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Spiral valve parasites of blue and common thresher sharks as indicators of shark feeding behaviour and ecology

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Abstract

This study documented the parasite faunas of the spiral valves of blue sharks *Prionace glauca* (L. 1758) and common thresher sharks *Alopias vulpinus* (Bonnaterre, 1788) caught in the California Current Large Marine Ecosystem (CCLME) north of the Mexican border. The spiral valves of 18 blue and 19 thresher sharks caught in the CCLME from 2009 to 2013 were examined for parasites. Seven parasite taxa were found in blue sharks and nine in threshers. The tetraphyllidean cestode *Anthobothrium* sp. (78% prevalence) was the most common parasite in blue sharks, and the phyllobothriid cestode *Paraorygmatobothrium* sp. (90% prevalence) was the most common in threshers. An adult nematode of the genus *Piscicapillaria* was found in threshers for the first time and may be a new species. Adult individuals of *Hysterothylacium* sp. were found in both shark species. The adult acanthocephalan *Rhadinorhynchus cololabis* and remains of the parasitic copepod *Pennella* sp. – both parasites of Pacific saury, *Cololabis saira* – were found in the intestines of threshers, indicating recent feeding on saury. This study paves the way for a more comprehensive examination, including more samples and a wider variety of shark species, to provide a greater understanding of shark feeding behaviour and possibly provide information on shark population biology.

KEYWORDS
blue shark, California, spiral valve parasites, thresher shark

1 | INTRODUCTION

Elasmobranchs are hosts to many metazoan parasites. The spiral valve or intestine is a suitable habitat for parasites and home to digeneans, nematodes, cestodes and, infrequently, monogeneans (Caira *et al*., 2012). The spiral valve is the most heavily parasitized internal organ of elasmobranchs and is the primary site occupied by cestodes, the most diverse group of elasmobranch parasites. It is rare to find a wild-caught elasmobranch that does not host at least one species of cestode in its spiral valve (Caira *et al*., 2012).

Despite the ubiquity of shark tapeworms, relatively little is known about the parasite faunas of pelagic sharks, in particular common thresher sharks *Alopias vulpinus* (Bonnaterre, 1788) (hereafter referred to as threshers). Cestodes are the most common helminths in the spiral valve of blue sharks *Prionace glauca* (L. 1758) (Caira *et al*., 2012; Curran and Caira, 1995; Henderson *et al*., 2002; Méndez and

Galván-Magaña, 2016). Less information is available for threshers, but some cestodes have been reported from the spiral valve (Love and Moser, 1983; Ruhnke, 1994; Yamaguti, 1952). The presence of parasites in the spiral valves of sharks can have adverse consequences (Borucinska and Caira, 2006; Borucinska and Dunham, 2000), but may also benefit host health by sequestration of heavy metals (Malek *et al*., 2007; Sures, 2004).

This study is the first on spiral valve parasites of blue and thresher sharks in the California Current Large Marine Ecosystem (CCLME) north of the Mexican border. It was not designed as a parasitological study; the shark spiral valves and their contents were collected as part of a larger Ph.D. project carried out by the senior author on the trophic ecology of nine top predators, including blue and thresher sharks, off California. They thus provided an opportunity to catalogue the intestinal parasite faunas of these sharks and to investigate possible links between parasites and shark diet.

2 | MATERIALS AND METHODS

2.1 | Sampling at sea

This study complied with all ethical requirements of the *Journal of Fish Biology* and local authorities. Sharks were killed during regular commercial fishery operations in tune with the Magnuson-Stevens Fishery Conservation and Management Act (MSA). Animal welfare laws, guidelines and policies were not applicable.

Spiral valves were collected during several fishing seasons from blue (2009, 2011, 2012) and thresher sharks (2011–2013) by the NOAA's West Coast Region Fishery Observer Program aboard Drift Gill Net (DGN) vessels.

These vessels operate within the U.S.A. Exclusive Economic Zone (EEZ) from the U.S.A-Mexico border (31° 20′N) to as far north as Washington State (48° 03′N), between 15 August and 31 January every year. In recent years, the majority of the vessels have operated in the Southern California Bight (SCB) between Point Conception, California, and the U.S.A-Mexico border. Fishing is carried out using 1.8 km [1000 fathom (fm)] long drift gillnets extending from roughly 11 to 100 m below the surface. Eighteen blue and 19 thresher shark spiral valves were collected during 26 observed trips and one shark tournament in the CCLME. Shark samples were dissected at sea.

