Latin American Journal of Aquatic Research, 53(5): 749-758, 2025
DOI: 10.3856/vol53-issue5-fulltext-3483

Research Article

Metazoan parasites of the red grouper, *Epinephelus morio*, in a pilot aquaculture system in Yucatán, Mexico

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ABSTRACT. The red grouper, *Epinephelus morio*, locally known as "mero rojo", represents one of the most important commercial fish species in the Yucatán Peninsula, although they have been overfished. Populations of this economically important fish have been studied in the wild, and the presence of a wide array of metazoan parasite taxa has been reported. The technology for producing red grouper seed for a complete aquaculture cycle is being assessed at the pilot system of the Unidad Multidisciplinaria de Docencia e Investigación (UMDI-UNAM) facility, in Sisal, in northwest Yucatán, Mexico. In two isolated events that occurred at the facility in 2021 and 2023, 14 individuals of *E. morio*, intended to be introduced into the system, died during the quarantine period; our sampling for parasites was opportunistic. Specimens were necropsied, and their metazoan parasites were recovered. Here, we report on the parasite fauna of these individuals. Parasite identification was conducted using morphological traits and, in some cases, molecular data. Nine species were found, including 1 monogenean, 3 trematodes, 1 cestode, 1 acanthocephalan, 2 nematodes, and 1 copepod. The highest prevalence of infection was observed in the acanthocephalan *Gorgorhynchus medius* and the monogenean *Pseudorhabdosynochus yucatanensis*, with rates of 70 and 75% for the first and second mortality events, respectively. The parasite fauna of fishes from the aquaculture system is akin to that of wild populations of *E. morio* in the Yucatán Peninsula. A brief discussion on the importance of considering parasitic diseases in aquaculture systems is presented, and we briefly discuss the potential zoonotic importance of the larvae of the nematode *Pseudoterranova* sp.

Keywords: *Epinephelus morio*; aquaculture; taxonomy; DNA; parasites, Sisal; Mexico

INTRODUCTION

The red grouper, *Epinephelus morio*, is a demersal fish that occurs at depths less than 100 m. It is distributed along the western Atlantic coast, from North Carolina, USA, to southern Brazil, including the Gulf of Mexico, the Caribbean Sea, and Bermuda (Froese & Pauly 2025). Adults are carnivores feeding upon a wide variety of fish, and occasionally crustaceans, whereas juveniles feed mainly on crustaceans (see Durruty-Lagunes 2014 and references therein). Red groupers are protogynous sequential hermaphrodites and lack sexual

Associate Editor: Mauricio Laterça

dimorphism (Brulé et al. 1999); females may exhibit sexual inversion to males, usually when they reach 30-35 cm (Giménez et al. 2003). Red groupers belong to the family Serranidae, are locally known as "mero rojo", and represent one of the most important commercial fisheries in the Gulf of Mexico (Rincón-Sandoval & López-Rocha 2024).

Since this important marine resource is overfished (Echazabal-Salazar et al. 2021), farming can be developed as a sustainable alternative to traditional fishing. The Unidad Multidisciplinaria de Docencia e Investigación at the Universidad Nacional Autónoma de Mexico (UMDI-UNAM) in Sisal, Yucatán, has implemented a research project aimed at producing red grouper seed for a complete aquaculture cycle. Grouper aquaculture has been developed in other parts of the world, particularly in Southeast Asia, with nine species of *Epinephelus* (Tupper & Sheriff 2008).

Besides the fact that parasites play a crucial role in ecosystems, they pose a significant limitation to the development and sustainability of aquaculture (Madsen & Stauffer 2024). Diseases may emerge through the exchange of pathogens with wild populations, evolution from non-pathogenic microorganisms, or the deliberate transfer of stocks (Murray & Peeler 2005, Madsen & Stauffer 2024). Some studies have described the parasite fauna of serranid fishes in the wild (e.g. Cribb et al. 2002), but relatively few have documented the parasite fauna of *Epinephelus* species in captivity (see Leong & Wong 1988, Seng & Yong 1990, Rückert et al. 2010, Truong et al. 2017). In particular, of the 37 species of parasites described from *E. morio*, 32 have been recorded in free-living populations in the Yucatán Peninsula (Fajer et al. 1979, Moravec et al. 1995a,b, 1997, 2010, Vidal-Martínez et al. 1995, 1997, 1998, Aguirre-Macedo & Bray 1996) (Table 1). The main objective of this study is to report on the metazoan parasite fauna of *E. morio* following two mortality events of broodstock specimens intended to be acclimatized under controlled conditions in the laboratory of marine fish reproduction at the Sisal UMDI-UNAM facility.

