

Research Article

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Parasite communities of the Pacific cutlassfish *Trichiurus nitens*: clues to its feeding ecology and population connectivity

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Abstract

The Gulf of California, one of the world's most biodiverse marine ecosystems, is also heavily exploited by fisheries. Among its fish fauna are species that, although currently underappreciated, may become commercially important in the future. Enhancing our biological knowledge of these species is crucial for monitoring population dynamics and community changes. Fish parasites offer valuable insights into host ecology, including feeding habits and population structure. In this study, we document the metazoan parasite fauna of *Trichiurus nitens* (Trichiuridae) from four locations in the eastern Gulf of California, Mexico. A total of 165 fish specimens were examined, revealing five parasite species identified using both morphological characteristics and molecular markers: the monogenean *Octoplectanocotyla travassosi*, the trematode *Lecithochirium sinaloense*, and three nematodes – *Anisakis typica* A, *Skrjabinisakis brevispiculata*, and *Spinitectus* sp. Among these, *L. sinaloense* was the most prevalent. Although parasite species richness was similar between small and large fish, overall parasite abundance was higher in larger specimens. Moreover, parasite assemblages did not vary significantly across the study locations. These findings suggest that *T. nitens* exhibits a specialized feeding strategy, relying on a narrow range of prey throughout its life, and that the oceanographic variability does not limit fish movement in the region. Future studies encompassing a broader geographical scale, additional fish size classes, and different climatic seasons are needed to further elucidate the ecological role of this species. This work provides novel insights into the host-parasite dynamics of *T. nitens* and establishes a valuable baseline for ecosystem monitoring under global change scenarios.

Introduction

Fish of the genus *Trichiurus* (Scombriformes: Trichiuridae), commonly known as cutlassfish or hairtails, are benthopelagic species that play an important ecological role as regulators of lower trophic-level populations. Their diet includes fish, crustaceans, and cephalopods, positioning them as key predators within marine ecosystems and contributing to the balance and energy flow in food webs (Shin et al., 2022; Yan et al., 2011). In addition to their ecological importance, cutlassfish hold substantial commercial value, particularly in East Asian countries such as China, India, Japan, and Korea, where they constitute a major component of global fisheries catches, supporting both local economies and food security (Ghosh et al., 2024; Liao et al., 2021; Shin et al., 2023; Watari et al., 2017). *Trichiurus* currently comprises 10 valid species (Froese and Pauly, 2024), with *T. lepturus* being the only circumtropical taxon. While *Trichiurus nitens* was historically synonymized with *T. lepturus*, recent studies recognize it as a distinct Eastern Pacific species (Burhanuddin and Parin, 2008; Fricke et al., 2024; Yi et al., 2022), ranging from California to Peru.

The Gulf of California is one of the most biodiverse marine ecosystems globally and an essential fishing ground for Mexico. It is home to a wide range of species, including many endemics, and supports critical habitats like mangroves, coral reefs, and seagrass beds. However, the region faces significant environmental pressures, including overfishing, habitat loss, and the impacts of climate change (Arreguín-Sánchez et al., 2017; Lluch-Cota et al., 2007; Páez-Osuna et al., 2016). Particularly, the eastern portion of the Gulf experiences high fishing effort (Moreno-Baez et al., 2015). This situation represents a threat for both the biodiversity of the Gulf and the sustainability of its fisheries, which are vital for the local economy and food security.

Trichiurus nitens is a documented component of fish assemblages in the Gulf of California (Amezcuca and Amezcuca-Linares, 2014). Despite its presence, the species has received

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Table 1. Sample characteristics of *Trichiurus nitens* collected from four locations in the eastern Gulf of California

| Location | Latitude N | Longitude W | Date | <i>n</i> | SST °C | TL ± SD (cm) |
|-------------|-------------|--------------|---------------|----------|--------|--------------|
| Yavaros | 26°30′72.3″ | 109°69′22.1″ | 02 May 2024 | 40 | 22.6 | 25.2 ± 2.4 |
| Topolobampo | 25°45′07.6″ | 109°42′73.1″ | 27 April 2024 | 20 | 22.9 | 74.9 ± 15.3 |
| Las Glorias | 25°03′39″ | 108°72′10.9″ | 26 April 2024 | 61 | 22 | 26.3 ± 2.8 |
| El Tambor | 24°70′11.8″ | 108°20′75.7″ | 25 April 2024 | 44 | 23.6 | 24.9 ± 3 |

n = sample size; TL = total length ± standard deviation; SST = sea surface temperature.

little attention in scientific literature. Technical reports indicate that it is commonly caught in the Gulf’s fishing grounds (Vallarta-Zárate *et al.*, 2023), yet its ecological relevance remains largely unexplored. This lack of research may be attributed to the fact that *T. nitens* holds no commercial value in the region, limiting its scientific attention. Nonetheless, it is known that environment pressures can change species abundances, potentially elevating previously overlooked species into more prominent ecological or economic roles (Link, 2007). Therefore, recognizing the ecological importance of underappreciated fish species is critical for tracking and maintaining the functional diversity of an ecosystem in a changing world (Link, 2007).

The ecology of a fish species can often be partially understood through the study of its parasites, as these organisms are intricately linked to various aspects of their host’s biology, including distribution patterns, habitat selection, and diet composition (Jacobson *et al.*, 2024; Timi and Poulin, 2020). For example, fish with broad dietary ranges tend to host more abundant, rich, and diverse communities of food-transmitted parasites compared to those with a restricted prey spectrum (Dallarés *et al.*, 2016; Knudsen *et al.*, 1996). Likewise, shifts in parasite populations or community structures can serve as indicators of host population structure (George-Nascimento and Oliva, 2015; Lester and Moore, 2015). In this context, the present study aimed to document the parasite fauna of *T. nitens* from four locations in the eastern Gulf of California, Mexico, providing clues to the species’ ecological characteristics, including its feeding habits and population connectivity.

Methods

Fish and parasites sampling

Fish samples were collected from fishing hauls conducted at four locations in the eastern Gulf of California during April–May 2024 (Figure 1 and Table 1). The hauls were performed as part of a research cruise aboard the R/V Dr. Jorge Carranza Fraser, operated by the Instituto Mexicano de Investigación en Pesca y Acuicultura Sustentables (IMIPAS). A midwater net with four equal panels (top and bottom footrope length: 48.17 m) was used, deployed at an average speed of 6.5 km/h for 45 minutes at a depth of 25–30 m, in water with an average temperature of approximately 23°C. In total 165 fish identified as *T. nitens* were collected and frozen for later examination. Species identification was carried out onboard the vessel by ichthyologists from IMIPAS.

