

Research Paper

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Determinants of diversity and composition of the tapeworm fauna of blue sharks, *Prionace glauca*: a geographical and host-specificity analysis

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Abstract

Blue sharks, *Prionace glauca*, are cosmopolitan, extremely vagile sharks and the species among elasmobranchs for which most surveys containing tapeworm community data are available worldwide. In this study we report on the tapeworm fauna of three samples of blue sharks ($n = 37$) from two new regions (one sample from Galicia, north-east Atlantic, and two from Valencia, western Mediterranean), and compared it with previous studies, assessing the relative role of the ecological and evolutionary factors in structuring local tapeworm assemblages. Nine cestode taxa were identified, of which four included adult specimens, that is, *Platybothrium auriculatum*, *Prosobothrium armigerum*, *Anthobothrium caseyi* and *Molicola horridus*. The abundance of these species, and Brillouin's diversity index, differed significantly among samples without a clear geographical signal. A comparison with six previous surveys revealed that tapeworm assemblages were composed of the same 'core' taxa, with mean species richness typically ranging from two to four species. Global records of adult tapeworms in blue sharks included: 15 taxa identified at species level, of which only eight (generalist trypanorhynchs) were shared with other sympatric host species; five mostly with other carcharhinids; and three with large lamnid sharks sharing the blue sharks' habitat. The composition of tapeworm communities of blue sharks is thus highly constrained by strong host specificity, with composition and abundance varying across localities depending on idiosyncratic environmental conditions.

Introduction

Cestodes make up the bulk of the intestinal helminths infecting sharks (Caira & Healy, 2012; Caira & Jensen, 2017) and represent, for several reasons, an ideal system to investigate the role of ecological and evolutionary factors in providing structure to parasite communities (Randhawa & Poulin, 2010; Rasmussen & Randhawa, 2018). First, there is substantial diversity within this parasite assemblage; over 650 spp. of tapeworms from approximately 180 genera and eight orders have hitherto been reported in sharks, and the estimated diversity is close to 1500 spp. (Caira & Jensen, 2017). Second, most of these species (with the exception of those belonging to the Trypanorhyncha) exhibit a high degree of host specificity, infecting a single species or a few closely-related host species (Caira & Jensen, 2014). Third, since cestodes are trophically-transmitted, the contacts of infective stages with sharks must be driven by both the relative degree of exploitation of the food web by these parasites (i.e. the number of intermediate and paratenic hosts they use) and by the dietary breadth of their final shark hosts (Palm & Caira, 2008; Rasmussen & Randhawa, 2018). In summary, both evolutionary (e.g. specificity) and ecological (e.g. passive contacts through hosts' diet) elements could play a variable role in defining the composition and diversity of tapeworm assemblages of sharks depending on the scale of analysis.

Over the last two decades, there has been an effort to unveil such community patterns at a global (i.e. macroecological) scale. Focusing on the component community level (i.e. samples of shark species as a whole), Randhawa & Poulin (2010) found few consistent host effects, although tapeworm species richness was significantly influenced by shark size after correcting for host phylogenetic effects. In a recent, more detailed re-analysis, a robust pattern did emerge, that is, the diet breadth of each shark species was a strong predictor of its tapeworm species richness, with a secondary influence of other host features such as size, trophic level, taxonomic distinctness of diet, or latitudinal or depth range (Rasmussen & Randhawa, 2018).

In contrast, analyses at host individual (i.e. infracommunity) level are still very scarce, mainly because few parasitological surveys of sharks report on proper infracommunity parameters (e.g. mean species richness, diversity indices, or mean abundance of each tapeworm species per host). Based on a limited dataset available, Penadés-Suay *et al.* (2017) recently investigated to what extent the potential dilution' effects of infective stages of tapeworms

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Table 1. Sampling features of blue sharks, *Prionace glauca*, collected in Iberian waters.

	Galicia	Western Mediterranean (stranded)	Western Mediterranean (captured)	Total
n	16	8	13	37
mean total length (cm) (standard deviation) [range]	202 (149.5–254.5) [130–284]	247 (175.9–318.1) [90–323]	[135–185]	[90–323]
number of males (%)	12 (75.0)	4 (50.0)	11 (84.6)	27 (72.8)
number of females (%)	4 (25.0)	4 (50.0)	2 (15.4)	10 (27.2)
number of juveniles (%)	6 (37.5)	1 (12.5)	13 (100)	20 (54.1)

Note that only the range of total length (cm) was available for the sample of sharks captured in the western Mediterranean.

in the pelagic–oceanic habitat could result in comparatively species-poor, low-abundance infracommunities in large oceanic sharks, regardless of the richness in the component community locally available. These authors failed to detect this specific host habitat effect, but their literature search incidentally revealed a striking finding, that is, there were just four species of sharks (for a global diversity of approximately 500 spp.) for which quantitative surveys of the whole tapeworm fauna had been carried out in at least two localities. This is unfortunate because the comparison of local parasitological surveys at a wide geographical range, with correspondingly varied environmental conditions, could shed much light on the ecological and evolutionary determinants of richness and composition at both component community and infracommunity levels.

The blue shark, *Prionace glauca* (Linnaeus, 1758), is likely the shark species for which more quantitative data exist on its tapeworm fauna at a global scale. Complete surveys on cestodes have been carried out in the Mediterranean Sea (Euzet, 1959), the North Atlantic (Curran & Caira, 1995; Henderson *et al.*, 2002), and the North (Méndez & Galván-Magaña, 2016; Preti *et al.*, 2020) and South (Escalante, 1986) Pacific. In addition, a great deal of parasitological records is available from the whole distribution range of this species (online supplementary appendix S1). Some of these studies have provided interesting insights on the microhabitat distribution of tapeworms within the intestine (Curran & Caira, 1995), tapeworm species associations (Henderson *et al.*, 2002), or the role of host specificity in imparting similarity to faunal composition among localities (Méndez & Galván-Magaña, 2016). What is lacking, however, is a comprehensive comparative analysis that accounts for the similarities and differences in composition and diversity of the tapeworm fauna, especially at infracommunity level, across localities.