Spiral valves were separated from the rest of the digestive tract by cutting around the pyloric sphincter anteriorly and the rectum posteriorly, then securing with plastic cinch ties. Samples were bagged, labelled and frozen. Data recorded included set and haul-back times, water depth, sea surface temperature (SST), location (latitude and longitude), fish length, sex and maturity state.

2.2 | Processing in the laboratory

Spiral valves were thawed and tamped with absorbent paper to remove excess water. They were then opened on a dissection tray with a longitudinal incision from the pyloric sphincter to the rectum along the ventral surface of the organ in proximity to the largest branch of the ventral blood vessel. This procedure allowed the spiral valve to be opened and unrolled in two similar halves. Contents were filtered with a mesh screen sieve with a mesh size of 0.3 mm, collected and rinsed with sea water. A microscope slide was used to scrape the internal tissue layers of the spiral valve to collect any parasites that may have been attached to the intestinal wall. All contents were added to a sea salt solution, and parasites were sorted, counted and identified under a dissecting microscope. All parasites observed were preserved in vials of 10% buffered formal saline, using separate vials for each shark. Vials containing parasites were examined by tipping the contents into Petri dishes and scanning them under a dissecting microscope at magnifications of ×60 to ×100. Different parasite taxa were placed in separate dishes and examined further at ×250 magnification. If necessary, individual parasites were stained with Mexican Red textile stain to enhance certain diagnostic features, and some nematodes were cleared in benzyl alcohol. Taxonomic identification was carried out with reference to specialized literature on cestodes (Healy, 2003; Khalil *et al*., 1994; Palm, 2004; Ruhnke *et al*., 2006; Ruhnke and Caira, 2009), nematodes (Arai and Smith, 2016; Bruce and Cannon, 1989; Deardorff and Overstreet, 1981; Moravec, 1987), Acanthocephala (Laurs and McCauley, 1964) and Copepoda (Hughes, 1973).

2.3 | Prevalence and mean intensity

To quantify the parasite infections, the prevalence and mean intensity of parasites were calculated according to Bush *et al*. (1997). Prevalence is the number of hosts infected with one or more individuals of a parasite species (or taxonomic group) divided by the number of hosts examined for that parasite species, and is commonly expressed as a percentage. Mean intensity is the average intensity of a parasite species among the infected members of a host species. Therefore, it is the total number of a particular parasite taxon found in a sample divided by the number of sampled hosts infected with that parasite. In some samples, parasites were too numerous to count so an approximation was used.

3 | RESULTS

Blue sharks (13 males and 5 females) examined ranged from 83 to 245 cm fork length (FL), and thresher sharks (6 males and 13 females) ranged from 101 to 283 cm FL. All spiral valves examined contained at least one parasite.

As mentioned in the "Introduction" section, this study was not designed specifically as a parasitological study. Freezing and thawing the spiral valves meant that many parasites were not in a condition that allowed for specific identification using finer diagnostic features. Small cestodes are particularly fragile and deteriorate quickly after death of the host. Most were, therefore, identifiable to only the generic level.

3.1 | Blue sharks

Table 1 lists the parasites found in blue sharks with their infection data. The most prevalent parasite was *Anthobothrium* sp., followed by *Prosobothrium* sp. Other parasites present were *Platybothrium auriculatum*(Figure 1), *Paraorygmatobothrium* sp., *Hysterothylacium* sp. (Figure 2), *Molicola* sp. and an unidentified phyllobothriid. All specimens of *Hysterothylacium* sp. found were male. The sample with the highest total number of parasites was from a male blue shark of 211 cm FL, which also contained the highest number of *Anthobothrium* sp. (300+). The largest blue shark in the sample was a male of 245 cm FL; its spiral intestine contained specimens of all the species of parasites found in the study, except for the unidentified phyllobothriid sp. (found in a male of 88 cm FL).