For parasitological examination, fish were thawed and measured for total length (TL, in cm). The external surfaces, gills, body cavities, and internal organs were then carefully examined under a stereomicroscope to detect metazoan parasites. All observed parasites were counted. Trematodes and monogeneans were processed using standard morphological identification

techniques (Salgado-Maldonado, 2009; Vidal-Martínez *et al.*, 2001). Nematodes and some trematodes were fixed and preserved in 96% ethanol for subsequent molecular identification.

Molecular identification

DNA extraction and amplification were carried out following established protocols (Hernández-Mena *et al.*, 2017; Shamsi *et al.*, 2017). For trematodes, the 28S rDNA region was amplified using primers 391 (5′-AGCGGAGGAAAAGAACTAA-3′) and 536 (5′-CAGCTATCCTGAGGGAAAC-3′) (García-Varela and Nadler, 2005; Nadler and Hudspeth, 1998). For nematodes, the ITS-1 region was targeted with primers SS1 (5′-GTTTCCGTAGGTGAACCTGCG-3′) and NC13R (5′-GCTGCGTTCCTTCATCGAT-3′), while the ITS-2 region used SS2 (5′-TTGCAGACACATTGAGCACT-3′) and NC2 (5′-TTAGTTTCTTTTCTCCGCT-3′) (Zhang *et al.*, 2007; Zhu *et al.*, 1998). PCR products were sequenced on an ABI 3730xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). The resulting sequences were analyzed, edited, and assembled using the software Geneious Pro 4.8.4 software (Biomatters Ltd., Auckland, New Zealand). Sequence similarities were determined via BLAST searches against the GenBank nucleotide database. All newly generated sequences have been deposited in GenBank (Table 2, Supplementary Table S1). For phylogenetic analyses, datasets were generated using Mesquite 3.62 (<https://www.mesquiteproject.org/>) with the newly obtained sequences in this study and sequences published in GenBank, including those selected in previous studies (Chan-Martin *et al.*, 2022; Mattiucci *et al.*, 2014). A total of two data matrices were generated: one for trematodes with DNA sequences of the 28S marker and another for nematodes with the ITS-1 and ITS-2 markers. In the case of nematodes, the ITS-1 and ITS-2 regions were combined into a single analysis. The matrices were aligned using the default parameters (Pairwise Alignment: SLOW/ACCURATE) of ClustalW (Thompson *et al.*, 1994) implemented on the website: <https://www.genome.jp/tools-bin/clustalw>. The nucleotide substitution model that best fit the aligned datasets was inferred with jModelTest v2 (Darriba *et al.*, 2012). The method used to determine phylogenetic relationships was maximum likelihood (ML), which was implemented in RAxML v. 7.0.4 (Stamatakis, 2006). The reliability of the phylogenetic relationships was assessed via non-parametric bootstrap analysis with 1000 replicates.

Parasitological metrics for population and community analysis

Parasite data were analyzed at both the population and infracommunity levels following Bush *et al.* (1997). At the population level, prevalence (percent of infected fish) and median intensity (median number of parasites per infected fish) were calculated for each parasite species at each location. At the infracommunity level, only