In this regard, the blue shark is also an interesting species for two reasons. First, it is a highly migratory, oceanic species which is widespread in temperate and tropical waters worldwide (Compagno, 2001). Individual blue sharks typically perform large-scale movements, covering thousands of kilometres within a few months or even weeks (Vandeperre *et al.*, 2014; Kai & Fujinami, 2020), although substantial inter-individual variability in linear distances covered may occur (see, e.g. Stevens *et al.*, 2010). Second, blue sharks are generalist predators whose diet may include, not only a number of teleost and cephalopod species, but also occasionally cetaceans, birds and crustaceans (Kohler, 1987; Henderson *et al.*, 2001; Biton-Porsmoguer *et al.*, 2017; and references therein). The specific diet composition has been observed to change substantially among localities, likely reflecting the relative availability of prey (Markaida & Sosa-Nishizaki,

2010). Thus, the tapeworm communities of blue sharks would theoretically be driven by factors tending to promote geographical similarity (i.e. a high host vagility; a narrow specificity typical from cestodes of sharks) or differentiation (a circumglobal host's geographical distribution; local variation of prey composition affecting host–parasite contacts).

Blue sharks are regularly caught by Spanish long-line fisheries operating in waters off Galicia, north-eastern Atlantic Ocean, and Valencia, eastern Mediterranean (Mejuto *et al.*, 2009a, b). This scenario provided us with the opportunity, firstly, to report on the intestinal helminth fauna of blue sharks in two new geographical areas, and to make a quantitative comparison of infracommunity data between them. Secondly, we used these data, along with those obtained for previous parasitological surveys on blue sharks worldwide, to perform a global assessment of the relative role of the ecological and evolutionary factors in structuring the local tapeworm assemblages of blue sharks.

Material and methods

Sample collection

Sampling of blue sharks was opportunistic and included both animals stranded and captured by long-line fisheries (table 1). The examination and collection of the intestines of the sharks captured by fisheries had to be carried out quickly, before the fish auction began, thus body length measurements of several individual fish could not always be taken (table 1). The intestine of 16 individuals were obtained at the port of Vigo (Galicia, Spain); this sample, which we will hereafter refer to as Galicia', was caught by long-line fisheries operating in the north-eastern Atlantic Ocean, between 40°N 20°W and 35°N 10°W; 13 sharks were caught in October 2012, and three in May 2013. Another sample of 13 sharks was caught in the western Mediterranean, in waters off the coast of Valencia (coordinates: 39°38'N 0° 44'E); this sample will be identified as Valencia (C). Finally, eight sharks were found stranded along the coast of Valencia and collected by the Valencian Community Stranding Network during the period 2013–2021; this sample will be named as Valencia (S). Blue sharks were considered juvenile when measuring less than 180 cm (males) and 220 cm (females), and adults otherwise (Compagno, 1984).

Due to logistic constraints, the intestine of all sharks had to be stored at –20°C for later analysis in the laboratory. After thawing, each intestine was rinsed with tap water under a 0.02 mm mesh and solid contents were collected. The intestine wall was also thoroughly examined for attached helminths. Parasites were

collected under a stereomicroscope, washed in 0.9% saline, examined to describe their main features, counted, and fixed and preserved in 70% ethanol. Cestodes were stained with iron acetocarmine (Georgiev, 1986), and mounted for examination. Specimens were identified based on Khalil *et al.* (1994) and specific Refs. (Healy, 2003; Palm, 2004; Ruhnke & Caira, 2009; Ruhnke, 2011). Voucher specimens are deposited at the Natural History Museum of London with accession numbers: *Anthobothrium caseyi*, NHMUK 2022.8.31.1; Tetracystidae fam. gen. sp., NHMUK 2022.8.31.2; *Platybothrium auriculatum*, NHMUK 2022.8.31.3; *Prosobothrium armigerum*, NHMUK 2022.8.31.4; and *Molicola horridus*, NHMUK 2022.8.31.5. Additional material from these specimens and the only specimens of *Scyphophyllidium* sp. and Trypanorhyncha fam. gen. sp. can be found at the Collection of the Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Spain.

Statistical analyses

For each helminth taxon, we recorded its prevalence (percentage of infected hosts in the sample), mean intensity (average number of worms in the sample of hosts infected with this taxon), and mean abundance (average number of worms in the total sample of hosts) following Bush *et al.* (1997). Species richness (i.e. the number of helminth taxa per individual shark) and Brillouin's diversity index were considered as infracommunity descriptors. The 95% confidence interval (CI) for prevalence was calculated with Sterne's exact method (Reiczigel, 2003). The 95% CI for mean abundance and mean intensity of each helminth taxon, as well as for mean species richness and mean Brillouin's diversity index, were obtained with the bias-corrected and accelerated bootstrap method using 10,000 replications (Rózsa *et al.*, 2000). Kruskal–Wallis tests were used to see differences between shark samples in the abundance of 5 cestode taxa (*A. caseyi*, *Scyphophyllidium* sp., *P. auriculatum*, *P. armigerum*, *M. horridus*) and two infracommunity descriptors (species richness and Brillouin's diversity index).

To globally compare the infracommunity diversity and composition of cestode faunas infecting blue sharks around the world, we searched all parasitological surveys for which at least the prevalence of all tapeworm taxa found in the intestine was reported. These surveys generally did not provide data on mean species richness per host; thus we calculated this parameter by summing up prevalence (expressed as decimals) of all intestinal tapeworm taxa in each sample (Penadés-Suay *et al.*, 2017). Differences of prevalence of specific taxa among localities were tested with exact Chi-square tests.

