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Parasite community of the pelagic thresher *Alopias pelagicus* (Lamniformes) as additional indicator of trophic network status and functioning

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The majority of marine parasites are trophically transmitted, exhibiting a complex life cycle, thus, parasite communities investigation is a valuable source of information on trophic network status. Parasite communities of sharks, which have high structural importance within trophic webs, might well be included among bioindicators of trophic network functioning. Here, we present the first study on parasite communities of the pelagic thresher *Alopias pelagicus*, in the eastern Pacific, a highly biodiverse area, subject to the threat of overfishing. Results indicated that the parasite community exhibited greater richness, abundance, and diversity compared to those reported in other shark species and locations, suggesting that the trophic network in the area may still be resilient to anthropogenic pressures. Differences found among sex, individuals of different size, and across sampling sites with different maximum depths confirmed that both biotic and abiotic factors influence parasite communities, which are known to be sensitive to such variables. Our findings supported the use of parasite communities in high trophic level predators as reliable and effective indicators of the trophic network status, advocating for their inclusion as an additional tool in biodiversity conservation.

Keywords Bioindicators, Eastern Pacific, Sharks, Helminths, Parasite community, Trophic network stability

Parasites represent one of the most successful modes of life in nature[1]; they are ubiquitous, comprise a significant proportion of world biodiversity and biomass[2,3]. They play an essential role in nature, as every ecosystem contains parasites, and virtually every metazoan hosts at least one parasite species[1]. Despite their ubiquity and abundance, the diversity of parasites is poorly known and underappreciated[1,4]. The parasite community in/on a specific host population is a highly complex and dynamic system, affected by biotic (host-related) and abiotic (related to host habitat) factors[5]. Elucidating the composition and structure of parasite communities can help to reveal ecological traits of the host and to understand the dynamic of infection of unknown or poorly known parasite species and the ecology of intermediate and final hosts[4,6,7].

In the marine realm, the majority of parasites are trophically transmitted (i.e. through feeding or predation) and have complex life cycles. They require a number of either invertebrate or vertebrate obligate intermediate hosts (and sometimes facultative paratenic, namely transport hosts), harboring only larval stages and a definitive vertebrate host to reach their adult stage[4]. The incorporation of parasite communities in the study of marine food webs is thus essential to understand predator–prey trophic interactions[7]. For example, the gastrointestinal helminth community may be used to provide information on trophic interactions and ontogenetic and seasonal shifts in host diet[4,6]. Furthermore, the study of parasite communities in marine ecosystems provides information on biodiversity and trophic network, as well as about health and/or deterioration of those ecosystems[7,8]. Perturbations in ecosystem structure and function affect trophic networks, which in turn influence parasite

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transmission dynamics, altering the composition and abundance of both host and parasite communities[9–13]. Generally, degraded habitats support fewer hosts and impoverished parasite communities, whereas stable habitats tend to support more hosts and richer parasite assemblages[9–13].

Sharks, being apical predators, have long been recognized of high structural importance within the marine ecosystem, and consequently in trophic webs[14]. Hence, parasite communities of sharks might well be included among the indicators of biodiversity, trophic network structure, status and health[5,10]. Despite their importance, studies thoroughly investigating parasite communities in ecologically important elasmobranch apical predator species are scarce, often limited to a specific taxonomic group infecting the gastrointestinal system (e.g. cestodes), or lacking relevant richness/diversity descriptors, crucial for evaluating communities and making temporal and spatial comparisons (sensu[15]).

The tropical eastern Pacific is an oceanic area with high primary production rates, sustaining every trophic level, up to apical predators. In particular, off the Pacific coast of Costa Rica, upwelling events periodically occur, forming a highly dynamic dome-like thermocline during the summer, named Costa Rica Thermal Dome[16,17]. Nutrient and oxygen distribution in this area is mainly determined by the localized upwelling of nutrient-rich, oxygen-poor water[17,18]. These oceanographic phenomena influencing the production of chlorophyll *a*, and consequently supporting a high zooplankton biomass, affect abundance and distribution of all marine organisms at higher trophic levels, including several apical predators[16,17].

Herein, we reported the first study on the parasite community of the pelagic thresher *Alopias pelagicus* (Lamniformes), an oceanic and tropical species restricted to the Indian and Pacific Ocean[19], listed as Endangered, with a decreasing population trend[20]. We focused on a population from the eastern Pacific, in an area off the coast of Costa Rica, rich in marine biodiversity and subjected to high fishing pressures[21,22]. In particular, the study aimed to: (i) investigate the parasite community structure in the pelagic thresher; (ii) explore the influence of some biotic and abiotic factors in shaping descriptors of parasite community; and (iii) discuss the use of parasite communities as potential indicators of trophic networks status at a larger scale.

Materials and methods

Sample collection

A total of 32 pelagic threshers were collected between June and October 2022 from off the Pacific coast of Costa Rica (Fig. 1). Pelagic threshers constituted the bycatch of commercial longline fisheries operating in the eastern Pacific Ocean. They were provided by the professional fishermen at the landing in Puntarenas or Cuajiniquil (Guanacaste). The samples were delivered to Incopesca based on the Incopesca Board of Directors Agreement AJDIP/309–2020. The samples were studied under the frame of a project (Resolution n. 384 of the Institutional Biodiversity Commission of the University of Costa Rica and permit n. ACG 019-2023) between Incopesca, the Universidad de Costa Rica, and the Stazione Zoologica Anton Dohrn.

Upon landing, sharks were sexed, measured (total length, TL), and weighed before (total weight, TW) and after evisceration (eviscerated weight, EW). Skin was visually inspected for macroscopic ecto-parasites, immediately after, head with the gills, heart, liver, gonads, and gastrointestinal tract were frozen (−20 °C)

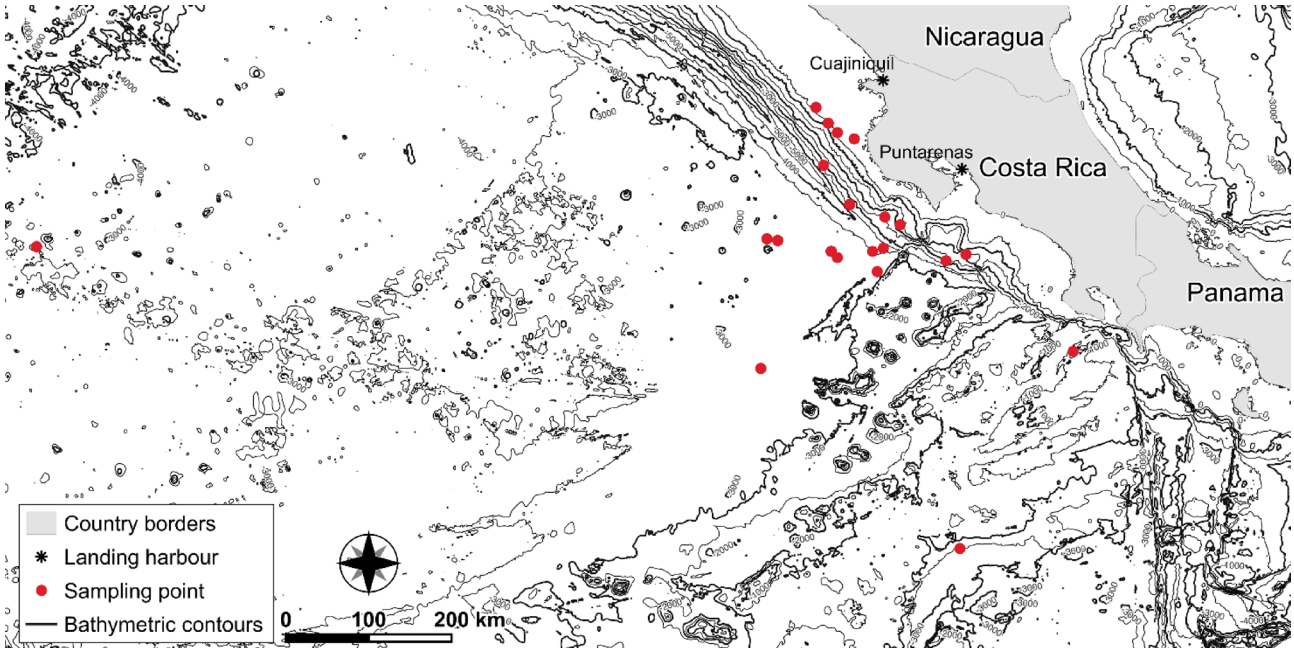

Fig. 1. Map of the Pacific Ocean area off Costa Rica coast where the pelagic threshers were sampled (21 unique sampling points, multiple sharks were caught in 16 points). Bathymetric values (GEBCO, 2024) are shown together with sampling point coordinates, as recorded by the fishing vessels, and landing harbors (Puntarenas and Cuajiniquil).