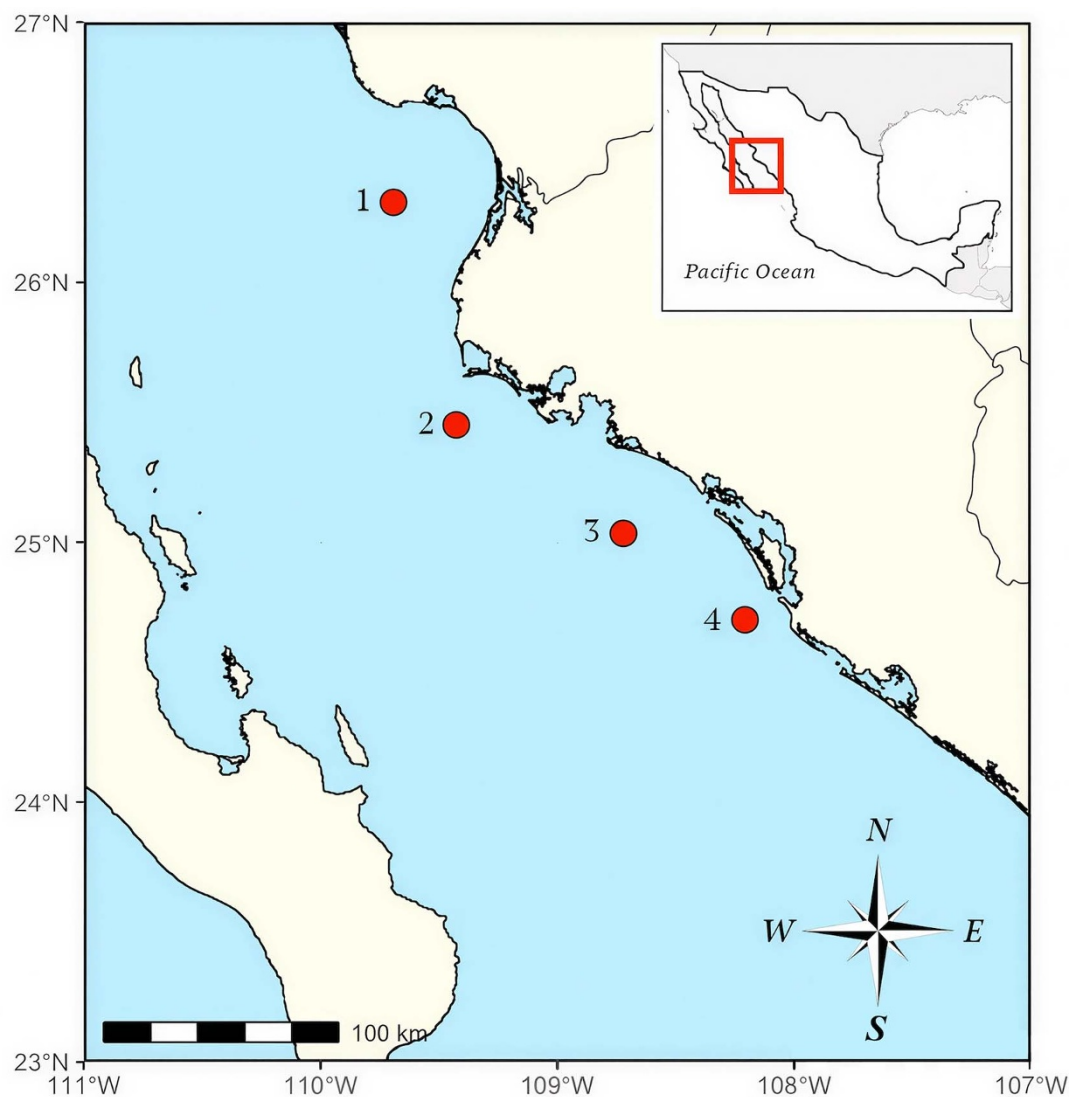


Figure 1. Study area with sampling locations across the eastern Gulf of California. 1: Yavaros; 2: Topolobampo; 3: Las Glorias; 4: El Tambor.

the species richness and the total number of parasite individuals were measured, as most fish were either uninfected or hosted only a single parasite species. Similarity in parasite assemblages among individual fish hosting parasites was quantified using Bray–Curtis distances, calculated on square-root-transformed abundance data to reduce the dominance of highly abundant taxa in the analysis. Uninfected fish were excluded from these analyses. To visualize patterns related to sampling locations, non-metric multidimensional scaling (nMDS) was performed using the similarity matrix. To enhance visualization, distances between the centroids of each sample were plotted by bootstrap averaging the original dataset (75 iterations with replacement; rho coefficient = 0.99). Statistical differences among locations were evaluated using a one-way permutational multivariate analysis of variance (PERMANOVA), incorporating fish TL as a covariate and ‘location’ as a factor. A sequential sum of squares (Type I SS) approach was applied to account for the covariate. All analyses were conducted using PRIMER v7 and the PERMANOVA + for PRIMER package (Anderson et al., 2008; Clarke and Gorley, 2015).

Results

Five parasite species were identified: the trematode *Lecithochirium sinaloense*, the monogenean *Octoplectanocotyla travassosi*, and three nematodes – *Anisakis typica* A, *Skrjabinisakis brevispiculata*, and *Spinitectus* sp. (Table 2). Identification was based on a combination of morphological and molecular data for the trematode, morphology alone for the monogenean and *Spinitectus*, and molecular data only for the two anisakids.

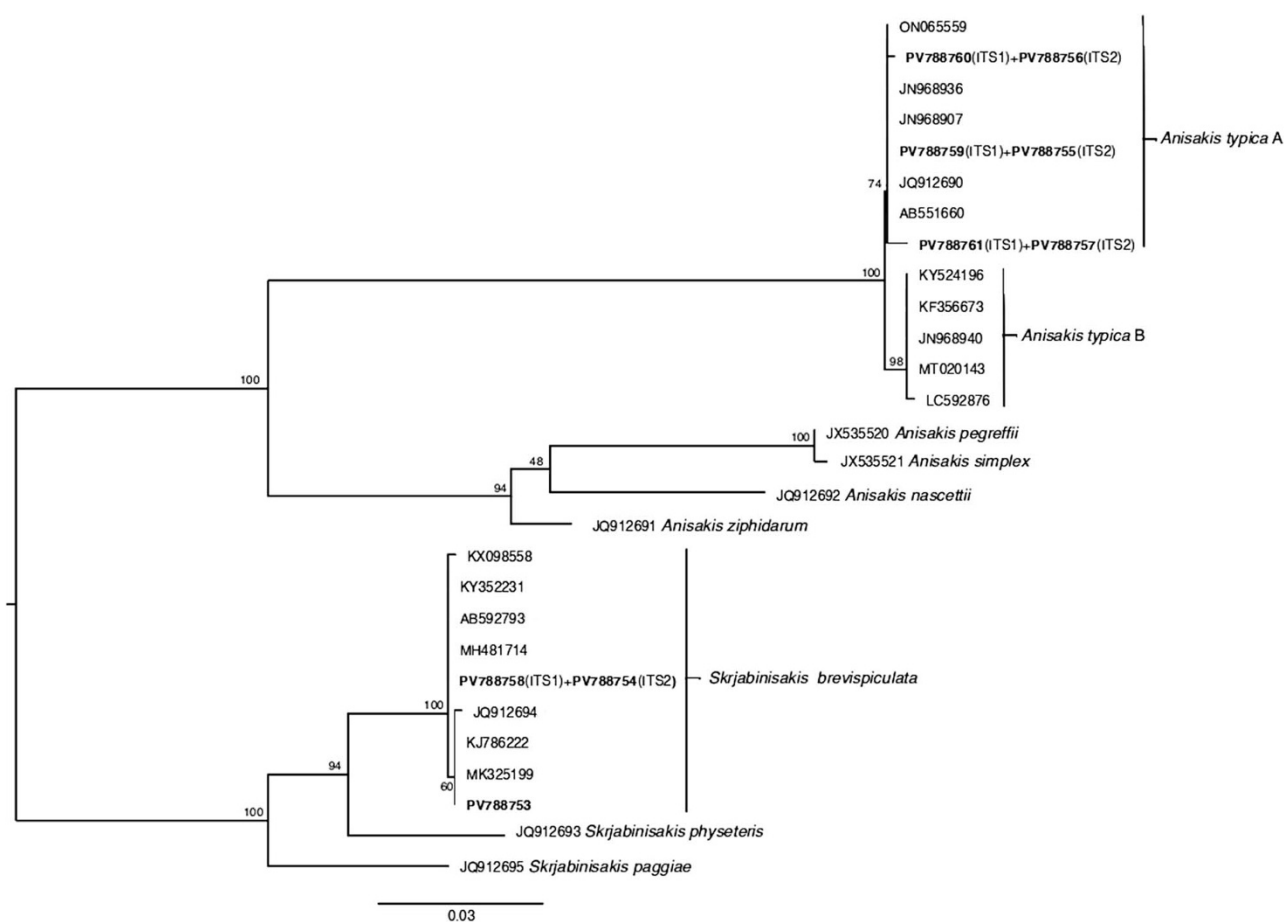
Anisakid larvae were initially separated into two morphotypes based on ventricular characteristics and body length: Anisakidae gen. sp. 1, approximately 1 mm in length, had a large ventricle relative to body size; Anisakidae gen. sp. 2, approximately 25 mm long, exhibited a small ventricle. This classification followed the ventricular size criterion proposed by Safonova et al. (2021). Molecular analysis (ITS-1 and ITS-2 regions) of three larvae from gen. sp. 1 and two from gen. sp. 2 confirmed that these morphotypes corresponded to distinct species: gen. sp. 1 showed 100% similarity to *A. typica* A and gen. sp. 2 to *S. brevispiculata* in BLAST, as supported by phylogenetic analysis (Figure 2, Supplementary Table S1).