MATERIALS AND METHODS

Specimens of *E. morio* examined in this study were obtained from the UMDI-UNAM facility at Sisal, as they were intended for an aquaculture research project. Two mortality events occurred in which the examined fish died during the quarantine period after being captured. The first event (event 1) occurred in November 2021, when 21 individuals of red groupers were captured at depths of 36-55 m using longlining off the coast of Sisal. Fish were maintained in 2,000 L tanks on the vessel and then transported to the UMDI-UNAM facility. Fish were kept in 18 m^3 tanks at a salinity of 35 with continuous aeration, water replacement, and fed a semi-moist diet supplemented with squid. A month later, despite prophylactic measures, 10 of the captured groupers died. A second mortality event (event 2) occurred in September 2023. Nine red groupers were captured by hook and line off the coast of Sisal, acclimatized, and transported with aeration to the UMDI-UNAM facility. Four of them died around 48 h post-capture.

A total of 14 red groupers were examined for parasites (mean total length, TL: 56.26 ± 7.28 cm; range: 37.5-77.97 cm), all of which were females. Ten of them corresponded to event 1 (mean TL 69.12 ± 5.32 cm; range of 61.9-77.97 cm), while four corresponded to event 2 (43.4 ± 9.25 cm; range of 37.5-54 cm). Fish from both mortality events were necropsied and their organs (gills, gonads, heart, gall bladder, urinary bladder, and gastrointestinal tract) separated in Petri dishes with 8.5% saline, and examined under the stereomicroscope. Trematodes, monogeneans, cestodes, and nematodes were recovered and washed in saline, killed with hot (nearly boiling) saline, and fixed in vials with 100% ethanol for morphological and molecular studies. Acanthocephalans were placed in distilled water for a few hours in the refrigerator and then fixed in 100% ethanol. Copepods were placed directly in vials with 100% ethanol.

Parasite processing for morphological examinations

Trematodes, acanthocephalans, and monogeneans were stained with Mayer's paracarmine, dehydrated through a graded alcohol series, cleared with methyl salicylate, and mounted on slides with Canada balsam. Nematodes and copepods were cleared with 50% glycerol. Specimens were identified to the lowest possible taxonomic level, and some of them were deposited in the Colección Nacional de Helmintos (CNHE), Mexico City (accession numbers 12397-12401). Ecological parameters were estimated following Bush et al. (1997).

Parasite processing for molecular analysis

For DNA extraction, some specimens were placed individually in tubes with a digestion solution and incubated overnight at 56°C. The digestion solution contained 10 mM Tris-HCl (pH 7.6), 10 mM NaCl, 20 mM Na2 EDTA (pH 8.0), 1% sarkosyl, and 0.1 mg mL^{-1} proteinase K. Following digestion, DNA was extracted from the supernatant using DNAzol reagent, according to the manufacturer's instructions. A fragment of the large subunit of ribosomal DNA (28S) was amplified via PCR using a series of primers (Table 2). PCR cycling conditions included denaturation at 94°C for 3 min, followed by 33 cycles of 94°C for 30 s, annealing at 52°C for 45 s, and extension at 72°C for 1 min, with a final extension of 7 min at 72°C. Contigs were assembled and base calling differences resolved using Geneious Prime v. 11.0.14 (Biomatters Ltd.). A standard nucleotide similarity search was performed using the nBLAST tool against the NCBI database for species identification (https://blast.ncbi.nlm.nih.gov/Blast.cgi). A sequence identity value ≥99% was arbitrarily considered valid to achieve a species-level designation. The obtained sequences were deposited in the GenBank database under the accession numbers (PV916722 - PV916727).

RESULTS

A total of 177 parasite specimens were collected from the 14 examined groupers, representing 9 taxa: 1 monogenean, 3 trematodes, 1 cestode, 1 acanthocephalan, 2 nematodes, and 1 copepod (Table 3). In event 1, 6 taxa were registered, whereas the 9 taxa were recovered in event 2. The habitat with the highest parasite species richness was the intestine, with five out of the nine taxa (Table 3).