P. auriculatum was identified to species by the acutely recurved base of the medial hook on the scolex (Figure 1), which distinguishes this species from other members of the genus *Platybothrium* (see Healy, 2003).

3.2 | Thresher sharks

Table 2 lists the parasites found in thresher sharks with their infection data. The most prevalent parasite was *Paraorygmatobothrium* sp., followed by *Lacistorhynchus dollfusi*. *L. dollfusi* was identified to species by the presence of basal hooks with long handles (Figure 3), which are absent in those of *Lacistorhynchus tenuis*, the only other member of this genus (Beveridge and Sakanari, 1987).

Other parasites present were *Anisakis* sp. larvae, *Rhadinorhynchus cololabis*, *Hysterothylacium* sp., *Piscicapillaria* sp. (Figure 4a,b) and *Molicola* sp. The sample with the highest number of parasites (665+) was a male thresher shark of 150 cm FL, which also contained the highest number of *Paraorygmatobothrium* sp. (650). A thresher shark female in the sample (236 cm FL) contained all the species of parasites found in the study except *Piscicapillaria* sp. and *Hysterothylacium* sp. As in blue sharks, all specimens of *Hysterothylacium* sp. found were male. Undigested but still identifiable remains, mostly anterior parts, of a *Pennella* sp. and of two unidentified caligid copepods were present in nine spiral valves.

Voucher specimens of a number of parasites found in this study were deposited at the Scripps Oceanographic Collections at the University of California San Diego under the following collection numbers: *Hysterothylacium* sp., SIO-BIC Nto76; *R. cololabis*, SIO-BIC BI1638; *Prosobothrium* sp., SIO-BIC Pt85; *Molicola* sp., SIO-BIC Pt86/SIO-BIC Pt87; *Paraorygmatobothrium* sp., SIO-BIC Pt88; *P. auriculatum*, SIO-BIC Pt89; *Anthobothrium* sp., SIO-BIC Pt90; *L. dollfusi*, SIO-BIC Pt91; *Paraorygmatobothrium* sp. SIO-BIC Pt92.

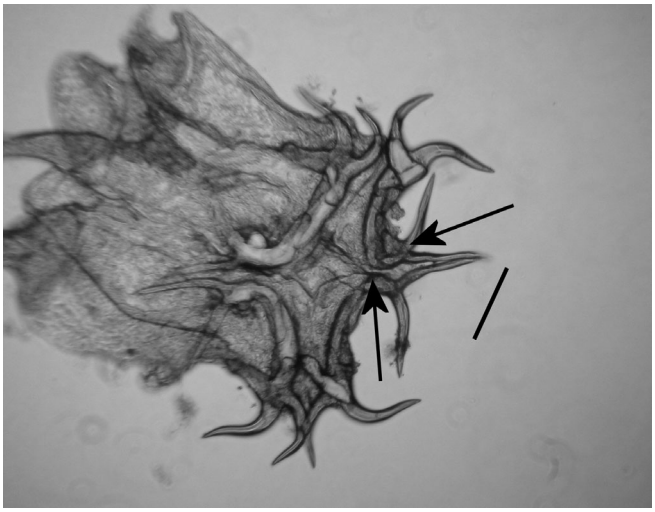

FIGURE 1 *Platybothrium auriculatum*. Scolex hooks showing acutely recurved base of medial hooks (arrowed). Scale bar = 10 μm

TABLE 1 Parasites recovered from the spiral valves of 18 blue sharks examined

Parasite	Pr (%)	MI (range)	*N*
Cestoda			
Tetraphyllidea			
Anthobothrium sp.	78	69.1 (1–300+)	14
Onchoproteocephalidea			
Prosobothrium sp.	67	28.0 (10–100+)	12
*Platybothrium auriculatum*Yamaguti, 1952	67	11.5 (1–40)	12
Phyllobothriidea			
Paraorygmatobothrium sp.	22	38.5 (4–100+)	4
Unidentified phyllobothriid	6	1.0	1
Trypanorhyncha			
Molicola sp.	11	3.0 (1–5)	2
Nematoda			
Ascaridoidea			
Hysterothylacium sp. Adult	11	3.5 (3–4)	2

Note. Pr, prevalence; MI, mean intensity; *N*, number of hosts infected.