We searched bibliography in the Shark References database (<https://shark-references.com/species/host-parasites-list>) and the Host–Parasite Database of the Natural History Museum (<https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/index.jsp>) to compile all existing records of adult cestodes infecting blue sharks. The references of each publication found were also checked for potentially missed records. We selected records in which tapeworms were identified to species level and in the intestine (not the stomach or the liver), excluding taxa that had been identified only to genus level or above because they were little informative to explore specificity patterns; moreover, these taxa typically involved sexually immature forms for which blue sharks likely act as putative non-hosts. Taxonomic nomenclature was updated when

necessary, using appropriate literature. For all compiled species, and also for their valid congeneric counterparts, we listed all hosts reported in the literature. The resulting inventory of host–parasite associations was placed on a cladogram of the elasmobranchs (adapted from Iglésias *et al.*, 2005; Naylor *et al.*, 2012; Amaral *et al.*, 2018) and visually interpreted for specificity patterns.

The software PERMANOVA + for PRIMER (Anderson *et al.*, 2008) was used to calculate infracommunity parameters, the free software 'Quantitative Parasitology' (Reiczigel *et al.*, 2019) to set the 95% CIs of infection parameters and the statistical package SPSS v. 22 for the remaining analyses (SPSS Inc., Chicago, IL). Statistical significance was set at $P < 0.05$.

Results

A total of 2726 helminth specimens were collected in the intestine of the 37 blue sharks, belonging to nine cestode taxa (table 2). All but one 278 cm-long male shark from Galicia harboured at least one cestode species. Adult specimens were detected in the sample of *A. caseyi*, *P. auriculatum*, *P. armigerum* and *M. horridus*, but not in the case of Tetracystidae spp. and Phyllobothriinae sp. 1 and 2. Only the scolex could be collected for single individuals of *Scyphophyllidium* sp. and Trypanorhyncha sp. and, therefore, it was not possible to confirm whether they were sexually mature. However, the length of the scolex (570 μm) and bothridia (ca. 530 μm) of *Scyphophyllidium* sp. was within that provided for the species specific to blue sharks, that is, *Scyphophyllidium prionacis* (see Ruhnke, 1994). Although we refrained to name it as such, we included it comparisons of abundance and infracommunity parameters between samples.

Five cestode taxa exhibited a prevalence >10%, of which four, *A. caseyi*, *P. auriculatum*, *P. armigerum* and Tetracystidae sp., were shared among the three blue shark samples, and one, *M. horridus*, occurred in both Galicia and Valencia (S) (table 2). The remaining four cestode taxa were found only in Galicia (table 2). The abundance of four of the five cestode taxa with adult specimens differed significantly between host samples (table 3). The *post-hoc* comparison revealed that the pattern of differences was not consistent in all taxa; the abundance of *P. auriculatum* and *P. armigerum* was significantly higher in Galicia compared with Valencia (C), whereas the abundance of *A. caseyi* was highest and smallest in the two samples from Valencia, and that from *M. horridus* was significantly higher in Valencia (S) compared with the two other samples (table 3).

In contrast, we did not detect significant differences in infracommunity species richness among the shark samples (table 3). Considering all cestode taxa, mean species richness (95% CI) was 2.69 (2.10–3.31) for Galicia, 1.75 (1.13–2.50) for Valencia (S) and 2.46 (2.00–2.92) for Valencia (C); when only species with adult specimens were selected, these figures were 2.13 (1.63–2.63), 1.63 (1.13–2.13) and 2.08 (1.72–2.39), respectively. In the case of Brillouin's diversity index, significant differences did show up only when all cestode taxa were considered, with values being 0.59 (0.41–0.78), 0.19 (0.04–0.34) and 0.50 (0.36–0.63), respectively. For the subset of cestode species with adult specimens, values of Brillouin's diversity index were 0.42 (0.27–0.56), 0.17 (0.04–0.33) and 0.43 (0.31–0.54).

Aside from the present study, we found six surveys reporting on the tapeworm fauna of the intestine of blue sharks; two and one from the North and South Pacific Ocean, respectively,

Table 2. Prevalence (P) expressed as percentage, and mean intensity (MI) of the cestode taxa found in the intestine of blue sharks, *Prionace glauca*, collected in Iberian waters.