When compared to GenBank records, the obtained sequence of the monogenean showed an identity of 85% with *Pseudorhabdosynochus* sp. The trematode showed an identity of 96% with *Lepidapedoides angustus*. Further morphological examination of the monogenean and the trematode, along with previously published records, allowed us to conclude that these species corresponded with *P. yucatanensis* and *L. levenseni*, respectively. The sequence of the cestode was 97.8% similar to that of *Phoreibothrium* sp.; since the recovered specimens were larval forms, we were unable to identify them morphologically to the species level. For the sequences of nematodes, BLAST search yielded an identity of 98% with *Philometra* sp., and 100% with *Pseudoterranova* sp. The last one was recovered as a larval form, hence limiting the achievement of species identification. Morphological examination, habitat within the host, and previous records also allowed us to conclude that *Philometra* specimens corresponded with *P. margolisi.* Finally, the acanthocephalan reached 100% similarity with sequences deposited in the GenBank for *Gorgorhynchus medius*. We were unable to obtain sequences for *Stephanostomum* sp., *Postporus epinepheli*, and *Hatschekia insolita*, which were identified morphologically.

Overall, ecological parameters of infection, including prevalence, mean intensity, and mean abundance, were higher in event 2, where fish died within less than two days after capture and transportation to the facility. In event 2, the monogenean *P. yucatanensis* (Fig. 1) reached a prevalence of 75%, with a mean intensity of seven parasites per infected host. In contrast, in event 1, the acanthocephalan *G. medius* was the species with the highest prevalence, at 70%, and a mean intensity of 32.1 parasites per infected host (Table 3). The trematode *L. levenseni* was found in both events, with relatively high prevalence and mean intensity values (Table 3).

DISCUSSION

Parasite species composition

Most of the recovered parasites were adult forms, and the red grouper is their definitive host. Only two of the nine parasite taxa we found in our study were larval parasites. The onchoproteocephalid tapeworm *Phoerobothrium* sp. uses groupers and other fish species as intermediate hosts, as the final hosts are sharks of the family Carcharhinidae (de Klerk et al. 2022, and references therein). We also recovered third-stage larvae of the nematode *Pseudoterranova* sp. This nematode requires pinnipeds (seals, sea lions, and walruses) to complete their life cycle, and is often found encysted in the flesh of fish paratenic hosts (McClelland 2002 and references therein).

The nine taxa of metazoan parasites reported in this study represent 27% of the parasite fauna previously reported for this host species across its geographical range. Taxa not identified to the species level are most likely to represent the species reported previously. For example, we report on the presence of the digenean *Stephanostomum* sp., which was previously reported as *S. dentatum* from red groupers in the same geographical area (Aguirre-Macedo & Bray 1996). The case of the acanthocephalan is interesting. The species was previously reported in red groupers as *Gorgorhynchus clavatus* although identification was based solely on morphological grounds (Moravec et al. 1995a, 1997, Vidal-Martínez et al. 1998). Novel molecular data obtained in our study clearly indicate that the individuals belong to *G. medius* as they are 100% similar to a sequence of that species from cystacanths obtained from the white grunt, *Haemulon plumierii*,