Table 2. Parasite infection parameters in *Trichiurus nitens* across four localities in the Gulf of California, Mexico

| Parasite/GenBank accession number | Site | | Yavaros | Las Glorias | El Tambor | Topolobampo |
|--------------------------------------|---------|----|----------------|-------------|----------------|----------------|
| Trematoda (A) | | | | | | |
| <i>Lecithochirium sinoense</i> | Stomach | P% | 27 (15–43) | 39 (27–52) | 40 (26–55) | 85 (63–95) |
| PV788762–68 | | MI | 1 (1–1) | 1 (1–1) | 1 (1–2) | 25 (19–34) |
| Monogenea (A) | | | | | | |
| <i>Octoplectanocotyla travassosi</i> | Gills | P% | 0 | 11 (5–21) | 2 (1–11) | 60 (36–79) |
| | | MI | 0 | 1 (1–2) | 1 ^a | 4 (3–5) |
| Nematoda (L) | | | | | | |
| <i>Anisakis typica</i> A | Stomach | P% | 0 | 9 (4–20) | 2 (1–11) | 15 (4–36) |
| PV788755–57, 59–61 | | MI | 0 | 2 (1–4) | 2 ^a | 1 ^a |
| <i>Skrjabinisakis brevispiculata</i> | Stomach | P% | 5 (1–16) | 0 | 0 | 0 |
| PV788753, 54, 58 | | MI | 1 ^a | 0 | 0 | 0 |
| <i>Spinitectus</i> sp. | Stomach | P% | 0 | 0 | 0 | 5 (2–23) |
| | | MI | 0 | 0 | 0 | 1 ^a |

A = adult; L = larva; P% = prevalence; MI = median intensity.

Note: Values within parenthesis represent 95% confidence intervals.

^aSample too small to calculate the confidence limits for median intensity.**Figure 2.** Maximum-likelihood phylogenetic tree of concatenated ITS-1 and ITS-2 sequences from anisakid nematodes. Terminal labels show species names and GenBank accession numbers (sequences from this study in bold). Bootstrap support values are shown at nodes. The tree was rooted with *Skrjabinisakis paggiae* and *Skrjabinisakis physeteris* as outgroups. Scale bar indicates nucleotide substitutions per site.

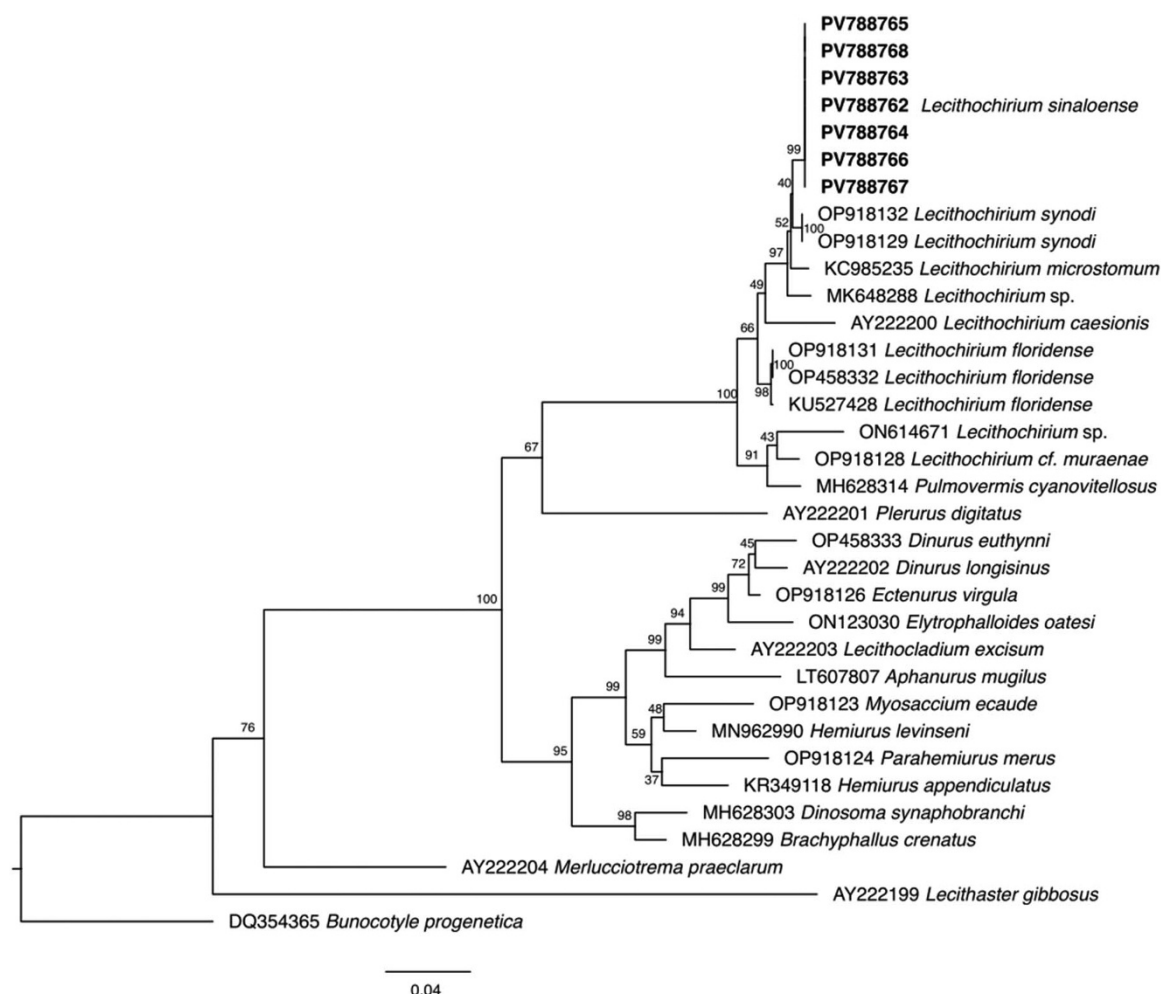


Figure 3. Maximum-likelihood phylogenetic tree of 28S sequences from hemiurids. Terminal labels show species names and GenBank accession numbers (sequences from this study in bold). Bootstrap support values are shown at nodes. *Lecithaster gibbosus*, *Merlucciotrema praeclarum*, and *Bunocotyle progenetica* were used as outgroup. Scale bar indicates nucleotide substitutions per site.