	Galicia (n = 16)			Valencia (stranded) (n = 8)			Valencia (captured) (n = 13)			Total (n = 37)		
	P	MI	MA	P	MI	MA	P	MI	MA	P	MI	MA
Tetraphyllidea												
<i>Anthobothrium caseyi</i>	62.5 (37.2–82.2)	11.6 [3–24] (7.1–17.1)	6.19 (2.88–11.4)	37.5 (11.1–71.1)	183[5–519] (5.0–354.0)	68.6 (1.25–264)	100 (77.5–100)	87.7 [4–332] (53.7–156)	87.7 (53.7–156)	70.3 (54.1–82.8)	69.4 [3–519] (37.9–139)	48.8 (26–98.8)
Tetraphyllidea fam. gen. sp.a	31.2 (13.2–56.4)	13.2 [3–25] (6.2–20.2)	4.12 (1.25–9.31)	12.5 (0.6–50.0)	19	2.38 (0–7.12)	38.5 (16.6–65.8)	14.2 [2–41] (5.4–28.8)	5.46 (1.54–16.5)	29.7 (17.2–45.9)	14.2 [2–41] (9.0–22.7)	4.22 (2–8.03)
Onchoproteocephalidea												
<i>Platybothrium auriculatum</i>	62.5 (37.2–82.2)	9.9 [3–27] (5.4–16.4)	6.19 (2.88–11.4)	12.5 (0.6–50.0)	5	0.625 (0–1.88)	23.1 (6.6–52.0)	3.3 [1–8] (1.0–5.7)	0.77 (0.08–2.69)	37.8 (23.4–54.1)	8.1 [1–27] (4.7–13.1)	3.08 (1.54–5.84)
<i>Prosobothrium armigerum</i>	68.8 (43.6–86.8)	18.5 [1–143] (4.5–68.4)	12.7 (2.88–49.1)	37.5 (11.1–71.1)	21 [12–34] (12.0–28.3)	7.88 (1.5–18.5)	84.6 (56.6–97.2)	26.9 [8–63] (19.3–37.4)	22.8 (14.7–33.5)	67.6 (51.3–81.5)	22.5 [1–143] (14.8–41.9)	15.2 (9.32–28.8)
Phyllobothriidea												
<i>Scyphophyllidium</i> sp.	6.2 (0.3–30.5)	1	0.06 (0–0.19)	–	–	–	–	–	–	2.7 (0.1–14.4)	1	0.03 (0–0.08)
Phyllobothriinae gen. sp. 1a	6.3 (0.3–30.5)	6	0.38 (0–1.12)	–	–	–	–	–	–	2.7 (0.1–14.4)	6	0.16 (0–0.49)
Phyllobothriinae gen. sp. 2a	6.3 (0.3–30.5)	10	0.63 (0–1.88)	–	–	–	–	–	–	2.7 (0.1–14.4)	10	0.27 (0–0.81)
Trypanorhyncha												
<i>Molicola horridus</i>	18.8 (5.3–43.6)	3 [1–5] (1.0–4.3)	0.56 (0.06–1.56)	75 (36.5–95.4)	10.3 [3–35] (4.3–24.7)	7.75 (2.88–20.2)	–	–	–	24.3 (13.0–40.5)	7.9 [3–35] (3.9–18.6)	1.92 (0.76–5.59)
Trypanorhyncha fam. gen. sp.a	6.2 (0.3–30.5)	1	0.06 (0–0.19)	–	–	–	–	–	–	2.7 (0.1–14.4)	1	0.03 (0–0.08)

Values between brackets and in parentheses indicate ranges and 95% confidence intervals, respectively.

aAdult cestodes from these species were not found.

Table 3. Results of Kruskal–Wallis tests (H) for differences in abundance of five cestode taxa and two infracommunity descriptors between three samples (corresponding to two degrees of freedom) of blue sharks, *Prionace glauca*, collected from Iberian waters, captured in Galicia (n = 16) and Valencia (C) (n = 13) and stranded along the coast of Valencia (S).

Descriptor	H	P	Post-hoc difference (<0.05)
abundance			
<i>Anthobothrium caseyi</i>	14,733	0.001	Valencia (C) vs. Valencia (S) and Galicia
<i>Platybothrium auriculatum</i>	8296	0.016	Valencia (C) vs. Galicia
<i>Prosobothrium armigerum</i>	7606	0.022	Valencia (C) vs. Galicia
<i>Scyphophyllidium</i> sp.	1169	0.559	
<i>Molicola horridus</i>	16,633	<0.001	Valencia (S) vs. Valencia (C) and Galicia
infracommunity			
all species			
species richness	4.285	0.117	
Brillouin's index of diversity	8.584	0.014	Valencia (S) vs. Galicia
species with adult specimens			
species richness	2.215	0.330	
Brillouin's index of diversity	5.228	0.073	

The comparison of species richness and diversity are made considering all cestode taxa and only the species for which at least one adult worm was found.

two from the North Atlantic Ocean and one from the Mediterranean Sea (table 4). Overall, 11 nominal taxa were reported, and there were significant differences between the eight host samples in all of them (exact Chi-square, $P < 0.05$). Only one species, that is, *P. auriculatum*, was shared among all host samples, although with obvious differences in prevalence and mean intensity (table 4). Species of *Anthobothrium* (particularly *A. caseyi* except in one case of undetermined identity), *Prosobothrium* (*P. armigerum* or *P. japonicum*) were found in all but one sample, and species of *Scyphophyllidium* (particularly *S. prionacis* except in one case of undetermined identity) in all but two samples. Two other taxa, that is, *Phoreiobothrium lasium* and *Molicola horridus*, occurred more idiosyncratically (table 4). Although mean infracommunity species richness ranked from 0.69 to 3.67 spp./host, values were remarkably similar in six of the eight surveys, around 2 to 2.7 spp./host (table 4).

We found 93 records of 15 intestinal cestodes infecting blue sharks that had been identified to species level (online supplementary appendix S1). A total of seven species, including one of ‘Tetraphyllidea’ (*A. caseyi*), four of Onchoproteocephalidea (*Pla. auriculatum*, *Pro. armigerum*, *Pro. japonicum* and *Phoreiobothrium* sp. [= *P. lasium*]), and two of Phyllobothriidea (*Pelichnibothrium speciosum* and *S. prionacis*), were reported only from blue sharks. For all these species, records encompassed at least the Pacific and Atlantic/Mediterranean basins, except *Phoreiobothrium* sp. (= *P. lasium*), for which records from the

Table 4. Comparison of infection parameters, and species richness, of adult cestode fauna found in the intestine of blue sharks, *Prionace glauca*, collected all over the world.

