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Octopus maya parasites off the Yucatán Peninsula, Mexico. I. Faunal assemblages

Sergio Guillén-Hernández[1,*], Atzelby López-Struck[1], Carlos González-Salas[1], M. Leopoldina Aguirre-Macedo[2]

[1]Universidad Autónoma de Yucatán, Campus de Ciencias Biológicas y Agropecuarias, Departamento de Biología Marina, Km. 15.5 Carretera Mérida-Xmatkuil, Apdo. Postal 4-116, Itzimná Mérida, Yucatán, México

[2]Centro de Investigación y de Estudios Avanzados del IPN, Departamento de Recursos del Mar, Carretera Antigua a Progreso Km 6 Cordemex, CP 97310, Mérida, Yucatán, México

ABSTRACT: The red octopus *Octopus maya* Voss et Solís-Ramírez, 1966 is an endemic species found exclusively off the coast of the Yucatán Peninsula, Mexico; its fishery is one of the most important along the Atlantic coast of Mexico and the Caribbean Sea. To date, the parasite fauna of *Octopus* spp. in southern Mexico remains unknown. In this study, we present the parasite fauna of *O. maya* from 8 localities along the Yucatán Peninsula. From August 2009 to June 2010, a total of 1202 specimens of *O. maya* were caught by artisanal fisheries and examined. Twenty parasite taxa were recorded from all octopus examined: 7 cestodes, 8 digeneans, 3 nematodes, 1 copepod and 1 coccidian. All taxa are new records for this host species, and the sampled locations represent new records of the geographic distribution of these parasite taxa. The gills and the intestine were the microhabitats in which the highest number of taxa were found. More than half of the parasites (13 taxa) that we found infected *O. maya* via its feeding habits, although a high number of taxa (n = 9) colonized via active transmission. Cestoda and Digenea were the taxonomic groups with the highest number of taxa. *Prochristianella* sp. showed the highest prevalence and mean abundance values in the localities where it was present. This work represents the first study on the parasite fauna of any cephalopod species in Mexico.

KEY WORDS: Red octopus · Cestode · Digenean · Parasite · Yucatán Peninsula · Mexico

INTRODUCTION

There is growing interest in the parasite communities associated with cephalopods. However, in Mexico, records of parasites of cephalopods are usually scarce and isolated (see Hochberg 1990, Furuya et al. 2002, Castellanos-Martinez et al. 2016). In particular, the parasite fauna associated with octopus species (*Octopus* spp.) in southern Mexico remains unknown. Most of the research conducted to date on octopus species in this region has been focused on different aspects of the biology and fisheries management of economically important species such as *O. maya* and *O. vulgaris*.

To date, most of the knowledge on the biology of cephalopods is derived from species such as *O. vulgaris* and *Sepia officinalis* studied in Europe and the Mediterranean Sea (Hanlon & Forsythe 1990). The geographic region with probably the most complete record of parasites present in cephalopods comes from northern Spain, followed by several countries (Nicaragua, Ecuador, Peru and Chile) in Central and South America where parasite records for this group have grown in recent years (Pascual et al. 1996, González et al. 2003, Pardo-Gandarillas et al. 2009). In the Yucatán Peninsula, Mexico, the octopus fishery is based on *O. maya* and *O. vulgaris*, although the former is economically more important due to its

*Corresponding author: ghernand@correo.uady.mx

higher capture volume. *O. maya*, commonly known as the red octopus, is an endemic species to the Yucatán Peninsula, and represents one of the most important fisheries along the Atlantic coast of Mexico and the Caribbean Sea (Voss & Solís-Ramírez 1966, Solís-Ramírez & Chávez 1986, Solís-Ramírez 1988, Pérez-Losada et al. 2002, Salas et al. 2006).

It is well documented that cephalopods act as intermediate, paratenic, or final hosts of macro-parasites such as helminths (monogeneans, digeneans, cestodes, nematodes and acanthocephalans) and crustaceans, as well as micro-parasites such as bacteria, viruses and coccidians (Hochberg 1990, Pascual et al. 1996, Vidal & Haimovici 1999, González et al. 2003). The role that cephalopods play in the life cycle of parasites may vary depending on the type of parasite since they may act as final hosts for protozoans, dicyemids and crustaceans, or as reservoir, second or third intermediate hosts of larvae of digeneans, cestodes, acanthocephalans and nematodes.