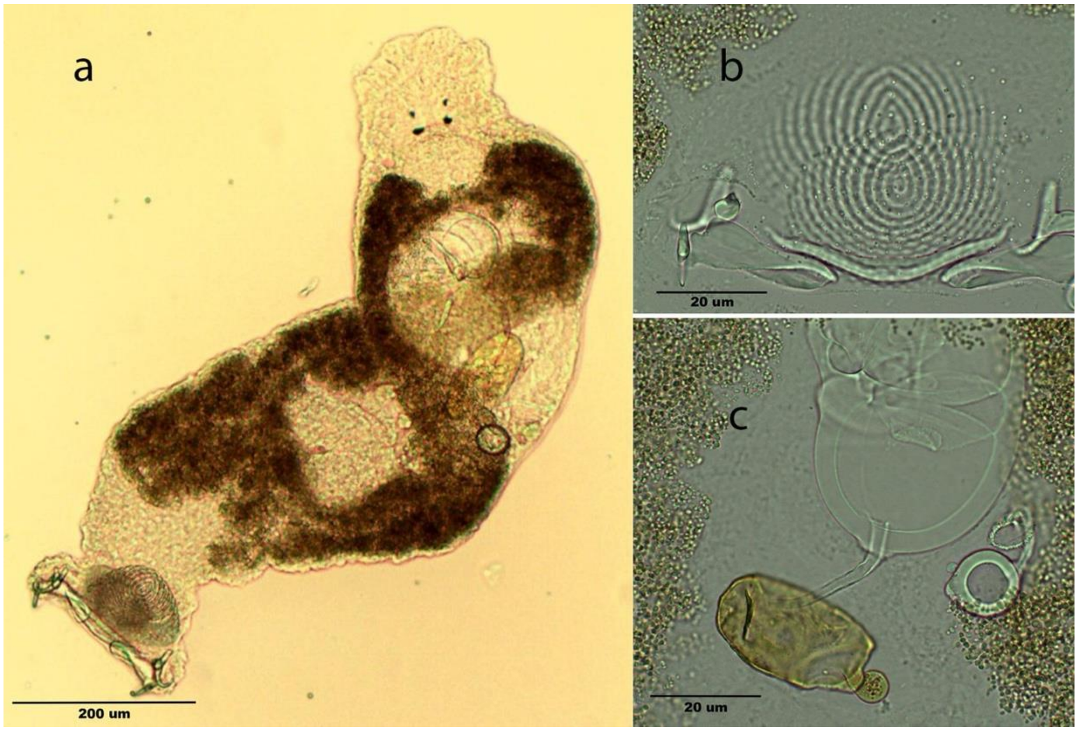

Figure 1. Photomicrographs of *Pseudorhabdosynochus yucatanensis* from the gills of breeding individuals of the red grouper, *Epinephelus morio*, from a pilot aquaculture system. a) Whole individual, ventral view, b) detail of the haptor showing the row pattern of the squamodisc, anchors, and bars, and c) detail of the male and female organs in the anterior end of the body (penis, vagina, and egg).

from the same geographical area (García-Varela et al. 2024). Certainly, molecular data are valuable for refining taxonomic identifications, and in some cases, for achieving a specific identification.

Parasite species richness

In this study, nine parasite taxa were identified in the two mortality events of individuals recently introduced to captive conditions or in the process of introduction, contrasting with the 37 metazoan parasite taxa reported from wild populations of the red grouper in the Yucatán Peninsula (Table 1). Some studies have reported on the parasite fauna of groupers (*Epinephelus* spp.) maintained in captivity compared to those sampled in the wild. In two species of groupers, *Epinephelus fuscoguttatus* and *E. coioides*, a higher diversity of parasite species was found in the wild (Rückert et al. 2010). In contrast, parasite diversity was higher in captive populations of *E. malabaricus* (Leong & Wong 1988). However, it has been shown that dominant parasite species might be found in these hosts regardless of the condition (wild or cultured) (Leong 1997). The lower parasite species richness of specimens intended for captive maintenance in our study may be attributed to factors such as the developmental stage and depth at which the specimens were captured, compared to those sampled in previous studies (e.g. Moravec et al. 1997). For instance, the specimens of the present study were adults (average length 56.25 cm) whereas the specimens studied by Moravec et al. (1997) were subadults with an average length of 23 cm. In this case, older fish living at greater depths exhibited a lower parasite species richness than fish occurring in nearshore habitats, which is in agreement with Marcogliese & Cone (1997). These authors argued that ontogenetic changes in feeding behavior, habitat, host size, and age may influence the parasite fauna. It has been reported that deep-water parasite fauna is less diverse than shallow-water faunas. For instance, the parasitic infection of the slope-dwelling rattail, *Coryphaenoides armatus*, decreases in the number of species and intensity as depth increases, which is associated with a decrease in macrofaunal abundance, as shown by Campbell (1990). Habitat depth might favor the loss of some species of parasites, along with the change in feeding ecology from juveniles to adults.

Table 1. Metazoan parasite taxa of *Epinephelus morio* along its distribution range in the western Atlantic coast. YU: Yucatán, CA: Campeche, QR: Quintana Roo, CU: Curacao, and CB: Cuba.