Region (Reference) [n]	North-eastern (NE) Pacific (1) [27]			South-eastern Pacific (3) [8]			North-western Atlantic (4) [12]			NE Atlantic (5) [159]			NE Atlantic (6) [16]			Western (W) Mediterranean (7) [22]			W Mediterranean (6) [21]		
	P	M	I	P	M	I	P	M	I	P	M	I	P	M	I	P	M	I	P	M	I
<i>Anthobothrium caseyi</i>	59	70	-	-	-	-	92	216	13	9	63	12	95	na	76	106					
<i>Anthobothrium</i> sp.	-	-	78	69	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Platybothrium auriculatum</i>	85	71	67	12	100	na	100	401	13	11	63	10	23	na	19	4					
<i>Prosobothrium armigerum</i>	-	-	-	-	-	-	92	39	43	18	69	19	23	na	67	26					
<i>Prosobothrium japonicum</i>	56	13	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Prosobothrium</i> sp.	-	-	67	28	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Scyphophyllidium prionacis</i>	67	80	-	-	100	na	83	354	-	-	-	-	55	na	-	-					
<i>Scyphophyllidium</i> sp.	-	-	22	39	-	-	-	-	-	-	6	1	-	-	-	-					
<i>Phoreiobothrium lasium</i>	-	-	-	-	-	-	-	-	-	-	-	-	9	na	-	-					
<i>Molicola horridus</i>	-	-	-	-	-	-	-	-	-	-	19	3	-	-	29	10					
<i>Molicola</i> sp.	-	-	11	3	-	-	-	-	-	-	-	-	-	-	-	-					
species richness	2.66	2.45	2.00	2.00	3.67	0.69	2.10	2.10	1.91												

P, prevalence; M, mean intensity; na, information not available.

References: 1, Méndez & Galván-Magaña (2016); 2, Preti et al. (2020); 3, Escalante (1986); 4, Curran & Caira (1995); 5, Henderson et al. (2002); 6, The current study; and 7, Euzet (1959).

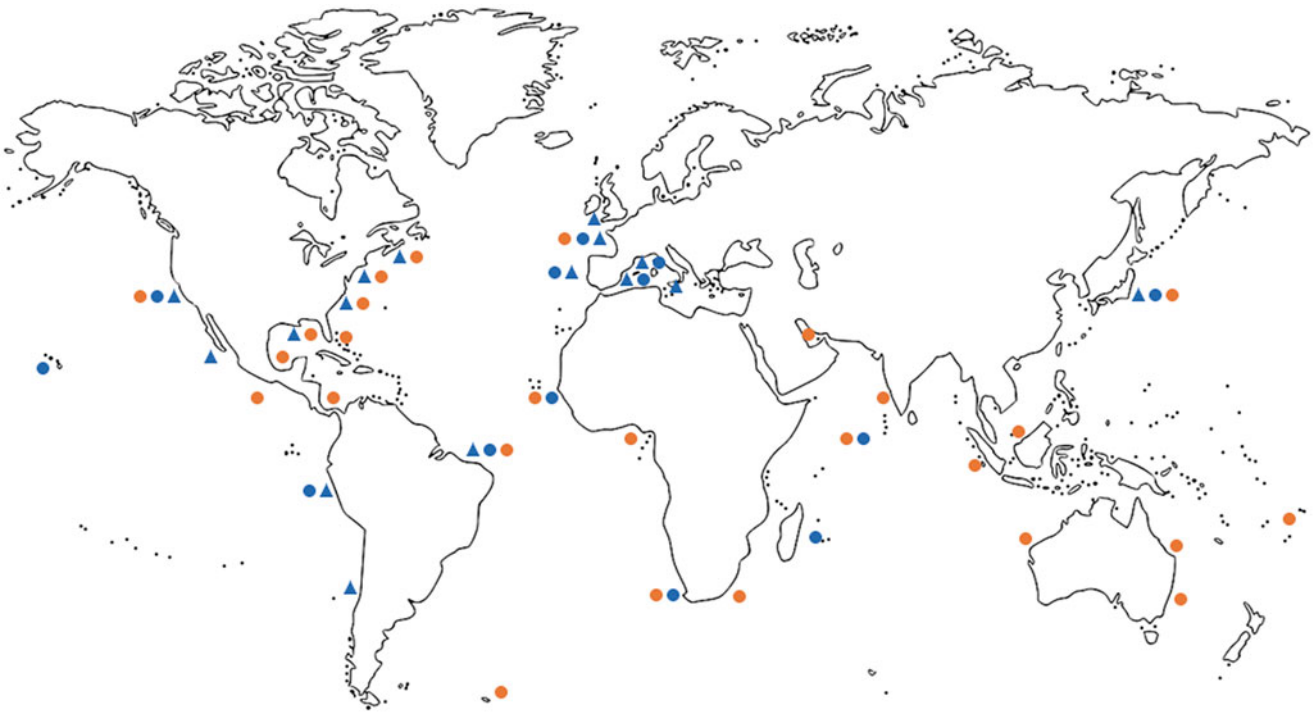


Fig. 1. Map showing the locations where adult cestode species that can be found in the intestine of *Prionace glauca* have been reported (see references in online supplementary appendix S1). Blue triangles indicate the ‘core’ species found only in *P. glauca* (see text); circles indicate species of the Trypanorhyncha that have been described infecting *P. glauca*; blue circles indicate records in *P. glauca*; and orange circles indicate records in other hosts.

Pacific Ocean were not found (fig. 1 and online supplementary appendix S1). In contrast, the eight species of Trypanorhyncha ever found in blue sharks were also reported from a wide range of elasmobranchs (from one to 19 species depending on the species), mainly of the family Carcharhinidae (online supplementary appendix S1). These species are also geographically widespread in tropical and temperate waters worldwide (fig. 1). It is important to highlight the case of the two species of *Nybelinia* described infecting blue sharks: *Nybelinia schmidtii* has only been reported also infecting shortfin mako sharks, *Isurus oxyrinchus* (Lamnidae); and *Nybelinia pintneri* infecting *I. oxyrinchus* and the milk shark, *Rhizoprionodon acutus* (Carcharhinidae).