individually in plastic bags until the analysis. Body condition index (BCI) was calculated as described by Le Cren[23] and discretized for statistical analyses. For each shark, GPS coordinates of fishing sites were provided, and the bathymetry of the sampling point was estimated through the GEBCO gridded bathymetric data[24] using QGIS 3.34.7[25]. Bathymetric values were subdivided in three categories (1: less than 1000 m depth; 2: between 1000 and 2000 m depth; 3: greater than 2000 m depth).

Parasitological analysis

After thawing, each organ was cut and the surfaces examined under a dissecting microscope (Axio Zoom V16, Zeiss, Switzerland). Then, each organ was individually washed in a basin and the washed material was sieved through an 88-µm mesh screen. The obtained washed material from each organ was examined under a dissecting microscope, and, when present, parasites were collected and counted[13,26].

For identification, crustaceans were clarified in 20% potassium hydroxide, and acanthocephalans, cestodes and trematodes were stained with Mayer's acid carmine, dehydrated through a graded ethanol series, cleared in methyl salicylate and mounted in permanent slides in Canada balsam[27]. Parasites were studied by light microscope and identified according to the available morphological identification keys. Larvae of ascaridoid nematodes that could not be identified to species level by morphological characters were treated as follows. Their anterior and posterior extremities were clarified in Amman's lactophenol, and identified to lower possible taxonomic level according to Berland[28] using a light microscope. A fragment of parasites' body of selected cestodes, for which morphological characterization at species level resulted problematic, together with ascaridoid larvae, were analyzed molecularly for species identification.

Molecular characterization of parasites morphologically unidentifiable at species level

Genomic DNA of selected samples, i.e. morphologically uncharacterized at species level, was extracted using Quick-gDNA Miniprep Kit (Zymo Research, USA) following the standard manufacturer-recommended protocol.

For ascaridoid larvae characterization, the ITS (Internal Transcribed Spacer) region of rDNA, including first internal transcribed spacer (ITS-1), the 5.8 S gene, the second transcribed spacer (ITS-2), and ~70 nucleotides of the 28 S gene, was amplified with the primers NC5 (forward; 5′-GTA GGT GAA CCT GCG GAA GGA TCA TT-3′) and NC2 (reverse; 5′-TTA GTT TCT TTT CCT CCG CT-3′)[29]. Polymerase chain reactions (PCRs) were carried out in a 25 µL volume containing 0.5 µL of each primer 10 mM, 3 µL of MgCl2 25 mM (Promega, USA), 5 µL of 5× buffer (Promega), 0.5 µL of DMSO 0.3 mM, 0.5 µL of dNTPs 10 mM (Promega), 0.3 µL of Go-Taq Polymerase (5 U/µL) (Promega), and 2 µL of total DNA. PCR temperature conditions were the following: 94 °C for 5 min (initial denaturation), followed by 30 cycles at 94 °C for 30 s (denaturation), 55 °C for 30 s (annealing), 72 °C for 30 s (extension), followed by post-amplification at 72 °C for 5 min.

A region of the LSU rRNA gene was amplified to characterize cestodes that were not morphologically identified at species level. According to Caira et al.[30,31], primers used for members of the family Litobothriidae were two sets, amplifying partially overlapping regions: - LSU5 (forward; 5′-TAG GTC GAC CCG CTG AAY TTA AGC A-3′) and ECD2 (reverse; 5′-CTT GGT CCG TGT TTC AAG ACG GG-3′); – 300 F (forward; 5′-CAA GTA CCG TGA GGG AAA GTT G-3′) and 1500R (reverse; 5′-GCT ATC CTG GAG GGA AAC TTC G-3′). In addition to these, for Phyllobothriidae members, additional primers targeting the same region were used, in combination, when amplification was not satisfactory: LSU55F (forward; 5′-AAC CAG GAT TCC CCT AGT AAC GGC-3′); ZX-1 (forward; 5′-ACC CGC TGA ATT TAA GCA TAT-3′); 1200R (reverse; 5′-GCA TAG TTC ACC ATC TTT CGG-3′)[31–33]. PCRs reactions, total volume of 25 µL, consisted of 0.6 µL of each primer 10 mM, 2 µL of MgCl2 25 mM (Promega), 5 µL of 5× buffer (Promega), 0.6 µL of dNTPs 10 mM (Promega), 0.2 µL of Go-Taq Polymerase (5 U/µL) (Promega), and 2 µL of total DNA. Thermocycling conditions followed those reported in Caira et al.[31] and Tkach et al.[34].

Successful PCR products were purified using Agencourt AMPure XP (Beckman Coulter, USA), following the standard manufacturer-recommended protocol. Clean PCR products were Sanger sequenced from both strands, utilizing all the selected primers, through an Automated Capillary Electrophoresis Sequencer 3730 DNA Analyzer (Applied Biosystems, USA) using the BigDye® Terminator v3.1 Cycle Sequencing Kit (Life Technologies, USA). The obtained contiguous sequences were assembled and edited using MEGAX v11[35]. Sequence identity was checked using BLASTn[36]. In case of uncertain species assignation, genetic distance among generated sequences and available data from GenBank was estimated with MEGAX v11[35].

Descriptors of parasite community

A component community comprised all parasite species recovered from the entire sample of pelagic thresher, while infracommunity referred to the parasites assemblage in one host individual[37]. Quantitative analyses were carried out at both component community and infracommunity level. The parasite species accumulation curve was constructed using the *vegan* package[38] in R[39]. Prevalence was defined as the number of hosts infected with one or more individuals of a parasite species. Abundance was measured as the number of individuals of a particular parasite species in/on a single host regardless of whether or not the host was infected[40]. Mean abundance was measured as the number of individuals of a particular parasite in the entire sample of the pelagic thresher divided by the total number of hosts examined (including both infected and uninfected hosts). Mean intensity was measured as the number of individuals of a particular parasite in the entire sample of the pelagic thresher divided by the total number of infected hosts.

Species richness, total mean abundance, Berger-Parker dominance index, and Brillouin index of diversity were used as overall descriptors of infracommunities. Total mean abundance was measured as the mean number of individuals of all parasite species, while species richness as the number of parasite species harbored by each shark specimen. To compare the present metrics to those retrieved from literature, we estimated them

for each of the following groups: full parasite community (ecto- and endo-parasites), full parasite community aggregated by taxonomic class, helminths (larvae and adult helminths), adult helminths (only adult endo-parasites), gastrointestinal helminths (larvae and adult endo-parasites found in the stomach and intestine), adult gastrointestinal helminths (only adult endo-parasites found in the stomach and intestine), and adult intestinal helminths (only adult cestodes found in the intestine). Similarly, to compare present data with the available literature on shark parasite communities, Simpson's evenness index and Bray & Curtis dissimilarity index were also calculated. All calculations were performed in R[39]; species richness, Berger-Parker, Brillouin and Simpson's evenness index were estimated using the package *tabula*[41].