Parasite taxa	Habitat	Locality	References
Digenea			
Allonematobothrium yucatanense	Fins	YU, CA, QR	Moravec et al. (1997)
Pyelosomum erubescens	Intestines	YU	Moravec et al. (1997)
Prosorhynchoides sp. (metacercaria)	Fins	YU, CA, QR	Vidal-Martínez et al. (1998)
Bucephalus sp. (metacercaria)	Fins	CA	Moravec et al. (1997)
Cardiocephaloides sp. (metacercaria)	Brain	YU, QR	Moravec et al. (1997)
Dollfustrema sp. (metacercaria)	Fins	YU, CA, QR	Moravec et al. (1997)
Helicometra torta	Intestine	YU, QR	Moravec et al. (1997)
Helicometrina nimia	Intestine	CA	Moravec et al. (1997)
Lepidapedoides levenseni	Intestine	YU	Moravec et al. (1997)
Lecithochirium floridense	Stomach	YU, CA, QR	Vidal-Martínez et al. (1998)
Postporus epinepheli	Intestine	YU, CA, QR, CU	Moravec et al. (1997), Vidal- Martínez et al. (1998), Nahhas & Cable (1964)
Rhipidocotyle sp. (metacercaria)	Fins	YU	Moravec et al. (1997)
Stephanostomum dentatum	Intestine	YU, CA, QR	Aguirre-Macedo & Bray (1996)
Stephanostomum sp. (metacercaria)	Head tissue, urinary bladder	YU, CA	Moravec et al. (1997)
Strigeidae gen. sp. (metacercaria)	Brain	YU, CA, QR	Vidal-Martínez et al. (1998)
Lecithochirium musculus	Stomach	CU	Nahhas & Cable (1964)
Lepidapedoides trachinoti	Intestine and caeca	CU	Nahhas & Cable (1964)
Monogenea			
Parancylodiscoides macrobaculum	Gills	YU, CA, QR, CB	Zhukov (1983), Kohn et al. (2006)
Pseudorhabdosynochus yucatanensis	Gills	YU, CA, QR	Vidal-Martínez et al. (1997)
Cestoda			
Callitetrarhynchus sp. (larva)	Intestine and stomach	YU, CA, QR	Fajer et al. (1979), Moravec et al. (1997), Vidal-Martínez et al. (1998)
Eutetrarhynchus sp. (larva)	Intestine	YU	Moravec et al. (1997)
Tylocephalum sp. (larva)	Stomach and caeca	YU, CA, QR	Moravec et al. (1997)
Tetraphyllidea sp.	Intestine	YU, CA, QR	Vidal-Martínez et al. (1998)
Acanthocephala			
Gorgorhynchus clavatus	Intestinal lumen	YU	Moravec et al. (1995a), Moravec et al. (1997)
Nematoda			
Anisakis typica (larva)	Mesentery	YU, CA, QR	Moravec et al. (1995a)
Anisakis sp.(larva)	Stomach	YU, CA, QR	Fajer et al. (1979)
Ascarophis mexicana	Intestine	YU, CA, QR	Moravec et al. (1995b), Moravec et al. (1997)
Capillariidae gen. sp.	Gills	YU	Moravec et al. (1995a)
Hysterothylacium eurycheilum	Intestine	YU	Moravec et al. (1995a)
Hysterothylacium sp. (larva)	Intestine	YU, QR	Moravec et al. (1995a)
Paracapillaria sp. (larva)	Intestine	YU, CA, QR	Vidal-Martínez et al. (1998)
Paracapillaria (Paracapillaria) epinepheli	Intestine	YU, CA	Moravec et al. (1996)
Philometra salgadoi	Ocular cavity	YU	Vidal-Martínez et al. (1995)
Philometra margolisi	Gonads	YU, CA, QR	Vidal-Martínez et al. (1998)
Philometra morii	Bucal cavity, nares	Tampa Bay, Florida. USA.	Moravec et al. (2010)
Phocanema decipiens	Mesentery	YU, CA, QR	Moravec et al. (1997)
Copepoda			
Hatschekia insolita	Gills	YU, CA, QR	Vidal-Martínez et al. (1998)

Moreover, the fish individuals sampled by Moravec et al. (1997) and Vidal-Martínez et al. (1998) included only specimens of *E. morio* collected from artisanal fisheries at several nearshore and shallow-water locations throughout the Yucatán Peninsula, in the states of Campeche, Yucatán, and Quintana Roo. Addi-

Table 2. Primers used for DNA sequencing.