For the trematode, 28S sequences were obtained from seven specimens. BLAST searches and phylogenetic analyses placed these specimens within the genus *Lecithochirium*, particularly as a sister species to *L. synodi* and *L. microstomum* (Figure 3, Supplementary Table S1). Morphologically, our specimens were identified as *L. sinaloense* by a combination of characters such as the presence of a presomatic pit glandular, the sucker ratio ($1:2.9-3.9 \times 1:2.7-3.5$), shape of the vitelline masses, and egg size ($21-23 \times 13-15$).

Among the five parasite species found in *T. nitens*, *L. sinaloense* was the only one occurring in all four sampling locations (Figure 4) and the most notable in terms of prevalence and infection intensity, followed by *O. travassosi*, while the nematodes were infrequently encountered (Table 2). Fish from three locations – Yavaros, Las Glorias, and El Tambor – were small, all measuring around 25 cm in length, and fish from Topolobampo were large, measuring an average of 75 cm (Table 1). In small fish, *L. sinaloense* reached a prevalence of 40% and median intensity of 1, whereas in large fish these values were 85% and 25, respectively. Likewise, in small fish, *O. travassosi* reached a prevalence of 11% and median intensity of 1, whereas in large fish these values were 60% and 4, respectively (Table 2).

The examined fish showed depauperate parasite infracommunities (Figure 5). About half of the small fish were free of parasites,

while the rest were parasitized by one or two species, with an average of fewer than three individual parasites per fish (Figure 5). In contrast, 90% of the large fish were parasitized by one to three species, with an average of 42 individual parasites per fish.

The analysis of infracommunity similarity across locations excluded Topolobampo, as fish sizes from this site were not comparable to those from the other three locations. The bootstrap-average-based nMDS ordination of infracommunities (Figure 6) did not reveal a clear separation among samples, with a low value of stress (0.03), indicating a good fit. This lack of differentiation was further supported by the PERMANOVA analysis (Table 3), which showed no significant differences among the parasite assemblages of fish from Yavaros, Las Glorias, and El Tambor.

Discussion

Comments on the parasite fauna of *T. nitens*

Thus far, no parasitological studies have focused on *T. nitens*, limiting direct comparisons. Of the 11 species of *Trichiurus*, parasitological research has predominantly focused on *T. lepturus*, likely due to its commercial importance. In fact, these studies often emphasize the identification of anisakid nematodes because of their zoonotic relevance (e.g., Cipriani et al., 2022; Kim et al., 2016).