According to the host specificity, parasite species were classified as specialists, defined narrowly as having the bulk of reproducing adults found only in a single host species or having been reported from a single host species, and generalists, when reported from a variety of related host species[42].

Statistical analyses

The Mann–Whitney–Wilcoxon Test or the Kruskal–Wallis H-test (depending on the numbers of levels) was performed to investigate whether descriptors of the parasite community (i.e. species richness, total mean abundance, Berger-Parker dominance index, Brillouin index, Simpson's evenness index) differed among individuals of different sex, BCI, and maximum depth of fishing coordinates; this was tested by species, and by groups (full parasite community aggregated by class, helminths, adult helminths, gastrointestinal helminths, adult gastrointestinal helminths, and adult intestinal helminths, see "Descriptors of parasite community" section for details). When significant results were observed, post-hoc analysis was performed using the Dunn test implemented in the *FSA* R package[43], to determine which levels of the independent variable differ from each other level. Potential relationships between total body length, total weight, BCI, sex, maximum depth of fishing coordinates and parasite species richness and abundance were explored using the Spearman correlation coefficient. This correlation approach was also used to investigate potential relationships among parasite taxa. Non-parametric testing was chosen to account for the non-normality of data, specific feature of parasite data, which are skewed count data[44]. All statistical analyses were performed in R[39]. The effects of sex, BCI and depth were further investigated using non-metric multidimensional scaling (nMDS), based on Bray & Curtis dissimilarity indices of non-transformed numbers of parasites, analyzed by species and aggregated by groups (full parasite community aggregated by class, helminths, adult helminths, gastrointestinal helminths, adult gastrointestinal helminths, and adult intestinal helminths, see "Descriptors of parasite community" section for details), implemented with the function *metaMDS* included in the *vegan* R package[38].

Literature review on shark parasite communities

A systematic literature review regarding the investigation of parasite communities in sharks was conducted to compare descriptors of parasite communities. Relevant databases were identified and selected: PubMed, Web of Science, Embase, Scopus, and Google Scholar. Search strings were created based on a priori knowledge about the topic and the review question (Table S1); search was performed in June 2024. Results were analyzed in R[39] with the *revtools* package[45]. Only published papers including at least two among the desired descriptors (species richness, heterogeneity/dominance, evenness, similarity/dissimilarity) were included in the final data set for comparison purposes (Table S2). Estimations performed on subsets of data not comparable with ours were discarded, as well as studies including lower than 10 individual hosts examined (Table S2).

Results

Component community

Biometrical data of the pelagic threshers used in the present study are listed in Table 1; according to data distribution, BCI discrete categories were: 1 = lower than 0.0024; 2 = between 0.0024 and 0.0027; 3 = greater than 0.0027. Biometrical data and information regarding sampling points were available for 27 out of 32 individual pelagic threshers.

All hosts were infected with at least one parasite; a total of 74894 individual parasites belonging to 24 taxa were identified, comprising four copepods (ecto-parasites) and 20 helminths (endo-parasites). The parasite species accumulation curve (Fig. 2) showed that the sample size was sufficient to evaluate quantitative characteristics of the infection at component, as well as the infracommunity level. Prevalence, abundance, and intensity of all parasite species, together with their degree of host specialization, location and stage are reported in Table 2.

A total of 6461 parasite individuals were ecto-parasites found on gills, except 13 individuals of *Echthrogaleus denticulatus* (Pandaridae) found on the skin. Ecto-parasites accounted for 8.6% of all parasites recorded. The

Host variables	Pelagic thresher ($n = 32$)
Sex	16 F, 9 M (7 unknown)
Total length (cm)	254.94 ± 18.40 (222–300)
Total weight (kg)	41.15 ± 8.32 (22.0–58.4)
Eviscerated weight (kg)	37.08 ± 6.75 (26.5–53.2)
BCI	0.0025 ± 0.0003 (0.0022–0.0035)

Table 1. Average values (± standard deviation and range in brackets) of morphological and physiological variables of the pelagic thresher examined for parasites. M, male; F, female; BCI, body condition index.

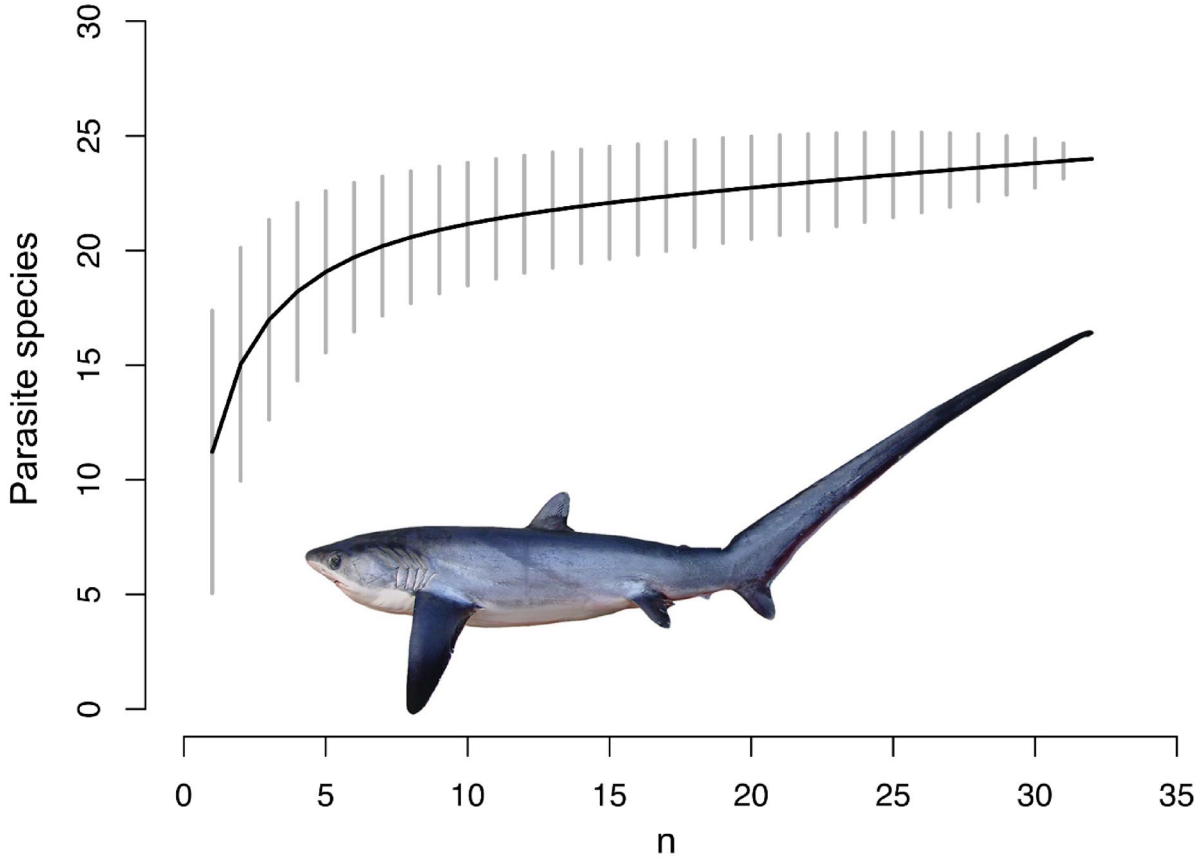

Fig. 2. Parasite species accumulation curve for the pelagic threshers analyzed in this study ($n = 32$). Grey bars: 95% confidence interval. The pelagic thresher silhouette is taken from https://fishider.org/.

most prevalent and abundant ecto-parasite was *Bariaka alopiae* (Eudactylinidae) representing 98.5% of all ecto-parasites.