In this study, we describe for the first time the parasite fauna associated with *O. maya* collected from 8 localities spanning most of the distribution range of this cephalopod along the Yucatán Peninsula (Mexico).

MATERIALS AND METHODS

From August 2009 to June 2010, specimens of *Octopus maya* were caught using artisanal fishing methods at 8 sites located offshore of the Yucatán Peninsula in Mexico (Fig. 1). Sites were separated in 2 regions, the Yucatán Coast and the Campeche Coast. Four sites were located off the coast of the state of Yucatán (Dzilam Bravo: 21° 19′ N, 88° 35′ W; Ría Lagartos: 21° 24′ N, 88° 02′ W; Progreso: 21° 19′ N, 89° 42′ W; Celestún: 20° 57′ N, 90° 34′ W), and 4 were off the coast of the state of Campeche (Champotón: 17° 49′ N, 89° 32′ W; Seybaplaya: 19° 38′ N, 90° 41′ W; Isla Arena: 20° 44′ N, 90° 40′ W; Campeche: 19° 56′ N, 90° 48′ W). Individuals were transported on ice to the laboratory of parasitology at the Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV) where we measured the mantle lengths and weights and determined sex for all captured individuals of *O. maya*. Samples were divided into 2 groups based on locality, with Champotón, Seybaplaya, Dzilam de Bravo and Rio Lagartos comprising one group, and Campeche, Isla Arena, Celestún and Progreso the other, since 2 laboratories were involved in the sample examination, following the same methodology.

First, a parasitological examination was conducted of both internal (alimentary canal, digestive gland, heart, gonads and gills) and external (mantle surface) organs using a stereomicroscope (Olympus SZ51 or Leica Zoom-2000) with magnification ranges of 0.8 to 4×. When samples were not examined immediately, octopus were frozen until their examination. Parasites were removed using a fine brush and counted; worms were fixed and preserved in hot 70% ethanol. Host data included mantle length, weight, sex and number of each parasite taxon. Helminths were then stained using Mayer-Paracarmin (Lamothe-Argumedo 1997) and mounted in Canada balsam for taxonomic identification. Nematodes were clarified in glycerin or lactophenol, then temporary mounts were made for morphological examination. Some larvae digeneans are very small, fragile and easily damaged or lost during the staining process; therefore, they were fixed and mounted on ammonium picrate.

The identification of different developmental stages of cestodes was based upon Palm (2004) and other specialized literature such as Campbell & Carvajal (1975) and Jensen & Bullard (2010). Digeneans were identified using information published by Yamaguti (1975), Gibson et al. (2002), Jones et al. (2005), Bray et al. (2008), and other specialized litera-

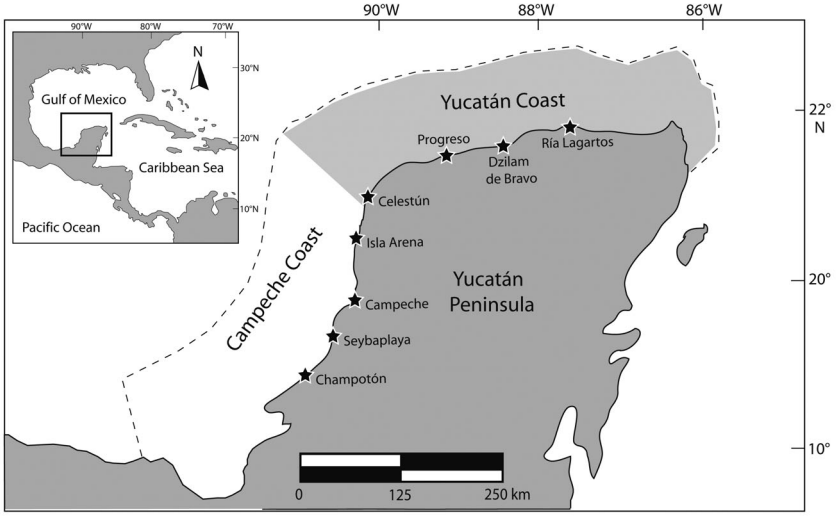

Fig. 1. Study area where specimens of *Octopus maya* were collected in the Campeche Coast (4 sites) and the Yucatán Coast (4 sites) along the Yucatán Peninsula (México)

ture. Finally, the identification of nematodes was based on the key proposed by Anderson et al. (2009) and Gibbons (2010). Parasites were then identified to lowest taxonomic level possible, and mean abundance, mean intensity and prevalence were estimated for each parasite taxon at each locality following Bush et al. (1997).