At genus level, the literature search revealed the following patterns (fig. 2 and online supplementary appendix S2): the monotypic genus *Pelichnibothrium* was exclusive to blue sharks, *Prosobothrium* (three spp.) was shared with Sphyrnidae (a single species), *Anthobothrium* (eight spp.) and *Platybothrium* (ten spp.) mostly with other Carcharhinidae and, finally, *Phoreiobothrium* (18 spp.) was shared with both Sphyrnidae and Carcharhinidae species. In the case of *Scyphophyllidium* (51 spp.) and most genera of the Trypanorhyncha, the bulk of species were allocated in the Carcharhinidae, but also occurred in a number of other families and orders of sharks and batoids (fig. 2 and online supplementary appendix S2). An exception was that of *Molicola* (three spp.), whose species only infect Lamniformes and blue sharks.

Discussion

In this study we surveyed the intestinal parasites of blue sharks in Iberian waters, where no previous records exist. None of the taxa identified at least to genus level is new for this host species, but as many as four tapeworm taxa could only be assigned to sub-

familial level at best. A potential concern is therefore, whether freezing of intestines could have damaged cestode specimens hampering a proper identification (e.g. Preti *et al.*, 2020). We are aware that freezing of organs is not recommended for taxonomic work on helminths, especially when dealing with delicate forms such as tapeworms. However, sampling of large sharks is often opportunistic and subject to trade-off with the stakeholders (fishers and staff of stranding networks). Perhaps not surprisingly, other parasitological surveys on blue sharks have also dealt with frozen samples (Henderson *et al.*, 2002; Preti *et al.*, 2020). Fortunately, the tapeworms from this study that could only be assigned to coarse taxonomic groups contained just immature specimens lacking diagnostic traits and for which the blue shark are putative non-hosts. We interpret that these immature forms are likely specific to other elasmobranchs and do not reproduce in blue sharks; thus, they could be considered as accidental parasites such as, for example, *Anisakis* spp. are in other sharks (Penadés-Suay *et al.*, 2017). The degree of preservation of samples of the remaining tapeworm taxa, all containing adults, allowed reliable specific identifications (see below) except for *Scyphophyllidium* sp. for which a single scolex could be collected. In any event, the voucher specimens deposited at the Natural History Museum of London will afford researchers further taxonomic re-examination, if necessary, for example, via molecular markers.

The ‘true’ tapeworm communities of blue sharks in Iberian waters were thus composed of four to five species (depending on whether *Scyphophyllidium* sp. is included). Three species were common to the three host samples analysed, being cosmopolitan parasites specific to blue sharks (online supplementary appendix S1). *Anthobothrium caseyi* can be differentiated from other congeneric species by their proglottid lacinations, which