A total of 68433 individuals were endo-parasites, accounting for 91.4% of all parasites. All endo-parasites were collected from the gastrointestinal tract, with the exception of 30 individuals of *Paronatrema davidbowiei* (Trematoda: Syncoeliidae) found on gills and into the aorta. The most abundant endo-parasites were cestodes, representing 99.8% of all endo-parasites, followed by the acanthocephalans (0.05%), nematodes (0.04%), and trematodes (0.04%). We identified 12 species of cestodes comprising two Trypanorhyncha (both from stomach), six Litobothriidea (from intestine) and four Phyllobothriidea (from intestine). The most abundant order of cestodes was Phyllobothriidea (with four putative species of *Scyphophyllidium*) followed by Litobothriidea, and finally Trypanorhyncha accounting for 65.0%, 34.6% and 0.3% of all cestodes recovered, respectively. Cestodes and trematodes were all adult stages, while acanthocephalans and nematodes were all larval stages, except an adult individual of *Piscicapillaria* sp. (Nematoda: Capillariidae).

Species of *Scyphophyllidium* well agreed with the diagnostic morphological features of the genus as amended by Caira et al.[32], as confirmed by the BLAST matches. Two of these were assigned to the morphological category 1 of its genus because they had globose bothridia, each with a proximal aperture. The other two species were assigned to the morphological category 8 of *Scyphophyllidium* because they had flat, unmodified bothridia, the surfaces of which have yet to be characterized using SEM. However, three of these taxa did not resemble any of the described species of the genus, so they were temporarily identified as *Scyphophyllidium* cat. 1 sp. 1, *Scyphophyllidium* cat. 8 sp. 1, and *Scyphophyllidium* cat. 8 sp. 2, respectively. One of the two species in morphological category 1 revealed 99.73% identity with the sequence of *Scyphophyllidium* sp. 6 (KF685771) sensu Caira et al.[32] and was considered conspecific. The newly obtained sequence was deposited in GenBank under the accession number PQ404916 (1421 bp). The other three *Scyphophyllidium* spp. returned the following BLAST matches: *Scyphophyllidium* cat. 1 sp. 1 97.73% identity with *Scyphophyllidium* sp. 6 (KF685771 – sensu[32]); *Scyphophyllidium* cat. 8 sp. 1 94.16% identity with *Scyphophyllidium bullardi* (GQ470001[33]); and *Scyphophyllidium* cat. 8 sp. 2 87.89% identity with *Scyphophyllidium* sp. 6 (KF685771 – sensu[32]), confirming that they were three distinct entities. Thus, the three newly obtained sequences were deposited in GenBank under the accession numbers PQ412549 (*Scyphophyllidium* cat. 1 sp. 1 – 1436 bp), PQ408639 (*Scyphophyllidium* cat. 8 sp. 1 – 1018 bp), and PQ412546 (*Scyphophyllidium* cat. 8 sp. 2 – 1208 bp). Distinctiveness of these *Scyphophyllidium*

Parasite	P(%)	Ab	In	Location in host	Parasite stage
Copepoda					
Bariaka alopiae	65.6	199.06 ± 221.27 (0–701)	303.33 ± 206.59 (5–701)	Gills	a
Echthrogaleus denticulatus	28.1	0.41 ± 0.71 (0–2)	1.44 ± 0.53 (1–2)	Skin	a
Gangliopus pyriformis	34.4	1.09 ± 2.32 (0–8)	3.18 ± 3.06 (1–8)	Gills	a
Pandarus sp.	18.7	1.34 ± 3.89 (0–17)	7.17 ± 6.62 (1–17)	Gills	a
Trematoda					
Elytrophallus mexicanus	6.2	0.09 ± 0.39 (0–2)	1.50 ± 0.71 (1–2)	Stomach	a
Paronatrema davidbowiei[§]	21.9	0.94 ± 2.84 (0–15)	4.29 ± 4.99 (1–15)	Gills, visceral cavity	a
Cestoda					
Litobothrium aenigmaticum[§]	78.1	45.41 ± 77.22 (0–302)	58.12 ± 83.26 (1–302)	Intestine	a
L. amplifica	96.9	393.44 ± 731.69 (0–4128)	406.13 ± 740.19 (4–4128)	Intestine	a
L. janovji	84.4	262.72 ± 674.41 (0–3528)	311.37 ± 725.65 (2–3528)	Intestine	a
L. nickoli[§]	40.6	10.12 ± 38.42 (0–216)	24.92 ± 58.42 (3–216)	Intestine	a
Litobothrium sp. 1	65.6	27.34 ± 38.47 (0–172)	41.67 ± 40.84 (1–172)	Intestine	a
Litobothrium sp. 2	34.4	1.28 ± 2.77 (0–12)	3.73 ± 3.72 (1–12)	Intestine	a
Heterosphyriocephalus encarnae[§]	75.0	5.09 ± 5.6 (0–19)	6.79 ± 5.50 (2–19)	Stomach	a
Nybelinia africana	40.6	1.91 ± 3.49 (0–17)	4.69 ± 4.15 (2–17)	Stomach	a
Scyphophyllidium cat. 8 sp. 1	81.2	186.69 ± 313.82 (0–1632)	229.77 ± 334.40 (4–1632)	Intestine	a
Scyphophyllidium cat. 8 sp. 2	78.1	552.62 ± 791.53 (0–2940)	707.36 ± 833.81 (8–2940)	Intestine	a
Scyphophyllidium cat. 1 sp. 1	87.5	442.31 ± 490.95 (0–1946)	505.50 ± 493.58 (48–1946)	Intestine	a
Scyphophyllidium sp. 6 (sensu Caira et al.[32])	87.5	206.53 ± 325.88 (0–1637)	236.04 ± 338.68 (6–1637)	Intestine	a
Acanthocephala					
Bolbosoma turbinella	43.7	1.09 ± 1.65 (0–6)	2.50 ± 1.65 (1–6)	Stomach	l
Nematoda					
Anisakis brevispiculata	3.1	0.03 ± 0.18 (0–1)	1.00 (1–1)	Stomach	l
Anisakis typica sp. A	28.1	0.50 ± 0.98 (0–4)	1.78 ± 1.09 (1–4)	Stomach	l
Anisakis ziphidarum	3.1	0.03 ± 0.18 (0–1)	1.00 (1–1)	Stomach	l
Lappetascaris sp.	15.6	0.34 ± 0.87 (0–3)	2.20 ± 0.84 (1–3)	Stomach	l
Piscicapillaria sp.	3.1	0.03 ± 0.18 (0–1)	1.00 (1–1)	Stomach	a

Table 2. Metazoan parasites of the pelagic thresher from the Pacific Coast of Costa rica. Prevalence (P) is expressed as percentage; mean abundance (Ab) and mean intensity (In) of infection are expressed as mean ± standard deviation followed by range in brackets. a, adult stage; l, larval stage. [§]: specialist parasite species[54].

spp. was supported by the analysis of genetic distance (Table S3; all the sequences used in the analysis are listed in Table S5).