RESULTS

In total, we examined 1202 individuals of *Octopus maya*, with more specimens sampled from localities along the Yucatán coast than from the coast of Campeche (Table 1). Average mantle length varied among localities, with the largest specimen recorded at Ría Lagartos (Yucatán) and the smallest one recorded at Champotón (Campeche) (Table 1). Accordingly, across all sampled localities, we observed a west-to-east gradient of increasing octopus size, from Champotón (western end of Campeche) where the smallest specimens were found, to Ría Lagartos (eastern end of Yucatán) where the largest specimens were collected (Table 1). The total number of parasite taxa recorded per locality ranged from 3 at Champotón to 14 in Campeche. There was no relationship between sample size and number of parasite taxa (Table 1).

As this is the first parasitological study performed on *O. maya*, all parasite taxa reported here are new records for this host species, and the sampled locations represent new records of the geographic distribution of these parasite taxa. All helminths recorded in this study were found in larval stages, and *Aggregata* sp. and *Octopicola* sp. were the only 2 taxa for which specimens in the sexual stage were recorded (see Table 2).

Twenty different parasite taxa were recorded among the octopus specimens (Table 2): 7 cestodes, 8 digeneans, 3 nematodes, 1 copepod and 1 coccidian. The intestine and gills were the micro-habitats where the highest number of taxa was recorded (10 and 8 taxa, respectively), followed by the esophagus (4 taxa), digestive gland, ink sac, cecum and mantle (3 taxa each), and finally the buccal mass (2 taxa). The parasite taxa that infected the highest number of microhabitats were *Prochristianella* sp. and *Eutetrarhynchus* sp., and *Prochristianella* sp. was generally the most frequent and abundant parasite found mainly in the buccal mass.

Table 1. *Octopus maya* sample size (n), mantle length (mean ± SD), number of parasites and taxa found at each locality

Locality	Sample size (n)	Mantle length (mm)	No. of parasites Individuals	Species
Campeche Coast				
Champotón	58	93.0 ± 36.3	1051	3
Seybaplaya	79	118.0 ± 16.1	2357	5
Campeche	60	94.5 ± 23.6	1125	14
Isla Arena	60	91.0 ± 40.2	28630	13
Yucatán Coast				
Celestún	203	113.3 ± 23.6	15130	12
Progreso	227	107.2 ± 44.0	169482	11
Dzilam de Bravo	255	120.6 ± 16.0	206438	8
Ría Lagartos	260	139.0 ± 15.4	169210	9

Table 2. Parasite micro-habitat and hosts involved in the life cycle of the parasite fauna found in *Octopus maya* from the Yucatán Peninsula. In: intestine; Es: esophagus; Bm: buccal mass; Gi: gills; Dg: digestive gland; Ce: cecum; Is: ink sac; Ma: mantle

Parasite species	Micro-habitat(s)	First intermediate host	Definitive host(s)
Apicomplexa			
Aggregata sp.	In, Es, Ce	Crustaceans	Cephalopods
Cestoda			
Prochristianella sp.	Bm, Es, Ce, In	Crustaceans	Sharks
Eutetrarhynchus sp.	Dg, Es, In, Is	Crustaceans	Rays, sharks
Nybelinia sp.	Bm, Es, In	Fishes	Sharks
Echeneibothrium sp.	Ce, In		
Prosobothrium sp.	Dg, Is		Sharks
Tetraphyllidea	Ce, In	Fishes	Fishes
Unidentified plerocercoid	Dg, Is, Gi		
Digenea			
Lecitochirium sp.	Gi	Gastropods	Fishes
Parvatrema sp.	Gi	Bivalves	Birds
Dollfustrema sp.	Ma	Bivalves	Fishes
Cryptogonimidae gen. sp.	Gi, In, Ma	Gastropods	Fishes
Podocotyle sp.	Gi	Gastropods	Fishes
Opecoeliidae gen. sp.	Gi	Gastropods	Fishes
Stephanostomum sp.	Ma	Gastropods	Fishes
Bucephalidae gen. sp.	Gi	Bivalves	Fishes
Nematoda			
Anisakidae gen. sp.	In	Copepods	Marine mammals
Spiruridae gen. sp.	In	Copepods	Turtles
Philometridae gen. sp.	In	Crustaceans	Fishes
Crustacea			
Octopicola sp.	Gi	Cephalopods	Cephalopods