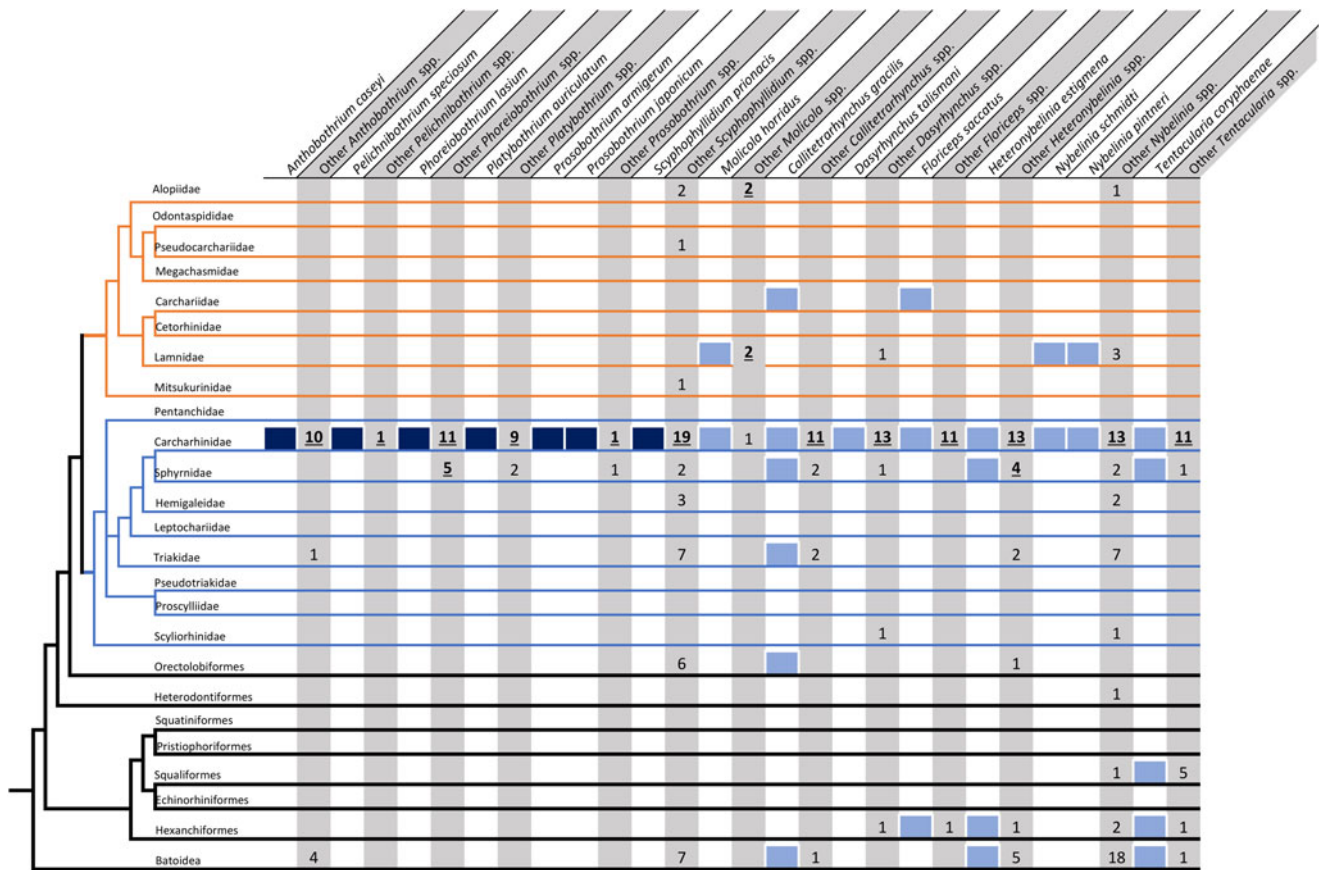


Fig. 2. Host–parasite associations of adult cestode taxa infecting the intestine of blue sharks, *Prionace glauca*, based on data from the literature. The phylogenetic tree of elasmobranchs (adapted from Iglésias *et al.* 2005, Naylor *et al.* 2012, Amaral *et al.* 2017), shows families of Lamniforms and Carcharhiniforms, along with the other orders of sharks and the Batoidea as a single group. Dark blue boxes indicate species specific to *P. glauca*, and light blue boxes indicate species also infecting other hosts (see online supplementary appendix S2). For the columns referring to other species of the cestode genera the boxes indicate number of other hosts described within the family, order or superorder: bold underlined numbers indicate the main host group (see online supplementary appendix S2). Numbers in the phylogenetic tree: 1. Lamniforms (in orange: 1.1 Alopiidae 1.2 Odontaspidae 1.3 Pseudocarchariidae 1.4 Megachasmidae 1.5 Carchariidae 1.6 Cetorhinidae 1.7 Lamnidae 1.8 Mitsukurinidae), 2. Carcharhiniforms (in blue: 2.1 Pentanchidae 2.2 Carcharhinidae 2.3 Sphyrnidae 2.4 Hemigaleidae 2.5 Leptochariidae 2.6 Triakidae 2.7 Pseudotriakidae 2.8 Proscylliidae 2.9 Scyliorhinidae), 3. Orectolobiformes, 4. Heterodontiformes, 5. Squatiformes, 6. Pristiophoriformes, 7. Squaliformes, 8. Echinorhiniformes, 9. Hexanchiformes, 10. Batoidea.

are approximately as long as wide (Ruhnke & Caira, 2009); *Pl. auriculatum*, by the acutely recurved base of the medial hook on the scolex (see Healy, 2003); and *Pro. armigerum* by its scolex formed by four glandular sessile discs (Khalil *et al.*, 1994). Two other cosmopolitan species of the order Phyllobothriidea have been reported exclusively in blue sharks, *Scyphophyllidium prionaci* and *Pelichnibothrium speciosum* (online supplementary appendix S1), but none of them were verified in this study. The scolex of the specimen assigned to *Scyphophyllidium* sp. superficially resembled that of *S. prionaci* but was in a very poor state of conservation, and the lack of proglottids precluded an unequivocal identification. Finally, we detected specimens of *M. horridus* in two of the three shark samples. This species had previously been detected in blue sharks from other Atlantic and Mediterranean localities (online supplementary appendix S1), and can be told from other species of the genus by its sequence of 8–10 macrohooks at the base of the tentacles (Palm, 2004).

Little geographical signal emerged when we compared the tapeworm assemblages of Atlantic and Mediterranean blue shark samples. This would be at odds with recent evidence showing certain degree of potential isolation of Mediterranean blue shark populations (Leone *et al.*, 2017). First, there were not

obvious differences in species composition at component community level. Even if we assume that the specimen of *Scyphophyllidium* collected in Galicia actually is a ‘true’ member of the community, that is, *S. prionaci*, its absence in the Mediterranean samples could hardly result from a true biogeographical gap, since Euzet (1959) reported *S. prionaci* in other localities from the western Mediterranean with high prevalence. Second, the geographical comparison of species richness or diversity at infracommunity level failed to be significant. Admittedly, the power of tests was low because host sample sizes were small, but we did detect significant differences when looking at infection parameters of most cestode species. However, these individual differences do not show a consistent geographical pattern.

Sampling heterogeneity could have blurred any potential geographical signal. For instance, *M. horridus* exhibited the highest infections in the Valencia (S) sample, which contained the largest, and presumably oldest, blue shark specimens; infections were intermediate in Galicia, which included a combination of both juvenile and adult sharks; and this parasite did not appear in the Valencia (C) sample, which was composed only of juveniles. It is therefore tempting to suggest that the host size/age influenced the likelihood of infection with *M. horridus*. In fact, this parasite

has been reported as plerocercoid in the liver of large pelagic teleosts, including the sunfish, *Mola mola*, and swordfish, *Xiphias gladius* (e.g. Palm, 2004; Fernández *et al.*, 2016; Ahuir-Baraja *et al.*, 2017), which are prey of large blue sharks (e.g. Bornatowski & Schwingel, 2008; Pope *et al.*, 2010; Markaida & Sosa-Nishizaki, 2010) but that can hardly be consumed by juvenile sharks. Similar changes in parasite abundance (both positive and negative) with host length have been reported in other shark species and seem to be clearly linked to ontogenetic dietary shifts (Randhawa & Brickle, 2011).