Similarly, of the three Litobothriidae, two *Litobothrium* species did not resemble any of the described species of the genus, so they were identified as *Litobothrium* sp. 1 and *Litobothrium* sp. 2. The sequences, of length 1402 bp and 1060 bp, respectively, were deposited in GenBank under the accession numbers PQ408638 and PQ408640. The last was identified as *L. aenigmaticum* (GenBank accession number PQ412945 – 1285 bp), validated by both morphological and molecular characterization (100% identity with *L. aenigmaticum* – KJ101600). Molecular analysis confirmed the two unknown species belonged to the assigned genus; BLAST results revealed 99.2% identity of *Litobothrium* sp. 1 with *L. aenigmaticum* (KJ101600), while *Litobothrium* sp. 2 showed 95.47% identity with *L. amplificum* (KF685906). Although the high identity percentage, *Litobothrium* sp. 1 was not considered the same as *L. aenigmaticum*, but a different species, on the basis of the analysis of genetic distance (Table S4; all the sequences used in the analysis are listed in Table S5). In general, p-distance and nucleotide differences were low among *Litobothrium* congeners, and *Litobothrium* sp. 1 presented a difference with *L. aenigmaticum* comparable with other undoubtedly different species (Table S4).

Among nematodes, a single damaged female specimen (not suitable for identification at species level) of *Piscicapillaria* was found. A total of 26 larvae of ascaridoids were found and molecularly characterized according to the obtained sequences as *Lappetascaris* sp. ($n = 10$), *Anisakis typica* sp. A ($n = 14$), *A. ziphidarum* ($n = 1$) and *Skrjabinisakis brevispiculata* ($n = 1$). In GenBank, these showed 100% identity with previously deposited sequences (accession numbers: MW697755, OP101843, JQ912691 and JQ912694, respectively). The newly obtained sequences were deposited in GenBank under the accession numbers PQ436342 (*Lappetascaris* sp. – 850 bp), PQ436341 (*A. typica* – 911 bp), PQ436340 (*A. ziphidarum* – 888 bp) and PQ436343 (*S. brevispiculata* – 853 bp).

Infracommunity

Descriptors of infracommunity for each of the groups considered are listed in Table 3. When considered the whole parasite community, the species richness ranged from 2 to 18 with the minimum and maximum number of parasite species observed in a single individual each. Most pelagic threshers (eight individuals) were infected with 11 parasite species, while, when considering only intestinal community, the species richness ranged from 2 to 10. The total mean abundance varied slightly ranging from 2340.44 (in the whole parasite community) to 2128.47 (in the intestinal community) (Table 3).

Brillouin index ranged from 2.02 in the full community to 1.85 when only adult intestinal helminths were considered; while Berger-Parker index value was 0.24 in the full community and 0.26 for each of the other groups (Table 3). Lowest and greatest evenness values were 0.27 (full community) and 0.56 (adult intestinal helminths), respectively. The degree of dissimilarity between hosts was highest in the full community (Bray & Curtis value of 0.52), while decreased in the other groups considered (Table 3).

Statistical analyses

Considering all adult helminths, the Kruskal–Wallis H-test showed that parasite community in female hosts had significantly lower values of Berger–Parker index ($H = 4.87$, $df = 1$, $p = 0.03$), i.e. more diverse communities (Fig. 3a); in addition, significant differences in Simpson's evenness values were observed among adult helminth communities from hosts sampled in areas of different depths ($H = 7.86$, $df = 2$, $p = 0.02$), with hosts from the shallowest and deepest areas having more even helminth communities (Fig. 3b). Post-hoc comparison indicated that the median evenness for the shallowest depth category was significantly different compared to the medium depth category; however, evenness of the communities from hosts sampled at lowest depth did not significantly differ from the first. These trends were also identified in the gastrointestinal helminth community subset (either only adults, or with the addition of larval forms): female hosts had significantly more even parasite communities (lower Berger–Parker index: $H = 4.88$, $df = 1$, $p = 0.03$); similarly, hosts from the shallowest and deepest areas had more even gastrointestinal helminth communities (lower Simpson's evenness: $H = 6.50$, $df = 2$, $p = 0.04$). Among all correlations, only parasite overall community evenness (Simpson's evenness index) and hosts' total length ($\rho\,(27) = 0.488$, $p = 0.05$) were significantly correlated in a positive direction (Fig. 3c).

nMDS analyses showed that parasite communities from hosts sampled in areas with different bathymetric values were different, although the clusters showed widely overlapping 95% confidence intervals (Fig. 4). There was no obvious clustering due to sex or BCI. This was observed when data were analyzed by species (stress = 0.149) (Fig. 4a), or by group (e.g. helminths: stress = 0.138; adult intestinal helminths: stress = 0.137), and especially when analysis was performed with parasite data aggregated by taxonomic class (stress = 0.044) (Fig. 4b).

Literature review on shark parasite communities

Nine studies, including the present, were included in Table 4 to compare descriptors of parasite communities of sharks. No other study considered the present species, and only an additional one was carried out in the Pacific Ocean, although in a different area. Among studies found in literature, three considered only adult intestinal parasites, and estimated only two descriptors. Nevertheless, the maximum number of indexes calculated was four, with no other than present study estimating the Bray & Curtis index. The geographic distribution of the studies was mainly restricted to the Western Mediterranean Sea and the species most frequently investigated were: *Etmopterus spinax*, *Galeus melastomus*, *Prionace glauca*, and *Scyliorhinus canicula*. Our results showed almost a tenfold difference regarding mean species richness, and remarkably lower Berger–Parker index values. Brillouin index, which was the only index estimated in all studies found in literature (together with mean species richness), ranged from 0.02 in the *G. melastomus* from the Gulf of Naples[13] to 0.74 in *Mustelus schmitti* from the Atlantic Ocean off the coast of northern Argentina[46], while the pelagic thresher parasite community presented much higher values. Only Espínola-Novelo et al.[47] reported evenness estimation and their values were in the same range as the present study.

Descriptors	Fpc	H	Ah	Gih	Agih	Aih
Mta	2340.44 ± 2217.49 (124-10307)	2138.53 ± 2146.36 (124–9654)	2136.53 ± 2145.46 (124–9645)	2137.59 ± 2146.44 (124–9654)	2135.59 ± 2145.53 (124–9645)	2128.47 ± 2145.61 (124–9635)
Species Richness	11.21 ± 3.13 (2–18)	9.75 ± 2.67 (2–15)	8.81 ± 2.64 (2–12)	9.53 ± 2.85 (2–16)	8.59 ± 2.30 (2–12)	7.34 ± 2.13 (2–10)
Brillouin	2.02	1.88	1.87	1.88	1.88	1.85
Berger-Parker	0.24	0.26	0.26	0.26	0.26	0.26
Simpson's evenness	0.27	0.28	0.38	0.30	0.30	0.56
Bray & Curtis	0.52	0.33	0.33	0.33	0.33	0.34

Table 3. Average values (± standard deviation) and range (values in brackets) of mean total abundance (Mta) of parasite infracommunities found in pelagic thresher ($n = 32$), and estimated descriptors of parasite community. Full parasite community (Fpc): ecto- and endo-parasites; helminths (H): larvae and adult helminths; adult helminths (Ah): only adult endo-parasites; gastrointestinal helminths (Gih): larvae and adult endoparasites located in the stomach and intestine; adult gastrointestinal helminths (Agih): only adult endo-parasites located in the stomach and intestine; adult intestinal helminths (Aih): only adult cestodes located in the intestine.