More than half of the parasites (13 taxa) that we recorded infected *O. maya* via its feeding habits (passive transmission), although a high number of taxa (9) colonized by active transmission (free-living larval penetration). Cestoda and Digenea were the taxonomic groups represented by the highest number of taxa, followed by nematodes. All cestode species infect this host species via passive colonization, whereas digeneans might be doing so actively.

Regarding the prevalence of each parasite taxon by location (Table 3), cestodes were the taxonomic group with the highest prevalence values. Within cestodes, the highest prevalence was observed for *Prochristianella* sp., with values ranging from 57% (Campeche) to 98% (Celestún). On the other hand, within digeneans, Cryptogonimidae showed the highest prevalence, with values ranging from 18.2% (Celestún) to 52% (Campeche). Nematodes exhibited prevalence values ≤5% (range: 0.4% in Ría Lagartos to 5% in Campeche), whereas the copepod *Octopicola* sp. exhibited values ranging from 0% (Champotón) to 100% (Celestún), and the coccidian *Aggregata* sp. from 17% (Champotón) to 69% (Dzilam de Bravo). The coccidian, the cestode *Prochristianella* sp. and the copepod *Octopicola* sp. showed high prevalence values at all locations where they were recorded.

The sampling locations with the highest number of taxa with prevalence values ≥10% were Isla Arena and Campeche (8 and 7 taxa, respectively) on the Campeche Coast, and Progreso and Celestún (8 and 7, respectively) on the Yucatán Coast. All other localities had 5 or fewer taxa with prevalence values ≥10%.

The taxa with the highest prevalence values (*Prochristianella* sp., Cryptogonimidae and *Octopicola* sp.) also had the highest mean abundance values (Table 4). Values observed for *Prochristianella* sp. were exceptionally high at localities where this parasite species was recorded, with the highest mean abundance observed at Celestún.

Table 3. Prevalence values of the parasites found in *Octopus maya* at each locality sampled

Parasite	Campeche Coast				Yucatán Coast			
	Champotón	Seybaplaya	Campeche	Isla Arena	Celestún	Progreso	Dzilam de Bravo	Ría Lagartos
Apicomplexa								
Aggregata sp.	17.0	41.0					69.0	62.0
Cestoda								
Prochristianella sp.	71.0	71.0	57.0	87.0	98.0	95.1	97.0	82.0
Eutetrarhynchus sp.			10.0	50.0	59.1	38.3	24.0	7.0
Nybelinia sp.			50.0	37.0	51.2	49.0	1.0	0.4
Prosobothrium sp.			18.0	27.0	23.6	16.8		
Echeneibothrium sp.	12.0	4.0					21.0	8.0
Tetraphyllidean		1.0			2.96	5.7	7.0	1.0
Unidentified plerocercoid			10.0	26.6	19.2	23.0		
Digenea								
Lecitochirium sp.					5.42	3.5	2.0	
Parvatrema sp.				2.0				
Dollfustrema sp.			7.0	3.0				
Cryptogonimidae gen. sp.			52.0	50.0		38.3		
Podocotyle sp.			5.0	13.3	16.7	22.0		0.4
Opecoeliidae gen. sp.			3.3	3.3	14.3	15.8		
Stephanostomum sp.			43.3	10.0				
Bucephalidae gen. sp.					0.99			
Nematoda								
Philometridae gen. sp.			3.0	1.6	0.5			
Spiruridae gen. sp.			3.0					
Anisakidae gen. sp.			5.0					0.4
Crustacea								
Octopicola sp.	0.0	44.0	13.3	98.3	100.0	95.6	20.0	21.0
Total number of taxa	3	5	14	13	12	11	8	9

