2). The mean number of species of helminth varied between 4.50 ± 1.29 in the infracommunities of *A. alba* from Coyuca and 5.9 ± 1.4 in those of *N. violacea*, while the mean number of individuals, 97.7 ± 84.0 (*N. violacea*) to 234.7 ± 318.2 (*A. alba* from Tres Palos), although only this second parameter varied significantly among the parasite infracommunities (one-way ANOVA, F=26.9, P <0.05; Table 2). The mean Brillouin diversity index varied significantly between *A. alba* from Coyuca, 0.91 ± 0.3 , and *N. violacea*, 1.5 ± 0.4 , (one-way ANOVA, F=11.8, P < 0.05).

Evenness was positively correlated with diversity values of all infracommunities (P<0.05), indicating that the most diverse infracommunities were those with a higher uniformity in species abundance. Mean qualitative similarity inside the infracommunities varied significantly from 21.3± 25.8 (*A. alba* from Coyuca) to 31.4±26.4 (*A. alba* from Tres Palos) (one-way ANOVA, F=4.62, P<0.05).

The ICI values indicated that common species (prevalence >50%, Fig. 1) registered the higher number of double or multiple co-occurrences with other helminth species (ICI >0.10, Table 1). The acanthocephalan, *S. hispida*, and the nematode, *C. multipapillatum*, were the only helminths that exhibited high ICI values in all the infracommunities (Table 1).

Discussion

Five of the species of adult helminths registered in the two species of fish-eating birds, *A. alba* and *N. violacea*, are new geographical host records for Coyuca and Tres Palos lagoons: *A. cornu*, *Ascocotyle* (*Phagicola*) sp., *Cloacitrema*

 Table 2
 Characteristics of the helminth component communities and infracommunities in two heron species A. alba and N. violacea (Ardeidae)

 from two coastal lagoons in Guerrero, Mexico

Parameters	Ardea Coyuca	Ardea Tres Palos	Nyctanassa Três Palos	χ^2	Р
Component community					
Total number of species	10	12	16	7.2	< 0.05
Total number of parasites	2,778	3,755	1,271	1,203.8	< 0.05
Shannon-Wiener Index	3.0	3.2	3.5	0.05	>0.05
Evenness	0.9	0.9	0.9	0.01	>0.05
Berger–Parker Index	0.8	0.5	0.3	4.2	< 0.05
Dominant species	A. (P.) longa	A. (P.) longa	P. cochlearii		
Infracommunity				ANOVA	P
Mean number of species	4.5±1.3	4.8 ± 2.0	5.9 ±1.4	2.7	>0.05
Mean number of individuals	198.43 ± 248.30	234.7 ± 318.2	97.8 ± 84.0	26.9	< 0.05
Mean value of Brillouin Index	0.9 ± 0.3	1.02 ± 0.33	1.5 ±0.4	11.8	< 0.05
Mean evenness	0.5 ± 0.3	0.52 ± 0.15	0.7 ± 0.2	1.9	>0.05
Jaccard Index	21.3 ±25.8	31.4 ±26.4	28.3 ± 16.9	4.6	< 0.05

Significantly different parameters are in bold (P<0.05)

ovatum, Haplorchis pumilio, and *Microparyphium facetum*. Helminths of the 14 remaining species had been registered previously in several species of fish from both lagoons (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007).

Considering the total parasite fauna registered in this study, the digeneans (15 species) were the dominant group in both species of host and in both lagoons (Table 1), which is similar to the general pattern reported for helminth communities of freshwater fish in Mexico (Salgado-Maldonado et al. 2001a, b; Salgado-Maldonado et al. 2004; Pineda-López et al. 2005), and particularly from Coyuca and Tres Palos (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007). Two of the three species of helminths considered as common in the two species of host as well as in both lagoons also have been recorded as larvae in previous studies. C. multipapillatum has been reported from ten species of fish and S. hispida has been reported from six species in Coyuca and Tres Palos lagoons (Violante-González and Aguirre-Macedo 2007, Violante-González et al. 2007). However, A. cornu has not been reported previously.

Immature individuals of *A. cornu* require invertebrates as intermediate hosts and use either fish or tadpoles as paratenic hosts (Yamaguti 1971; Navarro et al. 2005), so it is possible that this species uses tadpoles or frogs as paratenic hosts in coastal lagoons that have been studied because remains of amphibians were found in the stomach of some herons. *A. cornu* is considered to be a specialist because it matures only in herons (Ardeidae) (Navarro et al. 2005); our results are consistent with this hypothesis because this digenean was found in the two species examined for this study (Table 1) but not in cormorants (*P. brasilianus*), which are more abundant in the same area (Violante-González et al. 2011).