F	R	Forward sequence	Reverse sequence	Reference
502	536	CAAGTAC-CGTGAGGGAAAGTTGC	CAGCTATCCTGAGGGAAAC	García-Varela & Nadler (2005)
502	501	CAAGTACCGTGA GGGAAAGTT GC	TCGGAAGGAACCAGCTACTA	Smythe & Nadler (2006)
T01N	T30N	GATGACCCGCTGAATTTAA G	TGTTAGACTCCTTGGTCCGTG	Harper & Saunders (2001)
28Sy	28z	CTAASSAGGATTCCCTTAG-TAACGGCGAGT	AGACTCCTTGGTCCGT	Hillis & Dixon (1991)

Table 3. Metazoan parasites of the red grouper, *Epinephelus morio* recorded in this study from two mortality events under captivity, along with their corresponding ecological infection parameters. P: prevalence (%); MI: mean intensity, and MA: mean abundance. Habitat; Gi: gills; I: intestine, Go: gonads, M: mesentery. *Standard deviation not calculated since only one fish was infected with that parasite species. Standard deviation is indicated in parentheses.

Parasite taxa	Event 1			Event 2			Habitat
	P	MI	MA	P	MI	MA	
Monogenea							
Pseudorhabdosynochus yucatanensis	-	-	-	75	7.0 ± 2.6	5.25 ± 4.10	Gi
Trematoda							
Lepidapedoides levenseni	30	9.3 ± 6.6)	2.8 ± 5.5	50	19.5 ± 26.1)	9.75 ± 18.80	I
Postporus epinepheli	-	-	-	25	3.0*	0.75*	I
Stephanostomum sp.	-	-	-	25	1.0*	0.25*	I
Cestoda							
Phoreiobothrium sp.	10	15*	1.5*	50	20.5 ± 3.5	10.25 ± 12.0	I
Nematoda							
Philometra margolisi	20	2 ± 1.41	0.4 (0.96)	25	4.0*	1.00*	Go
Pseudoterranova sp.	10	1*	0.1*	25	1.0*	0.25*	M
Acanthocephala							
Gorgorhynchus medius	70	32.1 ± 43.8)	22.5 ± 39.03	-	-	-	I
Copepoda							
Hatschekia insolita	-	-	-	50	8.5 ± 4.94	4.25 ± 5.67	Gi

tionally, their sampling method accounted for a temporal variable, as they collected fish over a two-year period. Moravec et al. (1997) sampled fish from eight localities and collected 202 individual fish, whereas Vidal-Martínez et al. (1998) sampled 105 red groupers in seven localities. In the first case, 30 parasite species were reported, and in the second, 18 species were found. These results also contrast with our limited sample size of adult specimens (14) sampled from a single locality, and from which only 9 parasite species were identified.

Potential effects of parasites on grouper aquaculture

Here, we report parasite taxa that may threaten the survival and reproductive success of the individuals kept under captive conditions. Causative agents of disease in grouper aquaculture include skin and gill monogeneans, blood flukes, nematodes, caligid copepods, and isopods (Nagazawa & Cruz-Lacierda 2004). Fish treatments, such as the use of freshwater or certain chemical compounds, have been effective in controlling ectoparasite infections (Leong 1997, Do Thi Hoa 2007). Monogeneans are probably the most important parasites infecting groupers due to their high prevalence in both wild and cultured fish (Leong & Wong 1988, 1990, Ruckert et al. 2009, 2010, Palm et al. 2011, Kleinertz & Palm 2015, Truong et al. 2017). In our study, specimens of the monogenean *P. yucatanensis* were only found in event 2, as those from event 1 were subjected to a prophylactic freshwater body wash treatment for 10-20 min with constant aeration. The nematodes of the genus *Philometra* are also relevant, as they have been reported to cause chronic illness and severe damage to the reproductive organs in species of groupers such as *E. tauvina* and *E.*

chlorostigma in the Arabian Gulf (Mohamed et al. 2010). *Philometra* spp. found in muscle tissue, it also lowers the market value of the fish, severely affecting its profitability (Nagazawa & Cruz-Lacierda 2004). In the case of *E. morio*, infections by *Philometra* spp. have been reported in the eyes and gonads (Moravec et al. 1997, Vidal-Martínez et al. 1998). The specimens of *P. margolisi* were recovered from the gonads of the red grouper; however, we did not assess the damage they may have caused to the organ or the potential impact on the fish's reproduction. However, as Moravec et al. (1997) pointed out, *P. margolisi* is undoubtedly the most significant parasite affecting the host's reproduction, thereby endangering *E. morio* in aquaculture.