Table 4. Mean (± SD) abundance values of the parasites found in *Octopus maya* at each locality sampled. X: parasite present but individuals were not counted

Parasite	Campeche Coast				Yucatán Coast			
	Champotón	Seybaplaya	Campeche	Isla Arena	Celestún	Progreso	Dzilam de Bravo	Ría Lagartos
Apicomplexa								
Aggregata sp.	X	X					X	X
Cestoda								
Prochristianella sp.	18.0 ± 20.9	17.6 ± 24.6	4.9 ± 8.2	449.4 ± 500.7	1034.2 ± 1757	689.1 ± 917	791.3 ± 677.8	645.4 ± 877.7
Eutetrarhynchus sp.	0	0	0.21 ± 0.8	1.8 ± 2.6	4.1 ± 9.2	1.9 ± 5.45	2.6 ± 4.4	0.02 ± 1.1
Nybelinia sp.	0	0	1.2 ± 2.32	1.2 ± 1.8	1.9 ± 3.67	1.42 ± 2.32	0.008 ± 0.09	0.018 ± 0.3
Otobothium sp.			1.2 ± 2.32	1.2 ± 1.8	1.9 ± 3.7	1.42 ± 2.32		
Prosobothrium sp.			0.31 ± 0.8	1.55 ± 5.1	2.04 ± 7.7	0.62 ± 2.46		
Echeneibothrium sp.	0.12 ± 0.0	0.05 ± 0.2					0.55 ± 1.9	0.2 ± 1.1
Tetraphyllidean		0.21 ± 1.9			0.2 ± 1.3	0.41 ± 2.21	0.44 ± 2.45	0.03 ± 0.4
Unidentified plerocercoid			0.01 ± 0.13	0.8 ± 3.5	4.43 ± 23.3	5.2 ± 53		
Digenea								
Lecitochirium sp.					0.13 ± 0.7	0.40 ± 4.14	0.09 ± 1.13	
Parvatrema sp.				0.18 ± 1.4				
Dollfustrema sp.			0.36 ± 1.55	0.23 ± 1.56				
Cryptogonimidae gen. sp			10.0 ± 22.1	7.45 ± 15.4	1.21 ± 5.25	6.1 ± 19.6		
Podocotyle sp.			0.08 ± 0.42	1.2 ± 5.2	0.62 ± 2.0	1.1 ± 3.4		0.004 ± 0.003
Opecoeliidae gen. sp.			0.05 ± 0.3	0.12 ± 0.8	0.54 ± 2.13	0.52 ± 1.8		
Stephanostomum sp.			1.25 ± 1.63	0.28 ± 1.2				
Bucephalidae gen. sp.					0.04 ± 0.44			
Nematoda								
Spiruridae gen. sp.			0.01 ± 0.13		0.005 ± 0.07	0.02 ± 0.34		
Philometridae gen. sp.			0.01 ± 0.13	0.55 ± 4.2	0.005 ± 0.07			
Anisakidae gen. sp.			0.05 ± 0.21					0.004 ± 0.003
Crustacea								
Octopicola sp.	0.0	12 ± 26.4	0.28 ± 0.84	11.9 ± 62.3	57.5 ± 141.4	191.6 ± 191.6	7.6 ± 27.2	4.4 ± 11.8

DISCUSSION

We found a total of 20 parasite taxa associated with the red octopus *Octopus maya* in the Yucatán Peninsula, Mexico. All of these taxa represent new parasite records for this cephalopod species. Only *Prochristianella* sp. and *Octopicola* sp. were present at all or most of the sampled sites.