4 | DISCUSSION

4.1 | Parasites of blue sharks

The composition of cestode species in the blue shark in this study area is similar to that in previous studies. *Anthobothrium caseyi*, *P. auriculatum* and *Paraorygmatobothrium* sp. were found further south off the west coast of Baja California Sur, Mexico, where they each had a prevalence higher than 50% in a sample of 27 blue sharks (Méndez and Galván-Magaña, 2016). Curran and Caira (1995) examined the spiral valves of 24 specimens of blue shark collected off Montauk, Long Island, New York, and found *Prosobothrium armigerum* and *P. auriculatum*, both with prevalences higher than 90%. The same two species were also part of the spiral valve parasite load of a sample of 159 blue sharks reported by Henderson *et al.* (2002) in the North-East Atlantic Ocean.

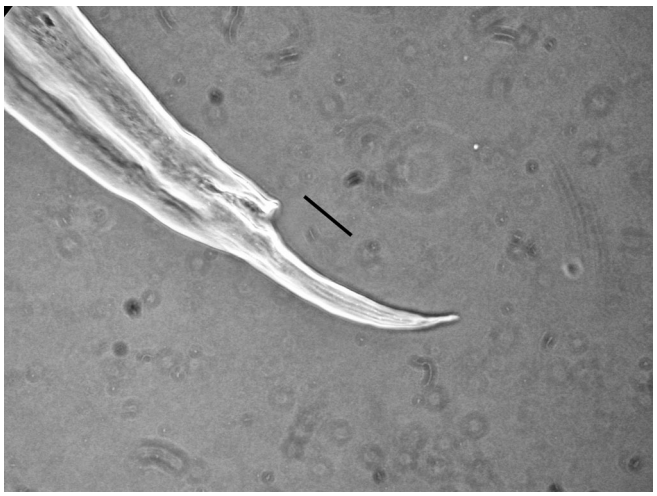

FIGURE 2 *Hysterothylacium* sp. Tail of male. Scale bar = 50 μm

Eight species are currently recognized in the genus *Anthobothrium* (see Caira *et al*., 2017b), one of which – *A. caseyi* – has been reported only from the blue shark. Caira *et al*. (2017a) recognized three species in the genus *Prosobothrium*, two of which – *Pr. armigerum* and *Pr. japonicum* – have been reported from the blue shark. Caira *et al*. (2017a) also recognized 10 species of *Platybothrium*, of which only *P. auriculatum* has been reported from the blue shark.

4.2 | Parasites of thresher sharks

After *Paraorygmatobothrium* sp., *L. dollfusi* was the second most prevalent cestode in the thresher. Its life cycle involves three hosts: a copepod, a teleost and an elasmobranch (Sakanari and Moser, 1989). The only other species in the genus – *L. tenuis* (van Beneden, 1858) – may have a purely Atlantic distribution (Beveridge and Sakanari, 1987).

Third-stage larvae of *Anisakis* sp.(p). were the second most prevalent nematodes in thresher sharks. Anisakid nematodes are known to infect over 200 pelagic fish species (Baldwin *et al*., 2011).

TABLE 2 Parasites recovered from the spiral valves of 19 thresher sharks examined

Parasite	Pr (%)	MI (range)	*N*
Cestoda			
Phyllobothriidea			
Paraorygmatobothrium sp.	90	213.7 (1–650)	17
Trypanorhyncha			
Lacistorhynchus dollfusi Beveridge and Sakanari, 1987	42	19.6 (1–50)	8
Molicola sp.	11	2.0 (1–3)	2
Nematoda			
Enoplida			
Piscicapillaria sp.	16	2.7 (2–4)	3
Ascaridoidea			
Hysterothylacium sp. Adult	16	4.0 (3.0)	3
Anisakis sp.(p). larvae	79	6.3 (1–54)	15
Acanthocephala			
Echinorhynchida			
Rhadinorhynchus cololabis (Laurs and McCauley, 1964)	42	5.6 (1–20)	8
Copepoda			
Siphonostomatoida			
Pennella sp. (partly digested)	47	2.1 (1–4)	9
Unidentified caligid (partly digested)	5	2.0	1

Note. Pr, prevalence; MI, mean intensity; *N*, number of hosts infected.