The heterophyids group (A. (P.) longa, A. (P.) sp., Centrocestus formosanus, and H. pumilio) were the best represented. In previous studies of the parasites of fish in México, heterophyids are the most frequent and abundant (Scholz et al. 2001), and the adults are frequently parasites of the intestine of aquatic birds (Sepúlveda et al. 1999; Scholz et al. 2001). In accordance with Scholz et al. (2001), at least two species of heterophyid (C. formosanus and H. pumilio) were introduced to Mexico, probably from Asia, with the accidental introduction of a thiarid snail, Melanoides tuberculata. To date, this snail is abundant in the coastal lagoons of Guerrero (Violante-González et al. 2009), and metacercariae of C. formosanus have been recorded co-occurring with Echinochasmus leopoldinae in the gills of Poecilia sphenops and Astyanax fasciatus (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007).

It is probable that the differences in the infection parameters of some species of helminths (Table 1) are the result of differences in the feeding behavior of each species of bird (Threlfall 1982). Nevertheless, the diet of both species is very similar, and it includes a wide variety of prey items as fish, tadpoles, frogs, snails, crustaceans, aquatic insects, and small mammals, *A. alba* is diurnal and *N. violacea* nocturnal. For example, five helminths were found with higher infection levels in *N. violacea* (*P. minimum*, *R. ondatrae*, *P. cochlearii*, *S. hispida*, and *C. multipapillatum*; Table 1), which feeds at night on a wider variety of species of fish that hide among the roots of the mangroves or under the submerged vegetation, being most easily captured during the night when they are more defenseless.

The parasite component communities were similar between species of host as between lagoons; i.e., they both exhibited a relatively low number of species (10 to 16 species) and were dominated by a single species [A. (P.) longa in A. alba and P. cochlearii in N. violacea] (see Table 2), which is the same pattern observed in the parasite communities of fish in these lagoons (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007). This could be attributed to the lack of migratory behavior in the birds from these coastal lagoons, which would limit exposure to other species of helminths from a wider geographical area (Threlfall 1982; Kennedy et al. 1986; Fedynich et al. 1997). Nevertheless, some differences among the component communities were evident. The richest and most diverse helminth community was that of N. violacea, possibly a result of this community being less dominated by a single species, in contrast to the communities of A. alba (Table 2).

One hypothesis in parasite communities suggests that parasite diversity is positively correlated with host abundance because hosts with larger populations will more readily sustain populations of adult helminths (Bell and Burt 1991; Takemoto et al. 2005). However, this hypothesis is not supported by our results because of the ten species of Ardeidae recorded in the locality, *A. alba* is the most abundant, while the population of *N. violacea* is the scarcest (unpublished data). The values of richness and diversity registered in the two heron species were similar to those reported in infracommunities of other piscivorous birds as cormorants in other localities (Threlfall 1982; Fedynich et al. 1997), and the same lagoons (Violante-González et al. 2011).

Overall, the results indicate that, even though species composition was similar between both species of host (they shared more than 70% of the species), the structure of the communities of both levels was not the same one. The helminth species responsible for the community structure were not the same ones in each community, possibly, as mentioned above, because of differences in the feeding behavior of each species (day/night habits), but as well this could be due to differences in the abundance of each species of fish as well as to infection levels of species of helminths in the two lagoons (Violante-González and Aguirre-Macedo 2007; Violante-González et al. 2007, 2009, 2010, 2011). The contribution of each of these three factors is yet to be studied. Acknowledgments This research was possible in part because of a collaborative project "Calidad Ambiental y Desarrollo Sustentable: Inventario Ambiental y Establecimiento de Indicadores Regionales" financed by the Programa de Mejoramiento del Profesorado (PROMEP). The authors thank Francisco Javier Aguilar Palma of the Marine Ecology Academic Unit (UAG) for his assistance with field and laboratory work. We are also grateful to Rogelio Aguilar Aguilar and David Osorio Sarabia (Universidad Nacional Autónoma de México, UNAM) for their assistance in identifying some of the species of helminths, as well as to Luís García Prieto (UNAM) who helped us obtain important bibliographic references for the realization of this manuscript. We thank an anonymous reviewer whose extensive and thoughtful comments substantially improved the manuscript.

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