Due to the diversity of parasites found in cephalopods (as shown in our study), Hochberg (1990) suggested that this host group plays a similar role to fishes in the transmission of parasites in marine environments. However, it is also interesting to note the absence in our study of groups like dicyemids, monogeneans, didimozoids, or acanthocephalans for *O. maya*, which have been reported previously in cephalopods. On the other hand, a histological study (M. L. Aguirre-Macedo unpubl.) revealed the presence of dicyemids in the excretory organs of *O. maya*. Nonetheless, monogeneans are a well represented group in marine fish from the coast of Yucatán, and their absence and the absence of dicyemids in *O. maya* may be explained by the fact that most of the samples were frozen before examination, which could have complicated the detection of these organisms, since members of both groups are very delicate. It is also possible that more protozoan parasites would have been detected if tissue samples had been prepared for histological examination prior to freezing and if the tissues had been examined microscopically. Didymozoids use 3 to 4 different hosts during their life cycle, and cephalopods are infected by eating larvae of this parasite present in invertebrates or fish (Hochberg 1990). Therefore, we speculate that the absence of didymozoids in *O. maya* might be because this cephalopod feeds on invertebrates or fishes that are not used as hosts by these parasites.

All parasite specimens found in this study were recorded in their larval stages, except *Aggregata* sp. and *Octopicola* sp. for which specimens in sexual stages were found. This suggests that *O. maya* may act as an intermediate or transport host in the

life cycle of many of these parasite taxa (Hochberg 1990, Pascual et al. 1996, Vidal & Haimovici 1999, González et al. 2003). Host species such as *O. maya* are thought to play a vital role in transferring parasites to final hosts such as elasmobranchs, bony fishes, sea birds and marine mammals (Hochberg 1990).

The diversity of parasites associated with *O. maya* in this study is greater than that reported for other species of cephalopods. For example, Pascual et al. (1996) published a list of parasites of 10 species of commercially exploited cephalopods in Spain, and the highest number of parasite species for a single cephalopod species (*O. vulgaris*) was 7. In addition, Cavaleiro (2013) reported 8 parasite species for *O. vulgaris* in Portugal. Finally, Pardo-Gandarillas et al. (2009) reported 6 parasite species in *Dosidicus gigas* in Chile. In comparison, we found a total of 20 parasite taxa, a much higher number, possibly related to a high diversity of invertebrates acting as first intermediate hosts on the coast of the Yucatán Peninsula.

Four of the 8 parasite taxa recorded in the digestive tract of *O. maya* were cestodes, suggesting that the oral cavity is the most common portal of infection. However, the presence of a high number of digeneans in other microhabitats (arms, mantle, gills, etc.) indicates that infection via cercarial penetration is also frequent. The diet of *O. maya* includes mainly crustaceans, mollusks and fishes (Boyle & Rodhouse 2005), which have been previously recorded as first intermediate hosts of the parasite taxa recorded in this study (see Table 1).

Although adult cestodes are rarely found in cephalopods, a great diversity of larval and post-larval forms of the orders Tetraphyllidea and Trypanorhyncha have been recorded for this host group (Hochberg 1990). Accordingly, Palm (2004) reported that the Gulf of Mexico is known for the large number of cestodes of the order Trypanorhyncha that parasitize invertebrates and fishes (teleosts and elasmobranchs). This may explain the high values of mean abundance and prevalence of this order in our *O. maya* samples.

The elevated taxonomic richness of parasites recorded in the digestive tract of *O. maya* also indicates that the diet of this cephalopod comprises a high diversity of organisms. The high prevalence values recorded for *Prochristianella* sp., *Eutetrarhynchus* sp., *Otobothrium* sp. and *Aggregata* sp. suggest that this octopus feeds recurrently on 1 or more species of invertebrates, which are used by these parasites as first intermediate hosts. Our results agree with previous work by Nigmatullin & Ostapenko (1976), Sánchez & Obarti (1993), Smith (2003), and Quetglas et al. (2005), thus indicating that crustaceans are the primary component of the diet of cephalopods of the genus *Octopus*. Preliminary results from a survey of the feeding habits of *O. maya* showed *Prochristianella hispida* as the only species found parasitizing shrimps in the Celestún, a brackish system in Yucatán, and there was no evidence of cestodes parasitizing 6 species of crabs in the same area (S. Guillén-Hernández & C. González-Salas unpubl.). These findings suggest that this cestode may infect shrimps when they move to the estuary and *O. maya* would then get the parasites when they prey on shrimps offshore. However, there are some aspects to consider in this life cycle: it has been proposed that the first intermediate host is a copepod, which is consumed by a shrimp or other type of crustacean (second intermediate host) and an elasmobranch as the final host (Palm 2004). We consider it more likely that the shrimp is infected by eating the eggs directly, and not by preying on a copepod, and that the elasmobranch would become infected by consuming the octopus. Therefore, the shrimp could be the first intermediate host, with the octopus as the second host and an elasmobranch as the final host. Nevertheless, for the *Prochristianella* larva that we found, more intensive study is needed to conclusively describe its life cycle, and identify it to the species level.