They have been reported frequently from the spiral valves of elasmobranchs, including the blue shark (Henderson *et al*., 2002), but no previous report from thresher sharks could be found. These nematodes use mainly euphausiids as first intermediate hosts, teleost fish or squid as second intermediate or paratenic hosts and cetaceans as definitive hosts (Smith and Wootten, 1978). *Anisakis* spp. larvae have been found parasitizing many teleost species, including the Pacific sardine (*Sardinops sagax*), in the California Current upwelling zone (Baldwin *et al*., 2011). The high number of larval *Anisakis* found in thresher sharks could have been acquired through their feeding on *S. sagax*, which is an important prey of threshers in the study area (Preti *et al*., 2012).

Three thresher samples contained a small number of *Piscicapillaria* sp., which represents a new host record. Moravec (1987) recognized six species in the genus *Piscicapillaria* (sub-genus *Piscicapillaria*), which has recently been added to by the description of a seventh species – *Piscicapillaria bursata* – by Moravec and Barton (2019). Specimens used in the study most closely resemble *Piscicapillaria baylisi* Moravec, 1987, particularly in the egg morphology: young *P. baylisi* eggs differ from those of the other six species in having strongly protruding polar plugs, as shown in Figure 4b. *P. baylisi* was described by Moravec (1987) from the nursehound, *Scyliorhinus stellaris*, caught in the English Channel. Given the different hosts and localities, the study's specimens from thresher sharks may prove to be a new species.

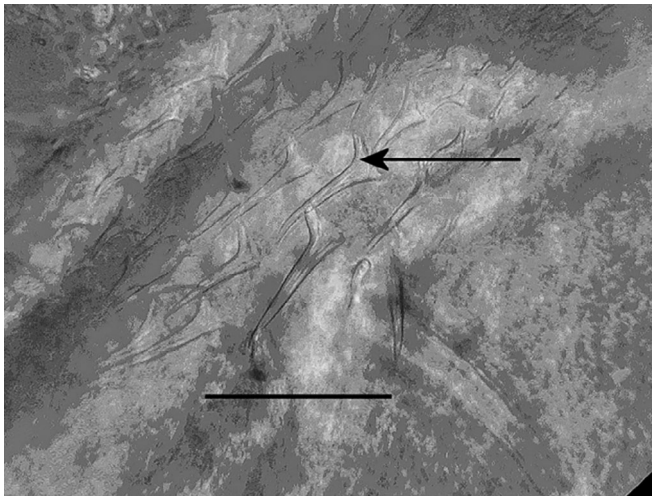

FIGURE 3 *Lacistorhynchus dollfusi*. Detail of basal armature of internal surface of tentacle. With the long handle of a basal hook arrowed. Scale bar = 50 μm

In this study the adult acanthocephalan *R. cololabis* was found for the first time in a shark. The Pacific saury *Cololabis saira* is the type host of this parasite, but it has also been reported from five other fish species: *Trachurus murphyii*, *Trachurus symmetricus* and *Brama japonica* (see Pozdynakov, 1994), steelhead trout *Oncorhynchus mykiss* (see Hughes, 1973) and cherry salmon *Oncorhynchus masou* (see Motora, 2016). Saury and *T. symmetricus* are two of the most common items found in the diet of threshers caught off California (Preti *et al*., 2012) and so are the most likely sources of the parasites found in the present study. Acanthocephala most frequently occur in teleosts but rarely in sharks and rays (Weaver and Smales, 2014). Many sharks and rays feed on bony fish that are definitive hosts of acanthocephalans, and the evidence suggests that these parasites can survive in the gut of sharks for a limited period of time (Weaver and Smales, 2014; results from this study). They are unlikely to live for long, however, because of the higher urea concentrations in the tissues of elasmobranchs than in bony fish and are thought to represent accidental infections (Smales *et al*., 2019; Williams *et al*., 1970).