As an additional observation, we report on the presence of the nematode *Pseudoterranova* sp. This parasite, as a member of the family Anisakidae, is considered a zoonotic risk. Infection in humans has been reported following the consumption of undercooked fish infected with larvae (Lima dos Santos & Howgate 2011, Brunet et al. 2017). Still, no records of anisakiasis in humans have been reported in the Yucatán Peninsula, even though its present in a variety marine fish consumed by local communities in Yucatán (Laffon-Leal et al. 2000). We acknowledge, however, that under controlled captive conditions, parasite life cycle could be interrupted, especially with food supplementation, which would eliminate the transmission to the groupers by the ingestion of the first intermediate host (crustacean), although this may be different in a sea-cage system.

Our results show that specimens incorporated from the wild into aquaculture facilities may be infected with several metazoan parasites. In this context, we emphasize the importance of implementing prophylactic and control measures to prevent the development of parasitic diseases at the UMDI-UNAM facility and at any other facility producing red grouper seed for a complete aquaculture cycle. Known treatments include freshwater baths to control skin monogeneans, copepods, or general parasites for 5-30 min (Nagazawa & Cruz-Lacierda 2004, Palm et al. 2015). Their use will depend on the parasite species and the general condition and tolerance of the fish. Maintaining groupers during quarantine in open filtered systems, as well as continuous disinfection of the materials used, will be essential to reduce the parasite load. Furthermore, controlling the type and source of food and cleaning the tanks will reduce, and sometimes eliminate, the presence of parasites in cultured organisms (Rückert et al. 2009). Checking for the presence of monogenean parasites in the system is also advisable; the use of cotton threads has been successfully employed in previous studies (Grano-Maldonado et al. 2010, 2011, 2015, Enriquez-Benavides et al. 2025).

In conclusion, all the information gathered about commercially important fish species is necessary for the adequate management of these species. In this context, and due to their commercial importance, all stakeholders play a crucial role in regulating the catch trends of the red grouper in the Yucatán Peninsula by adopting responsible fishing and consumption practices (Hernández-Delgado et al. 2024). Aquacultural practices also become a complementary approach.

Credit author contribution

C. Canul-Cámara: conceptualization, field work, writing-original draft, sequencing and data curation, parasite identification; C. Durruty: conceptualization, field work, writing-original draft, funding acquisition, project administration, supervision, and editing; B. Solórzano-García: conceptualization, field work, writing-original draft, sequencing and data curation; G. Pérez-Ponce de León: conceptualization, field work, writing-original draft, funding acquisition, project administration, supervision, and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare that they have no conflicts of interest.

Data availability

Sequence data were deposited in GenBank under the accession numbers PV916722-PV916727.

ACKNOWLEDGMENTS

We thank the following individuals for their support during the sampling and processing of fish for acclimatization at the UMDI-UNAM facility: Sr. José Alonzo, M.Sc. Estefania Suárez Wegan, Nelson Mauricio Cruz Estrella, and Dr. Manuel Valenzuela Jiménez. We thank Norberto Colín for allowing us to use the Molecular Biology lab of ENES-Mérida. We also thank Dr. Leopoldo Andrade Gómez for his assistance during fieldwork, Laura Marquez and Nelly López from the Laboratorio Nacional de La Biodiversidad, Instituto de Biología UNAM, for their help in obtaining DNA sequences, and Dr. Haseeb Randhawa for the critical review of an earlier version of this manuscript. We also thank the financial support of the Project "Biotechnology of the red grouper *Epinephelus morio*" (SEPASY-UNAM) to CDL, and PAPIIT UNAM IN200824 to GPPL.

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Received: June 17, 2025; Accepted: August 12, 2025

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