Of particular interest are the high mean abundances of the tapeworm *Prochristianella* sp. at the 8 sampled locations. This finding could be indicative of constant recruitment of this parasite throughout the lifetime of the octopus. In support of this argument, we found increasing abundances of this parasite from localities with small mean octopus size to localities with larger octopus sizes. Guillén-Hernández et al. (2018) showed that *Prochristianella* sp. can cause severe damage to the salivary glands of *O. maya*. These results suggest that the geographical distribution of the intermediate host of this parasite in Campeche and Yucatán probably closely matches the distribution of *O. maya*, and is thus a very common item in the diet of this octopus.

On the other hand, most digeneans colonize the host mainly by active penetration of cercariae into the host tissues. Because prevalence values of the metacercaria stages in most cases were less than 10%, it is highly probable than these infections are accidental and that *O. maya* does not play an important role in digenean transmission as an intermediate host. It has been suggested that members of the genus *Aggregata* (*A. octopiana*) can cause malabsorption syndromes in cephalopods (Gestal et al. 2002), and that *Octopicola* sp. attached to the gills may cause problems in oxygen uptake. It would be interesting in the future to

consider the possible negative effect of these 2 parasites together with *Prochristianella* sp. on the health status of the octopus population.

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LITERATURE CITED

Anderson RC, Chabaud AG, Willmott S (2009) Keys to the nematode parasites of vertebrates. Archival Volume. CABI, London

Boyle P, Rodhouse P (2005) Cephalopods: ecology and fisheries. Blackwell Publishing Company, Oxford

Bray RA, Gibson DI, Jones A (2008) Keys to trematodes, Vol III. Natural History Museum and CABI, London

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Campbell RA, Carvajal J (1975) A revision of some trypanorhynchs from the western north Atlantic described by Edwin Linton. J Parasitol 61:1016–1022

Castellanos-Martinez S, Aguirre-Macedo ML, Furuya H (2016) Two new species of dicyemid mesozoans (Dicyemida: Dicyemidae) from *Octopus maya* Voss & Solis-Ramirez (Octopodidae) off Yucatan, Mexico. Syst Parasitol 93:551–564

Cavaleiro MNC (2013) Parasite fauna of *Octopus vulgaris* (Cephalopoda: Octopodidae) and *Platichthys flesus* (Actinopterygii: Oleuronectidae): morphology, systematics, life history strategies and ecology. PhD thesis, Universidade Do Porto

Furuya H, Damian RT, Hochberg FG (2002) *Dicyema shorti* n. sp. (Phylum Dicyemida) from *Octopus burryi* (Mollusca: Cephalopoda: Octopodida) in the Gulf of Mexico. J Parasitol 88:325–329

Gestal C, Abollo E, Pascual S (2002) Observations on associated histopathology with *Aggregata octopiana* infection (Protista: Apicomplexa) in *Octopus vulgaris.* Dis Aquat Org 50:45–49

Gibbons LM (2010) Keys to the nematode parasites of vertebrates, supplementary volume. CABI, Cambridge

Gibson DI, Jones A, Bray RA (2002) Keys to the Trematoda, Vol 1. CABI and The Natural History Museum, London

González A, Pascual S, Gestal C, Abolo E, Guerra A (2003) What makes a cephalopod a suitable host for parasite? The case of Galician water. Fish Res 60:177–183

Guillén-Hernández S, González-Salas C, Pech-Puch D, Villegas-Hernández H (2018) *Octopus maya* parasites off the Yucatán Peninsula, Mexico. II. Salivary gland damage by cestodes. Dis Aquat Org 130:45–50