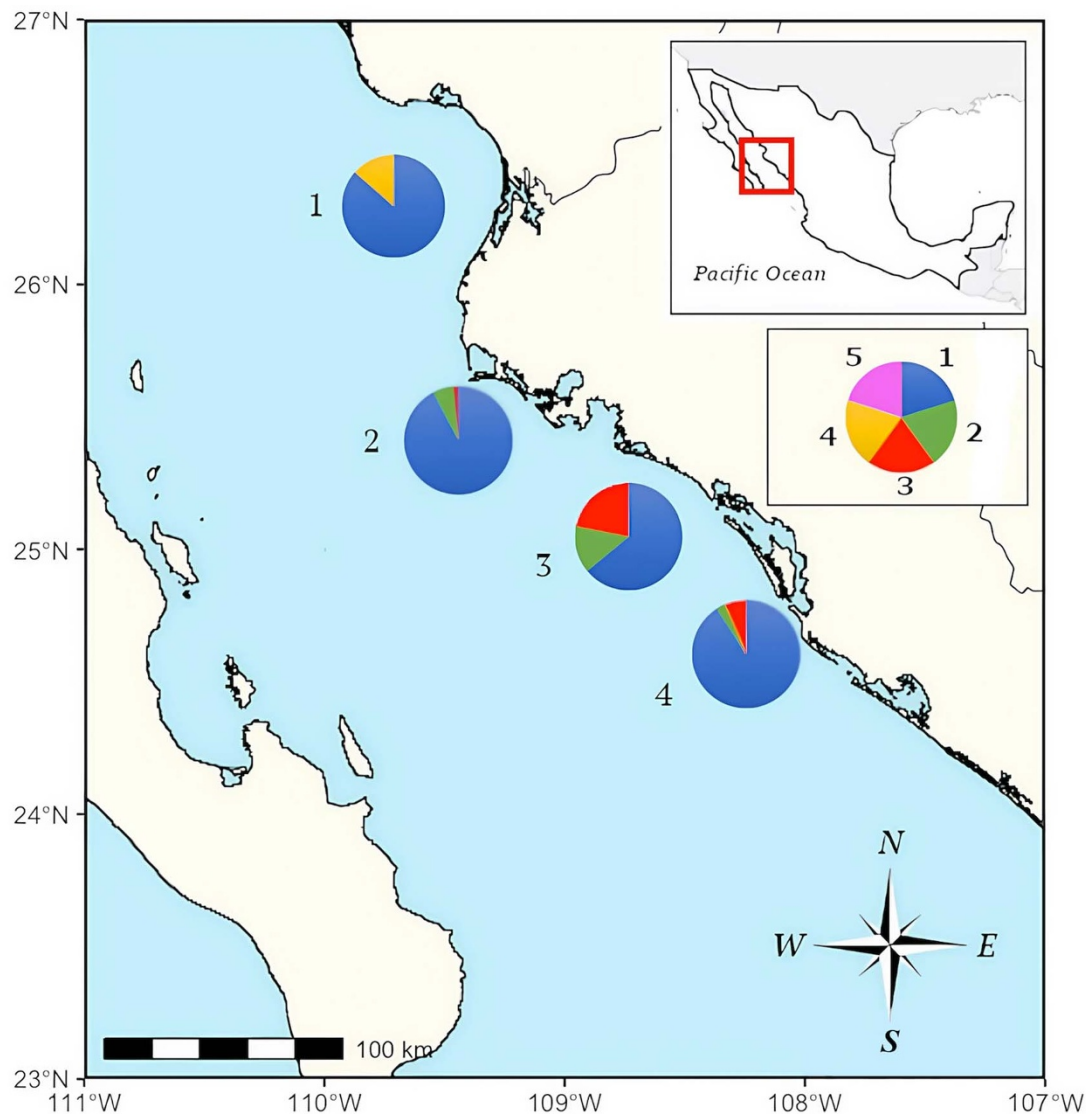


Figure 4. Spatial variation in parasite community composition of *Trichiurus nitens* across sampling locations in the Gulf of California. Pie charts represent the relative abundance (%) of each parasite species, coded by colour: (1) *Lecithochirium sinaloense* (blue), (2) *Octoplectanocotyla travassosi* (green), (3) *Anisakis typica* (red), (4) *Skrjabinisakis brevispiculata* (yellow), and (5) *Spinitectus* sp. (pink). Size proportions reflect actual abundance ratios among species at each site.

The parasite species identified in this study have previously been reported in other fish host species and geographical regions. *Anisakis typica* (s.l.) is one of the most common anisakid nematodes in warm temperate and tropical waters, occurring as an adult in various dolphin species and as a larva in multiple fish species worldwide, including *T. lepturus* from Korea and the Southwest Indian Ocean (Cipriani *et al.*, 2022; Lee *et al.*, 2009; Mattiucci *et al.*, 2022). Previous studies have reported *A. typica* (s.l.) in the fish *Trachinotus rhodopus* (Carangidae) from Puerto Ángel, Oaxaca, and in the dolphin *Stenella longirostris* (Delphinidae) from La Paz, Baja California Sur (Aguilar-Aguilar *et al.*, 2001; Martínez-Flores *et al.*, 2023). Thus, the present study further confirms the presence of *A. typica* (s.l.) in the Mexican Pacific, including the Gulf of California.

The phylogenetic analysis provides additional resolution for this taxon. Our sequences clustered within *A. typica* sp. A, as defined by Cipriani *et al.* (2022), who also reported the occurrence of *A. typica* sp. B in sympatry with sp. A in *T. lepturus*. This placement indicates

phylogenetic affinity with Indo-Pacific populations and suggests that *A. typica* sp. A has a broader distribution than previously documented, now including the Eastern Pacific. In our material, *A. typica* sp. B was not detected. The detection of *A. typica* sp. A in the Gulf of California expands both the known host range (now including *T. nitens*) and the geographic distribution of this lineage. Cipriani *et al.* (2022) already emphasized that *A. typica* sp. A shows a worldwide distribution, and our findings are consistent with this interpretation. These results are relevant not only for clarifying the diversity and phylogeography of anisakid nematodes, but also for food safety considerations, since *Anisakis* larvae are zoonotic.

Skrjabinisakis brevispiculata is currently the valid name for *Anisakis brevispiculata*, which has been found in kogiid whales as definitive hosts and in several fish species as intermediate hosts across the Atlantic and Indo-Pacific regions (Cabrera-Gil *et al.*, 2018; Cipriani *et al.*, 2024; Safonova *et al.*, 2021). In our phylogenetic reconstruction, the sequences obtained from *T. nitens*