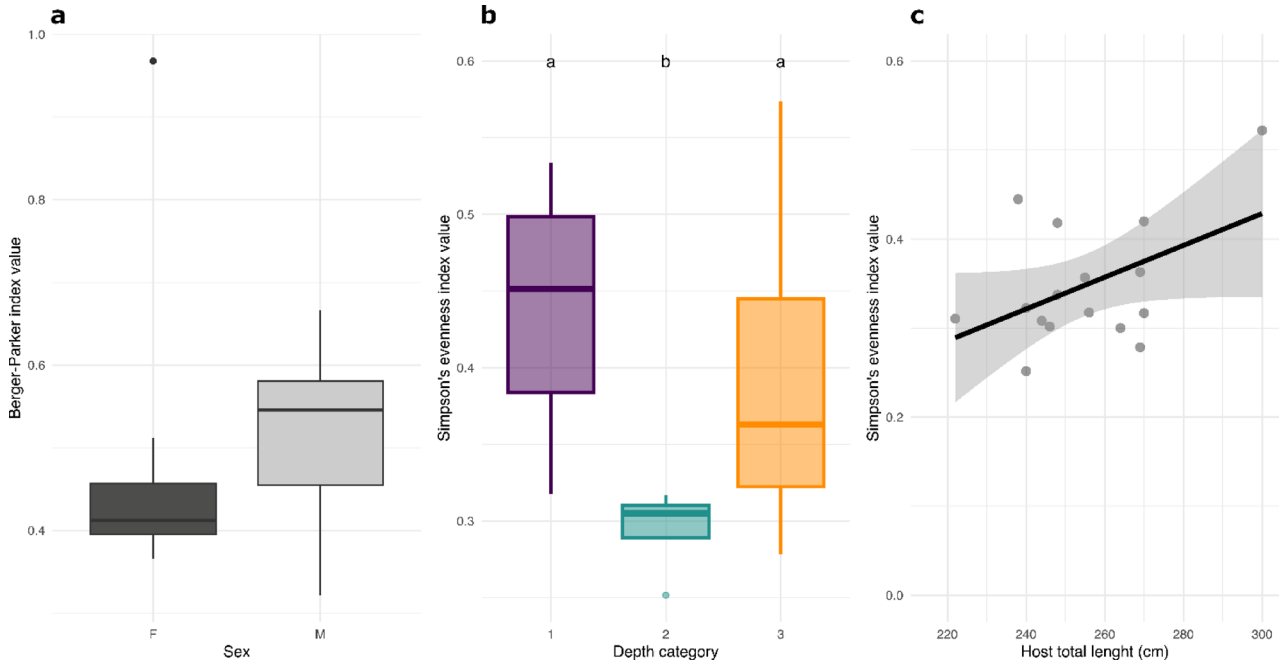

Fig. 3. Box and whisker plots showing differences of Berger–Parker (**a**) and Simpson's evenness index (**b**) between sexes (F: female; M: male) and the three maximum depth of fishing coordinates categories, respectively. Lower and upper box boundaries are 25th and 75th percentiles, respectively; line inside box is the median; lower and upper error lines are 10th and 90th percentiles, respectively; filled circles show data falling outside 10th and 90th percentiles. Analyses performed on adult helminths only. Lowercase letters on top of each box represent results of post-hoc analysis. (**c**) Scatterplot showing values of pelagic thresher individual lengths and correspondent Simpson's evenness index values of parasite community. Smoother is fitted through ranked data (Spearman rank correlation: $\rho\,(27) = 0.488$, $p = 0.05$); 95% confidence intervals.

Discussion

The present study revealed an unexpectedly rich component community comprising 24 taxa, including four ecto- and 20 endo-parasites. With the exception of ecto-parasites (all copepods with direct life cycle), the other taxa were all trophically transmitted helminths with a complex life cycle. The pelagic thresher serves as a definitive host for at least 14 endo-parasites (12 cestodes, the trematode *Paronatrema davidbowiei* and the nematode *Piscicapillaria* sp.), while the acanthocephalan *Bolbosoma turbinella*, the trematode *Elytrophallus mexicanus*, and the ascaridoid nematodes *Anisakis* spp., and *Lappetascaris* sp. should be considered as accidental findings. Indeed, *Bolbosoma* and *Anisakis* species mature only in marine mammals [48],[49], whereas adult forms of *Lappetascaris* spp. and *E. mexicanus* are known only from pelagic teleost fishes[50]. Likely, all these accidental parasites were acquired through the ingestion of squids and Scombridae fishes. Indeed, these prey items that represent the natural intermediate hosts of these parasites were largely observed in the gastric content of the present sharks during dissections. Although these taxa were accidental, their finding in the pelagic thresher revealed, for the first time, the occurrence of these parasites, and evidence of their life cycle, in Pacific waters of Costa Rica.

The parasite community of the pelagic thresher was unquestionably dominated by adult cestodes (99.8% of sampled endo-parasites, and 91.2% of all parasites), with *Scyphophyllidium* spp. (Phyllobothriidea) numerically dominating the assemblages. Recorded cestode taxa belonged to three distinct orders, which are typically found in the gastrointestinal tract of Carcharhiniformes and Lamniformes: Litobothriidea (six spp.), Phyllobothriidea (four spp.) and Trypanorhyncha (two spp.). The life cycle of the members of these three orders is currently unknown, although some assumptions can be made to understand the presumed infection routes.

For Litobothriidea, it has been proposed that life cycle might include two or three intermediate hosts, and possibly some paratenic ones[51]. Currently, Litobothriidea (all belonging to the genus *Litobothrium*) comprises nine species parasitizing the spiral valve of four species of lamniform sharks within the families Alopiidae, Mitsukurinidae, and Odontaspididae[51,52]. The *Litobothrium* spp. recorded here included four known species (i.e. *L. aenigmaticum*, *L. amplificum*, *L. janovii*, and *L. nickoli*), previously detected in the same host from Indo-Pacific area, and two unidentified species (named here *Litobothrium* sp. 1 and *Litobothrium* sp. 2). The latter two did not morphologically resemble any other species in this genus; additionally, molecular analyses unequivocally assigned both taxa to the *Litobothrium* genus. Thus, most likely both represented yet undescribed species.

Phyllobothriidea comprises parasites of the spiral valve of sharks and, occasionally, of rays. A three-host life cycle has been proposed for members of this order, with copepods acting as first, and cephalopods (mostly squids) and fish as second intermediate and/or paratenic hosts[32]. All members of this order collected here well agreed with the diagnostic morphological features of the genus *Scyphophyllidium*[32]. However, both