Hanlon RT, Forsythe JW (1990) Diseases caused by microorganisms. In: Kinne O (ed) Diseases of marine animals, Vol 3: Introduction, Cephalopoda, Annelida, Crustacea, Chaetognatha, Echinodermata, Urochordata. Biologische Anstalt Helgoland, Hamburg, p 23–46

Hochberg FG (1990) Diseases caused by protistans and metazoans. In: Kinne O (ed) Diseases of marine animals, Vol 3: Introduction, Cephalopoda, Annelida, Crustacea, Chaetognatha, Echinodermata, Urochordata. Biologische Anstalt Helgoland, Hamburg, p 47–202

Jensen K, Bullard SA (2010) Characterization of a diversity of tetraphyllidean and rhinebothriidean cestode larval types, with comments on host associations and life cycles. Int J Parasitol 40:889–910

Jones A, Bray RA, Gibson DI (2005) Keys to the Trematoda, Vol 2. CABI and The Natural History Museum, London

Lamothe-Argumedo R (1997) Manual de técnicas para preparar y estudiar los parásitos de animales silvestres. AGT Editor, Mexico City

Nigmatullin ChM, Ostapenko AA (1976) Feeding of *Octopus vulgaris* Lam. from the northwest African Coast. CM1976/K6. ICES, Copenhagen

Palm HW (2004) The Trypanorhyncha Diesing, 1863. PKSPL-IPB (Center for Coastal and Marine Resources Studies – Bogor Agricultural University) Press, Bogor

Pardo-Gandarillas MC, Lohrmann KB, Valdivia AL, Ibañez CM (2009) First record of parasites of *Dosidicus gigas* (d'Orbigny, 1835) (Cephalopoda: Ommastrephidae) from the Humboldt Current system off Chile. Rev Biol Mar Oceanogr 49:397–408

Pascual S, Gestal C, Estévez JM, Rodríguez H, Soto M, Abollo E, Arias C (1996) Parasites in commercially-exploited cephalopods (Mollusca, Cephalopoda) in Spain: an updated perspective. Aquaculture 142:1–10

Pérez-Losada M, Guerra A, Sanjuan A (2002) Allozyme divergence supporting the taxonomic separation of *Octopus mimus* and *Octopus maya* from *Octopus vulgaris* (Cephalopoda: Octopus). Bull Mar Sci 71:653–664

Quetglas A, González M, Franco I (2005) Biology of the upper-slope cephalopod *Octopus salutii* from the western Mediterranean Sea. Mar Biol 146:1131–1138

Salas S, Mexicano-Cíntora G, Cabrera MA (2006) ¿Hacia dónde van las pesquerías en Yucatán? Tendencias, retos y perspectivas. CINVESTAV, Mérida

Sánchez P, Obarti R (1993) The biology and fishery of *O. vulgaris* caught with clay pots in Spanish Mediterranean coast. In: Okutani T, O'Dor RK, Kubodera T (eds) Recent advances in cephalopod fishery biology. Tokai University Press, Tokyo, p 477–487

Smith DC (2003) Diet of *Octopus vulgaris* in False Bay, South Africa. Mar Biol 143:1127–1133

Solís-Ramírez MJ (1988) El recurso pulpo del Golfo de México y del Caribe mexicano. In: SEPESCA (ed) Los recursos pesqueros del país. XXV Aniversario del INP, México, p 463–478

Solís-Ramírez MJ, Chávez EA (1986) Evaluación y régimen óptimo de pesca de pulpo en la Península de Yucatán. Anal Inst Cienc Mar y Limnol UNAM 13:1–18

Vidal E, Haimovici M (1999) Digestive tract parasites in rhynchoteuthion squid paralarvae, particularly in *Illex argentinus* (Cephalopoda: Ommastrephidae). Fish Bull 97:402–405

Voss GL, Solís-Ramírez MJ (1966) *Octopus maya*, a new species from the Bay of Campeche. Bull Mar Sci 16: 615–625

Yamaguti S (1975) A synoptical review of the life histories of diagenetic trematodes of vertebrates with special reference to the morphology of their larval forms. Keiguaku Publishing Co., Tokyo

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