The partly digested remains of parasitic copepods of the genus *Pennella* were found in the spiral valves of nine threshers. These were

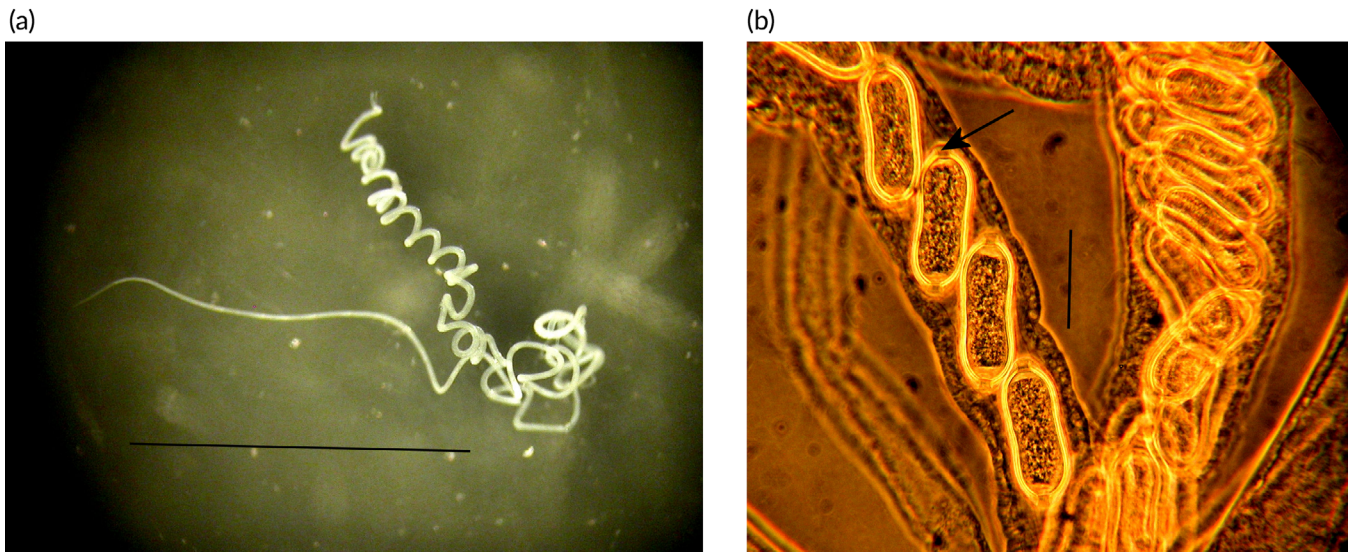

FIGURE 4 *Piscicapillaria* sp.: (a) whole nematode; (b) eggs, with the protruding polar pugs. Arrowed. Scale bars: a = 1 mm, b = 50 μm

morphologically similar to the *Pennella* sp. found on Pacific saury as described by Suyama *et al*. (2019). The carapace also had the distinctive black colour described by Kurochkin (1978) and Nagasawa (1984) as a feature of the saury parasite. This finding provides further evidence of recent feeding by these threshers on saury. One thresher spiral valve contained the remains of two caligid copepods. These are very common ectoparasites of many species of marine fish and would have been ingested with the prey.

4.3 | Parasites common to both shark species

Blue and thresher sharks shared two cestode genera (*Paraorygmatobothrium* and *Molicola*) and one nematode species (*Hysterothylacium* sp.).

Paraorygmatobothrium sp. was the most prevalent cestode taxon of thresher sharks with up to 650 parasite individuals found in one spiral valve. This is one of the most speciose of the phyllobothriid genera, with 21 species recognized by Ruhnke *et al*. (2017). *Paraorygmatobothrium prionacis* is the only species to have been reported from blue sharks, whereas two species, *Paraorygmatobothrium exiguum* and *Paraorygmatobothrium filiforme*, have been reported from thresher sharks (Ruhnke, 1994; Ruhnke *et al*., 2017). The poor condition of the specimens used in this study did not allow for specific identification.

Three species are currently recognized in the trypanorhynch genus *Molicola* (see Beveridge *et al*., 2017). Palm (2004) lists the blue shark as a host for *M. horridus* and the thresher as a host for *M. uncinatus*. The tentacles were not everted in any of the specimens, so specific identification was not possible.

Two blue shark and three thresher shark samples contained small adult nematodes of a species of *Hysterothylacium* ranging in length from 5 to 10 mm. Some specimens from blue sharks were dead and degenerating, but most from both shark species were intact, although their state of preservation was not ideal for identification purposes.