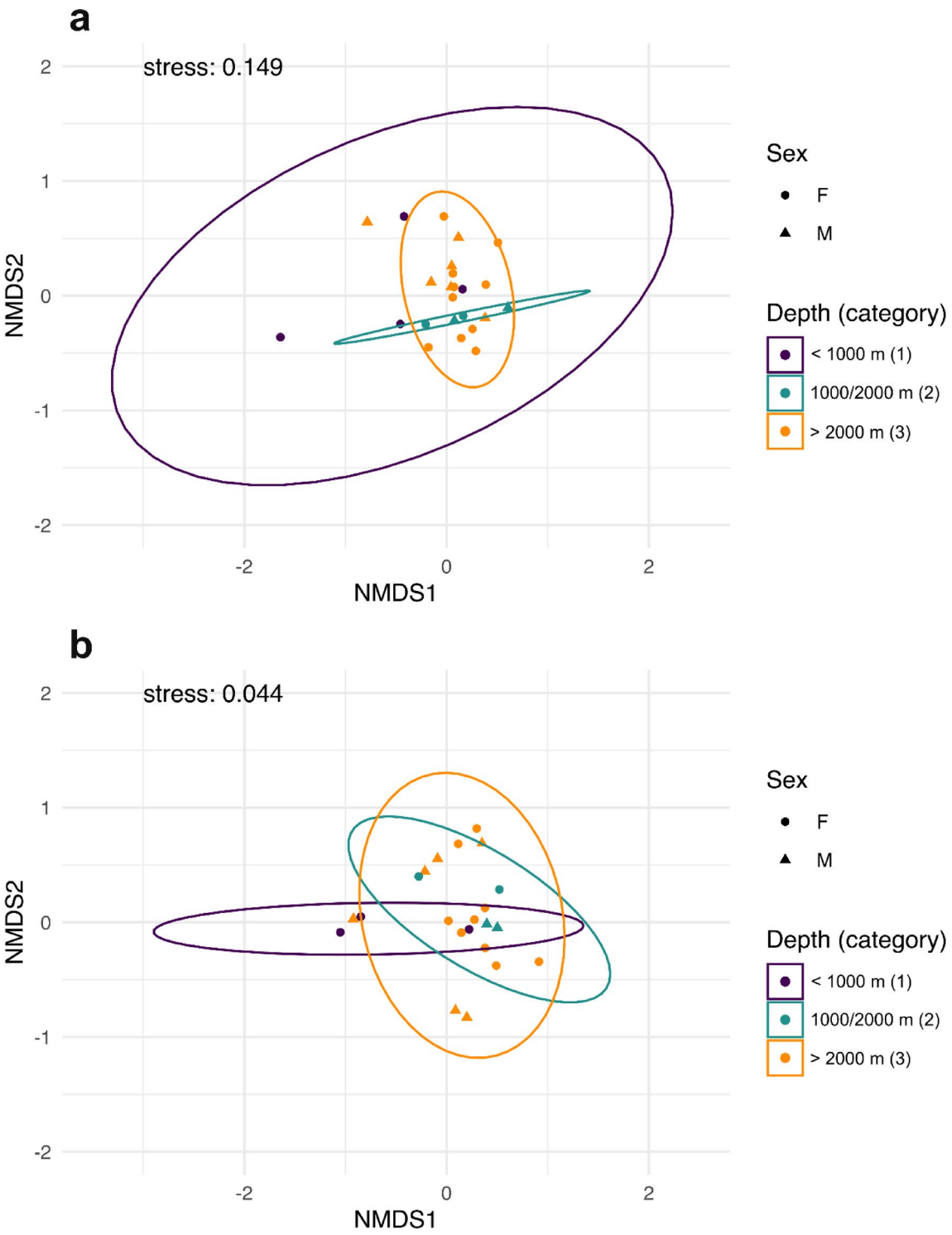

Fig. 4. Two-dimensional nMDS ordination plot based on Bray & Curtis dissimilarity indices of non-transformed numbers of parasites analyzed by species (**a**) and aggregated by class (**b**) recorded in the pelagic thresher. Shapes represent males and female individuals; different colors represent different bathymetric values at individual sampling locations. Ellipses indicate clusters with confidence intervals of 95%.

morphological and molecular analyses did not assign the present four species to any of the currently valid *Scyphophyllidium* species. A single species (named here *Scyphophyllidium* sp. 6 (cat. 1) sensu Caira et al.[32]), was genetically very close (99.72% identity) to an undescribed species found by Caira et al.[30], named previously *Marsupiobothrium* sp. 1 and later *Scyphophyllidium* sp. 6 in Caira et al.[32]. This was identified in the pelagic thresher from Pacific of Mexico, and was here considered conspecific. The other three species showed 97.63%,

Species	*n*	Mean total abundance	Species richness	Berger-Parker	Brillouin	Simpson's evenness	Bray & Curtis	Geographic location	References
Pelagic thresher *Alopias pelagicus*	32	2340.44	11.21	0.24	2.02	0.27	0.52	Costa Rica (Eastern Pacific Ocean)	This study
		2128.47	7.34	0.26	1.85	0.56	0.34		
Largenose catshark *Apristurus nasutus*	13	5.00	0.92	–	0.13	0.32	–	North-Central Chile (Pacific Ocean)	47
		–	–	–	–	–	–		
Portuguese dogfish *Centroscymnus coelolepis*	10	928.00	2.50	0.85	0.25	–	–	Balearic Sea (Western Mediterranean Sea)	74
		–	–	–	–	–	–		
Southern lanternshark *Etmopterus granulosus*	120	2.35	1.06	–	0.26	0.42	–	North-Central Chile (Pacific Ocean)	47
		–	–	–	–	–	–		
Velvet belly *Etmopterus spinax*	11	10.45	0.73	0.93	0.05	–	–	Balearic Sea (Western Mediterranean Sea)	74
		–	–	–	–	–	–		
Velvet belly *Etmopterus spinax*	30	5.30	1.70	0.60	0.30	–	–	Spain (North–east Atlantic Ocean)	75
		–	–	–	–	–	–		
Velvet belly *Etmopterus spinax*	29	9.50	1.20	0.60	0.20	–	–	Spain (North–east Atlantic Ocean)	75
		–	–	–	–	–	–		
Velvet belly *Etmopterus spinax*	39	5.54	1.25	0.95	0.08	–	–	Gulf of Naples (Western Mediterranean Sea)	13
		–	–	–	–	–	–		
Blackmouth catshark *Galeus melastomus*	53	0.18–2.29	0.14–0.90	0.88–1.00	0.08–0.11	–	–	Balearic Sea (Western Mediterranean Sea)	74
		–	–	–	–	–	–		
Blackmouth catshark *Galeus melastomus*	23	34.33–87.89	1.67–3.38	0.85–0.95	0.14–0.28	–	–	Balearic Sea (Western Mediterranean Sea)	87
		–	–	–	–	–	–		
Blackmouth catshark *Galeus melastomus*	91	182.90	1.27	0.99	0.02	–	–	Gulf of Naples (Western Mediterranean Sea)	13
		–	–	–	–	–	–		
Narrownose smooth-hound *Mustelus schmitti*	20	–	–	–	–	–	–	Northern Argentina (coastal Atlantic Ocean)	46
		–	3.00	–	0.74	–	–		
Blue shark *Prionace glauca*	16	–	–	–	–	–	–	Galicia, Spain (North–eastern Atlantic Ocean)	69
		–	2.69	–	0.59	–	–		
Blue shark *Prionace glauca*	13	–	–	–	–	–	–	Gulf of Valencia (Western Mediterranean Sea)	69
		–	2.46	–	0.50	–	–		
Lesser spotted dogfish *Scyliorhinus canicula*	13	29.14–80.56	1.17–1.44	0.96–0.99	0.03–0.09	–	–	Balearic Sea (Western Mediterranean Sea)	87
		–	–	–	–	–	–		
Lesser spotted dogfish *Scyliorhinus canicula*	102	32.61	1.55	0.96	0.10	–	–	Gulf of Naples (Western Mediterranean Sea)	13
		–	–	–	–	–	–		
Nursehound *Scyliorhinus stellaris*	28	6.93	0.93	0.79	0.07	–	–	Gulf of Naples (Western Mediterranean Sea)	26
		–	–	–	–	–	–		

Table 4. Comparison of descriptors of shark parasite communities found in literature with those of pelagic thresher (this study). For each species, top row refers to complete parasitological examination, bottom row only adult intestinal parasites. *n*: number of hosts examined. Range is provided when the host population was analyzed in subgroups (e.g. season).

94.16%, and 87.89% identity, respectively, with the sequence of *Scyphophyllidium* sp. 6 found by Caira et al.[30], and were here considered congenerics.

Both species of Trypanorhyncha found in the stomach of the present sharks belonged to the superfamily Tentacularioidea. *Heterosphyriocephalus encarnae* is a specialist parasite of the pelagic thresher[53]. In contrast, *Nybelinia africana* is a generalist parasite in Carcharhiniformes and Lamniformes[54]. For membersof Tentacularioidea, it has been suggested a life cycle including four or more hosts, with copepods as first, euphausiids or schooling fish as second intermediate, and fish as third or more intermediate or paratenic hosts[55].

The feeding ecology of the pelagic thresher shark has been previously investigated[56–58], and the present findings further illuminate trophic links between prey items and the occurrence of specific parasite taxa. The presence of parasites with complex life cycles suggests that squid and pelagic fishes constitute key components of the pelagic thresher's diet. This was in agreement with results of studies from the Indo-Pacific waters reporting squids, scombrids, and lanternfish as the most common prey items found in the stomach of pelagic threshers[57–59].