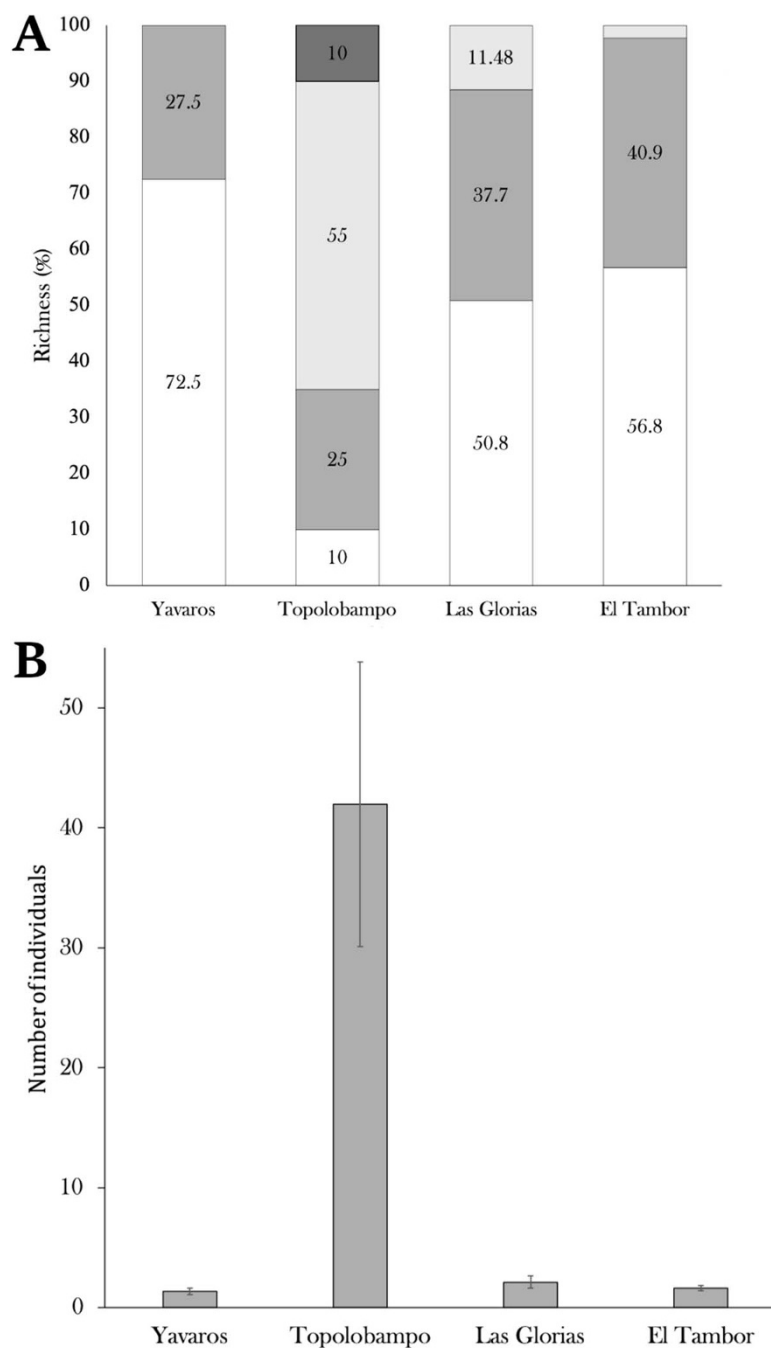


Figure 5. Parasite infracommunities of *Trichiurus nitens* across four localities in the Gulf of California, Mexico. (A) Relative parasite species richness represented in greyscale: white = 0 parasite species, medium grey = 1 parasite species, light grey = 2 parasite species, dark grey = 3 parasite species. (B) Average number of parasite individuals (bars indicate standard error).

clustered with sequences of *S. brevispiculata*, supporting the identification of this species in the Gulf of California. To our knowledge, there are no previous records of *S. brevispiculata* in the Mexican Pacific. Its presence in *T. nitens* can be explained by the wide geographic distribution of at least two of its definitive hosts, *Kogia breviceps* and *Physeter macrocephalus*, as well as one of its intermediate hosts, *Xiphias gladius*, all of which extend into the Mexican Pacific. This study represents new host and geographical records for *S. brevispiculata*.

A single specimen of *Spinitectus* sp. was found in all fish examined. Molecular analysis was precluded by DNA degradation. Morphologically, the specimen was identified as *Spinitectus* sp. following Moravec et al. (2023), based on its characteristic transverse rows of conical, pointed cuticular spines –

a diagnostic feature distinguishing this genus from other nematodes. The low prevalence could suggest accidental acquisition through trophic interactions. This nematode has been reported in other marine fish from the Mexican Pacific, typically at very low prevalence; however, in some species, such as *Euthynnus lineatus*, prevalence can range from moderate to high (Miranda-Delgado et al., 2019; Santos-Bustos et al., 2018; Villalba-Vasquez et al., 2022). Despite its occurrence, *Spinitectus* has only been identified at the genus level. According to Moravec et al. (2023), species-level identification of *Spinitectus* remains challenging due to the inadequacy of existing species descriptions.

Currently, three valid species of monogeneans belong to the genus *Octoplectanocotyla*: *O. aphanopi*, *O. travassosi*, and *O.*

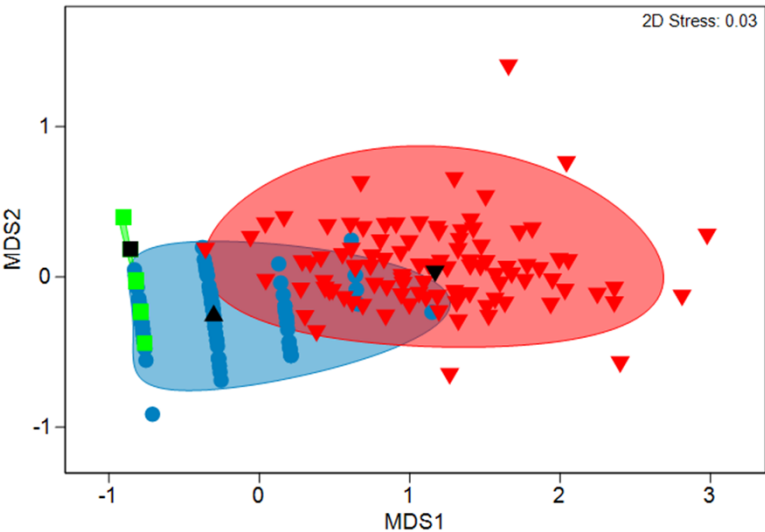


Figure 6. Non-metric multi-dimensional scaling plot (nMDS) of bootstrap averages of parasite infracommunities in three samples of *Trichiurus nitens* from the Gulf of California, based on Bray–Curtis dissimilarity of square root-transformed data of abundance. Black full symbols represent the overall centroids across all repetitions. Blue circles: El Tambor; red triangles: Las Glorias; and green squares: Yavaros. Colours areas represent 95% confidence regions.

Table 3. PERMANOVA results of square-root-transformed abundance of parasites of *Trichiurus nitens* in three samples from the Gulf of California, based on the Bray–Curtis dissimilarity measure with host length as covariable. *P*-values obtained after 9999 permutations

| Source | df | SS | MS | Pseudo F | <i>P</i> (perm) |
|------------------------|----|--------|--------|----------|-----------------|
| Host length | 1 | 300.71 | 300.71 | 0.2562 | 0.721 |
| Locality | 2 | 5123 | 2561.5 | 2.1824 | 0.0886 |
| Host length x Locality | 2 | 754.11 | 377.06 | 0.32125 | 0.7802 |
| Residual | 54 | 63381 | 1173.7 | | |
| Total | 59 | 69559 | | | |

df = degrees freedom; SS = sum of squares; MS = mean square.

trichiuri. The morphology of the monogeneans found in *T. nitens* aligns with *O. travassosi*, originally described by Carvalho and Luque (2012) from specimens collected on *T. lepturus* in Brazil. According to these authors, *O. travassosi* differs from its congeners by possessing a third pair of small hooks between the outer and inner pairs, as well as six large and two small genital spines. These distinguishing structures were observed in specimens from *T. nitens*; however, further detailed morphological and molecular analyses are required to confirm the presence of *O. travassosi* in the Mexican Pacific.