In any event, inter-sampling heterogeneity in infection levels has not only been observed in this study, it is indeed a salient feature of our broad-scale geographical comparison. We observed that infracommunity species richness tended to be similar across localities, but infection levels of all cestode species showed significant, sometimes extreme variations. As expressed by Henderson *et al.* (2002), this variability seems inevitable because infection rates are determined by a multitude of biotic and abiotic factors. Of particular significance are the local differences in the diet of blue sharks (see, e.g. references in Markaida & Sosa-Nishizaki, 2010; Loo-Andrade *et al.*, 2017), and in the number of intermediate/paratenic hosts available. Cephalopods and teleosts are the key prey groups of blue sharks (Markaida & Sosa-Nishizaki, 2010; Hernández-Aguilar *et al.*, 2016; Córdova-Zavaleta *et al.*, 2018) and both types of prey have also been reported as hosts for larvae of *Anthobothrium* spp. (Dollfus, 1923; Jensen & Bullard, 2010; Schwerdt, 2015; Tedesco *et al.*, 2020); *Prosobothrium* spp. (Avdeeva, 1989; Williams & Bunkley-Williams, 1996; González & Kroeck, 2000); and *Scyphophyllidium* spp. (Gaevskaya & Schuhgalter, 1992; Schuhgalter, 1992; Jensen & Bullard, 2010). However, it is not possible to morphologically identify the larval stages to species level, except for the Trypanorhyncha (Palm, 2004; Palm & Caira, 2008) and, therefore, this precluded a quantitative assessment of the potential communities of intermediate/paratenic hosts at a local or even regional scale. In this context it is worth mentioning that as many as one-quarter of species for the Trypanorhyncha seem to use only one to two prey species as intermediate/paratenic hosts (Palm & Caira, 2008). Accordingly, local variation in the consumption of these prey can generate dramatic differences in the infection rates of the definitive host.

At a global geographical scale, tapeworm communities of blue sharks were composed of approximately ten cestode taxa, seven of which (those belonging to the Phyllobothriidea, Onchoproteocephalidea and 'Tetraphyllidea') are exclusive to this host species, corroborating the general pattern of specificity observed for these orders (Caira & Jensen, 2014). These exclusive species share two fundamental traits. First, they appear to have a cosmopolitan distribution as their host species. The only exception is the enigmatic *Phoreiobothrium* sp., which has apparently only been referred to in an article from the Mediterranean (Euzet, 1959). The species was identified as *P. lasium*, but re-examination of the specimens suggests that it is an exclusive species infecting blue sharks yet to be described (Euzet, 1959; Caira *et al.*, 2005). Second, all the cestode species unique to blue sharks belong to genera whose bulk diversity appears in carcharhinids with diverse ecologies.

These patterns would suggest that a group of cestode species has geographically accompanied the blue sharks with apparently little diversification (with perhaps the exception of *P. japonicum* in the Pacific Ocean). As noted above, blue sharks are highly migratory and exhibit limited genetic structure across populations sampled from disparate oceanic regions (Madigan *et al.*, 2021).

Accordingly, this pool of tapeworm species would potentially appear, in any sampling location, with greater or lesser prevalence and intensity, thus providing similarity to infracommunity composition and diversity, such as observed. The additional occurrence of trypanorhynchan cestodes in these communities would be less predictable depending on both the composition of the local elasmobranch community and the patterns of cestode exchange through the food web. Conversely, the quantitative differences in tapeworm faunas across localities would result from: (a) the variability of the local transmission rate of each cestode species (which, in part, would depend on the host diet and the density of intermediate/paratenic hosts); and (b) the mobility of blue sharks with respect to the life span of the parasites. This factor is important because satellite tracking data indicate that blue sharks can travel thousands of kilometres in a few months (Vandepierre *et al.*, 2014; Kai & Fujinami, 2020). Indeed, in the Atlantic Ocean, long-term tagging data indicate such an extensive range of movements that the whole population of blue sharks are considered as a single stock (Kohler & Turner, 2019). This suggests that parasites acquired in a specific region could be transported to very remote sampling areas, thus contributing, at first glance, to homogenize parasite assemblages. Nevertheless, the persistence of the carried parasites in these areas would depend on the local occurrence of appropriate intermediate hosts to guarantee the completion of life-cycles; otherwise, the parasites would gradually be lost (see, e.g. Torchin *et al.*, 2003; Diamant, 2010).

As a final remark it is interesting to note that, for the cestode order with a more broad-based pattern of host preference, that is, the Trypanorhyncha, there are two putative instances of host-switching, that is, *Molicola horridus* and *Nybelinia schmidtii*. Both species reproduce in two phylogenetically unrelated hosts, that is, the blue shark and the shortfin mako shark, two cosmopolitan species which share prey in a common oceanic habitat. It is interesting to put the overall specificity patterns of tapeworms from blue sharks in a broader context. In a recent study, Beer *et al.* (2019) found a substantial number of co-speciation events among tapeworm assemblages in skates, leading to narrow specificity to single host species. Indeed, this might be the case for the 'core' tapeworm species that have exclusively been reported in blue sharks; note, however, that the narrow specificity of many tapeworms from elasmobranchs does not necessarily imply strict co-speciation (Caira & Jensen, 2001). On the other hand, Beer *et al.* (2019) also detected that a combination of ecological factors (*inter alia*, host size and diet) could account for a non-negligible number of host-switching events in the skate-tapeworm associations they studied, similarly as noted here for *M. horridus* and *N. schmidtii* in blue sharks. Thus, a salient point that can be drawn from this evidence is that, for blue sharks, and probably other elasmobranchs, the influence of ecological factors upon their tapeworm communities is idiosyncratic and also constrained by historical factors, that is, the strong host specificity of most of their tapeworm species. Such 'Gleasonian' features could explain why only a few generalizations have been found on the ecological factors that provide structure to tapeworm communities of sharks (Randhawa & Poulin, 2010; Rasmussen & Randhawa, 2018).

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0022149X22000803>

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Ethics statement. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals, as samples were obtained from commercial captures or stranded animals.

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