Female threshers were observed to have a more diverse infracommunity of trophically transmitted helminths than males. They showed a more evenly distributed community, which is considered more diverse than a community with the same number of species but dominated by few species[60], suggesting that females feed on a wider spectrum of available prey items. The pelagic thresher usually segregates by sex and location depending on the season, with females gathering in high productivity areas, especially during reproductive season[19,61]. Our results might reflect the different feeding strategies and ranging behavior of females during the sampling season,

which indeed coincided with the reproductive season of that population[62]. This was also confirmed by the occurrence of several pregnant females in our sample. This hypothesis is supported by data on pelagic thresher feeding ecology from a contiguous area, where females were found to have a greater diversity of prey[56], mostly linked to their energy requirements compared to males to support larger sizes and reproduction-associated energy costs[19,63,64].

Herein, a positive relationship between parasite infracommunity evenness and host total length was found, suggesting an increased parasite diversity with host size. A previous metanalysis found, in elasmobranchs, a positive significant relationship between host size and cestode richness[65]. To explain these results, it has been proposed that larger hosts, having a greater and more diversified food intake, increase the likelihood of acquiring more diverse parasite species, as well as indirectly shaping parasite community structure through their ranging and feeding preferences[66,67]. Furthermore, significant differences in helminth infracommunity evenness (i.e. diversity, since species count did not significantly differ) were observed in hosts sampled in the three areas characterized by different depths. These areas might represent different habitats with different prey species communities that are exploited in a different way by the pelagic thresher. Movement ecology of pelagic thresher remains largely unknown, but it has been observed performing vertical migration, most likely to feed[68]. Hence, the differences found in the trophically transmitted helminth communities in the three groups of individuals suggested that the pelagic threshers might exploit different taxa of prey items through their vertical range. This was in agreement with results obtained by Penadés-Suay et al.[69] who found that the composition and abundance of cestode communities of blue sharks varied across localities depending on idiosyncratic environmental conditions. Similar results were also found in a teleost fish (*Alepocephalus rostratus*), in the deep slope of the Catalan Sea, where differences in helminth communities related to distinct depths were explained with the dietary shift of the host at greater depths[70]. In addition, host latitudinal and depth range seemed associated with the diversity of endo-parasite assemblages in both elasmobranch and teleost fishes[71–73]. The result of our multivariate analysis also highlighted differences in parasite community structure among individuals sampled at different depths, emphasizing the influence of idiosyncratic environmental conditions.

Remarkable differences mainly linked to copepods and cestodes were observed when we compared the present results with similar studies performed on other shark species. In particular, the total mean abundance of the full community found in the pelagic thresher was about threefold higher than that recorded in *Centroscymnus coelolepis* from Balearic waters[74], and about thirteenfold higher than that recorded in *Galeus melastomus* from the Gulf of Naples[13]. Similarly, the mean species richness of the full community was almost ten times higher than full community mean species richness reported for *Etmopterus spinax* from Atlantic Spain[75]; in addition, the mean intestinal species richness was more than twofold higher than that recorded in *Mustelus schmitti* from the Atlantic of Argentina[46] and *Prionace glauca* from the Atlantic of Spain[69]. Rasmussen and Randhawa[73], in a metanalysis restricted to intestinal cestodes of 91 shark species, found that each shark species harbored 6.26 cestode species on average. Despite that result was obtained dividing all cestode species found globally in sharks by the number of shark species in their database, in the present study, cestode mean species richness was still higher (7.34). Brillouin and evenness indexes, i.e. community diversity, were here remarkably higher when compared to other studies (see Table 4). In the present case, species evenness (as well as similarity among hosts) increased when considering only cestode species.

Compared to previous studies, the present high values of parasite infracommunities (abundance and diversity) could be related to the high diversity and abundance of lower trophic levels (including many intermediate hosts) in the study area[16,17], which is facilitating the completion of distinct parasite life cycles[4,10,73,76]. Indeed, the eastern Pacific, off the coast of Costa Rica, is a very productive area, rich in marine biodiversity and recognized as the area with highest level of regional endemism compared to any comparably sized region in the world[77]. The dynamic interactions between hosts and their environment, which has long been identified as a driver of fish parasite communities[65,78], also seemed to shape parasite communities of the pelagic thresher. Present findings indicated that the trophic network, of which the pelagic thresher represents an apical node, might be more stable than those observed in other locations, and might be tolerant to current anthropogenic pressures.

In conclusion, the present study analyzed for the first time the parasite community of the pelagic thresher. The species composition showed a pattern similar to that reported for other sharks but showed higher richness, abundance and diversity at the infracommunity level. Differences found among females and males of pelagic thresher, and among hosts sampled at sites with different depths, confirmed that distinct biotic and abiotic factors can affect some descriptors of parasite community. Eastern Pacific off the Costa Rican coast is among the largest fishery areas in the world[79], of which data on overfishing and bycatch mortality of megafauna seem to depict a threatened ecosystem (e.g.[22,80]). Generally, overfishing pauperizes marine biodiversity, and it has been also shown to have a negative effect on richness, abundance and diversity of parasites with complex life cycles[81]. However, the high abundance and diversity of parasite community found in the pelagic thresher suggest that the trophic network remains stable and potentially healthy, as it continues to support a rich array of host species involved in the life cycles of numerous heteroxenous parasites. It is plausible that the high productivity of the eastern Pacific—driven by oceanographic processes that sustain an exceptionally diverse marine ecosystem—combined with ongoing efforts to improve marine resource management, may be mitigating the negative impacts of fishing pressure.

Marine parasite communities can thus be considered effective bioindicators of environmental conditions and trophic network status[9,11]. Indeed, modifications of structure – as well as diversity – of fish parasite communities have been observed in environmental alterations[7,9,11–13,82]. Values of parasite communities have also been employed to evaluate temporal changes in a fish stock to assess the effectiveness of protection measures implementation[8,83]. Compared to other direct methodologies of trophic network investigation, parasite community analysis is less costly than stable isotope analysis and may offer greater reliability than stomach content analysis[84]. Trophically transmitted parasites, such as helminths, exhibit limited seasonal or interannual

variation, generally have lifespans appropriate to the temporal scale of ecological studies, and display high microhabitat specificity within hosts. As a result, they can provide insights into long-term feeding patterns, even when the host's stomach is empty[84,85]. Although this approach requires taxonomic expertise, this limitation can be addressed through integrative taxonomy, including cost-effective molecular tools (e.g. DNA barcoding)[84]. Given these advantages, and the nestedness nature of parasite communities[67], monitoring efforts might be conducted either systematically or opportunistically—such as through the analysis of bycatch hosts—to detect temporal trends or early signs of trophic network disruption.

Thus, the present study provides further evidence that the analysis of parasite communities of high trophic level organisms, in relation to their biotic and abiotic variables, yields valuable insights into host ecology and trophic network dynamics. Our findings strongly support the utility of parasite communities of high trophic level predators as reliable and effective indicators for assessing the status of trophic interactions and investigating broader ecological networks, as well as advocating for their inclusion as an additional tool for biodiversity conservation and ecosystem monitoring efforts[86].

Data availability

Data is provided within the manuscript or supplementary information files.

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M.S.: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing—original draft, Writing—review and editing. F.O.: Formal analysis, Methodology, Visualization, Writing—original draft, Writing—review and editing. L.M.C. and M.P.: Formal analysis, Methodology. B.P.C. and J.M.C.R.: Resources, Writing—review and editing. M.M.A.: Formal analysis. A.R.: Conceptualization, Writing—review and editing. A.S.B.: Conceptualization, Formal analysis, Funding acquisition, Investigation, Writing—review and editing.

Declarations

Competing interests

The authors declare no competing interests.

Ethical approval

No approval of research ethics committees was required to accomplish the goals of this study.

Additional information

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