The morphology of the tail is an important diagnostic feature for distinguishing species of ascaridoid nematodes, including the genus *Hysterothylacium*. The tails of all the specimens had a distinctive shape: long, conical and tapering to a fine point which was slightly bent ventrally with no terminal mucron (Figure 2). Three papers reported the descriptions of ascaridoid nematodes with apparently identical tail morphology:

1. The tail of a female *Hysterothylacium* identified as *Hysterothylacium incurvum* (Rudolphi) by Deardorff and Overstreet (1981) (see Figure 56 of these authors), was based on material collected from three different species of billfishes (Xiphiidae and Istiophoridae).
2. Bruce and Cannon (1989) examined Deardorff and Overstreet's (1981) material from white marlin *Kajikia albida* and found that it was not conspecific with their material of *H. incurvum* collected from swordfish *Xiphias gladius*. They proposed the new generic name *Maricostula* for *H. incurvum* and other species of *Hysterothylacium* reported from billfishes and considered the newly named *Maricostula incurva* to be specific to swordfish. They also described a new species *Maricostula cenatica* from striped marlin *Kajikia audax*. Their description of the female tail of *M. cenatica* is again identical in form to that in this study's material. More recently, Moravec and Justine (2005) considered the features used by Bruce and Cannon (1989) for the separation of *Maricostula* to be questionable and of specific rather than generic importance. On this basis they relegated *Maricostula* to the status of a junior synonym of *Hysterothylacium*.
3. We also noted the same distinctive tail morphology in *Hysterothylacium*-type HB larvae from yellowfin tuna *Thunnus albacares* as described and illustrated by Deardorff *et al*. (1982).

The only species of adult *Hysterothylacium* previously reported from either shark species is *Hysterothylacium hospitum*, described from a blue shark caught off Hawaii by Solovjeva and Pozdnjakov (1984). This study's specimens were markedly different from this species in both size and morphology. Further study must await the collection of fresh material prepared specifically for morphological and molecular description. It is possible that these forms are a new species of *Hysterothylacium* specific to one or both of these shark species, or more likely that they represent accidental infections resulting from predation on the normal host species.

Blue and thresher sharks presented a distinct qualitative difference in the parasite assemblages of their spiral valves. Blue sharks were predominately infected with cestodes and a small number of nematodes, whereas thresher sharks presented a more diverse parasite fauna with specimens belonging to various taxonomic groups (Cestoda, Nematoda, Acanthocephala, Copepoda). This difference in parasite faunas is likely due to the differences in diet between the two predators because intestinal parasites are acquired trophically and also reflect the regions where the sharks spend most time. Blue sharks are known to migrate throughout the Pacific, whereas threshers are more coastal (Compagno *et al*., 2005). Blue sharks are recorded to feed regularly on a wide variety of teleost and cephalopod species and, sporadically, even mammals (Kohler, 1987).

5 | CONCLUSIONS

The spiral intestines of blue and thresher sharks were hosts to seven and nine taxa of parasites, respectively. Blue shark intestines were predominately infected with cestodes and a small number of nematodes, whereas thresher sharks presented a more diverse parasite fauna. Blue and thresher sharks shared one nematode species (*Hysterothylacium* sp.) and two cestode genera (*Paraorygmatobothrium* and *Molicola*). The difference in the composition of parasite species indicates the different feeding and migratory behaviours of these two predators. The occurrence of two parasites (*R. cololabis* and *Pennella* sp.) of Pacific saury in threshers indicates recent feeding on saury, whereas the high prevalence of *Anisakis* sp. in the same host may be a result of intensive feeding on Pacific sardine; both saury and sardine are important components of the diet of threshers in the study area.

The *Piscicapillaria* sp. found in threshers and the *Hysterothylacium* sp. found in both shark species are new host records and may represent new species. This study is a preliminary attempt to catalogue and analyse the intestinal parasite faunas of blue and thresher sharks in the CCLME north of the Mexican border. A wider study including more samples and more shark species would offer an opportunity to understand more about feeding behaviour and migrations and possibly provide information on shark population biology.

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CONFLICT OF INTEREST

None.

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