Lecithochirium sinaloense was previously reported from *Cynoponticus coniceps* in the Mexican Pacific (Bravo-Hollis, 1956), and to our knowledge, no additional records of this trematode exist. Our specimens resemble *L. sinaloense*, particularly based on a combination of characters: shape of the vitelline masses, presomatic pit glandular, sucker ratio and egg size. This species belongs to the ‘synodi’ group, which includes several very similar species. Bray (1991) mentions that the species in this group could well be synonyms. However, *L. sinaloense* (and therefore our specimens) can be distinguished from *L. synodi* by having larger eggs (20–23 in length vs. 12–16 in *L. synodi*) and by the average sucker ratio (1:3.1 in *L. sinaloense* vs. 1:1.3 in *L. synodi*) (Bravo-Hollis, 1956; Bray, 1991; Manter, 1931). Additionally, Bray (1991) explicitly mentions that *L. sinaloense* may be a synonym of *L. acutum*; however, we differ since *L. acutum* generally has smaller eggs (e.g., 15 × 10 in Chauhan, 1954; see Bray, 1991 for further

measurements). Genetically and phylogenetically, our specimens are also distinct from specimens that have been identified as *L. synodi* from Brazil. Clearly, resolving the taxonomic problem of the ‘synodi’ group requires a more thorough review of the species that comprise the group, supported by DNA sequences and phylogenetic analysis. However, we have decided to adopt a conservative position regarding the taxonomic validity of *L. sinaloense*, since there are underlying morphological differences, which are compatible with the specimens collected in this study.

The parasite community of *T. nitens* in our study area showed low richness (five taxa), consistent with patterns observed in other mesopelagic vertical migrators (Woodstock et al., 2020). While *T. lepturus* populations may show variable parasite richness across regions, for instance, 6 taxa in Taiwan (Shih, 2004) vs. 14 in Brazil (Carvalho and Luque, 2011), our findings align with the typically depauperate communities reported for bathypelagic fishes. This pattern may reflect ecological constraints of the mesopelagic zone, including greater host spacing and lower nutrient availability that limit parasite transmission (Woodstock et al., 2020). Consistent with the findings of the present study, a trematode (*Lecithochirium microstomum*) was the most abundant parasite reported in *T. lepturus* from Brazil. Notably, the Brazilian fish measured approximately 100 cm in length, whereas the Taiwanese specimens and most of those examined in this study measured approximately 25 cm. Such differences in fish size may explain the higher parasite species richness reported in Brazil. In fish populations, larger individuals typically harbour richer parasite communities because they have had more time to accumulate parasites, access a wider range of habitats, and consume a more diverse diet, all of which can increase exposure to a broader array of parasite species (Guégan and Hugué, 1994; Pérez-del Olmo et al., 2008; Poulin, 2007). Nonetheless, in the present study, the 20 larger fish (75 cm in length) did not exhibit higher parasite species richness, although they did harbour a greater number of parasite individuals. This observation supports the idea that the decay in similarity of parasite communities as a function of ontogenetic distances becomes more apparent when using abundance-based metrics rather than those based solely on presence/absence data (Timi et al., 2010). The absence of a clear correlation between parasite richness and host size has been documented in several studies (e.g., González and Poulin, 2005; Norton et al., 2003). While our

data show a similar pattern, we emphasize that our sample lacked sufficient representation across size classes for robust statistical analysis.

Parasites of *T. nitens* as indicators of fish feeding ecology

The lack of obvious variation in parasite species across the size range studied (25–75 cm) suggests that *T. nitens* maintains a specialized feeding strategy throughout ontogeny. This aligns with a previous study which identified *T. lepturus* as a specialist feeder, with larger individuals narrowing to only three prey types: Clupeiformes, Mugiliformes, and Perciformes (Gomathy and Vivekanandan, 2017). Another study also revealed that *T. lepturus* strongly prefers one of three selected fish species (Chiou et al., 2006). Broader evidence from other fish species supports the parasite-diet link. For instance, Knudsen et al. (1996) demonstrated that infections by three food-transmitted parasite species reflected the specialization of Arctic charr on specific prey items. In contrast, Kleinertz et al. (2012) found that the diversity of the parasite community mirrored the variety of prey items consumed by European sprat. Similarly, Dallarés et al. (2016) observed that the high abundance, richness, and diversity of parasites in greater forkbeard correlated with its broad dietary range. However, further targeted research is necessary to confirm the hypothesis of feeding specialization in *T. nitens*.

Based on our findings, it is also plausible to suggest that *T. nitens* primarily feeds in the pelagic zone, where intermediate host availability is limited compared to benthic zones (see Dallarés et al., 2014, and references therein). On the other hand, our results do not allow us to determine the specific prey consumed by *T. nitens*. Of the five parasite species found in *T. nitens*, four are food-transmitted (one trematode and three nematodes). Inferring how these parasites are transmitted to *T. nitens* is challenging, as they can use a variety of invertebrate and fish species as paratenic hosts through their indirect life cycles, which are not totally understood (Gibson and Bray, 1986; Mattiucci et al., 2022; Moravec et al., 2023).

Parasites of *T. nitens* as indicators of host population structure

The similarity in parasite assemblage structure across sampling locations could reflect connectivity among host populations, based on two established ecological patterns: first, some parasite species tend to occur only in specific host populations; second, the abundance of certain parasite species can vary among host populations where they are present (Poulin and Kamiya, 2015). In general, similarity among parasite communities in marine fish tends to decline with increasing geographical distance, due to oceanographic variability that can act as a barrier to the distribution of both fish and their parasites (Oliva and González, 2005; Vales et al., 2011). This decay in similarity depends, among other factors, on the spatial scale of the study, environmental constraints, and the dispersal abilities of the organisms (Poulin and Kamiya, 2015).

Our study area is characterized by pronounced environmental complexity (Marín-Enríquez et al., 2024). Despite this heterogeneity, which might theoretically limit host movement, we observed homogeneous parasite assemblages across sites. This pattern could suggest sufficient host connectivity to maintain shared parasite faunas, or limitations of parasite tags to resolve subtle population structure in this system. Our study design did not include a geographically distinct reference population to test the method's resolution. The maximum sampled distance (~260 km between Yavaros and El Tambor) falls within ranges where parasite tags

have detected structure elsewhere (Poulin and Kamiya, 2015), but conclusions remain provisional without complementary data (e.g., genetics, otolith chemistry). Future studies should integrate these approaches to validate potential connectivity.

Conclusion

To the best of our knowledge, this study represents the first parasitological investigation of *T. nitens*. The depauperate parasite community, comprising one monogenean species, one trematode, and three nematodes, suggests that *T. nitens* may exhibit a specialized feeding strategy. Moreover, the homogeneous parasite assemblages across our 260-km study area suggest potential connectivity among *T. nitens* populations, though we emphasize that this interpretation requires validation through complementary approaches (e.g., genetics, otolith chemistry). Although *T. nitens* remains underappreciated, our findings provide valuable insights into its ecology, which could inform future fisheries management. Additionally, these parasitological data serve as a useful baseline for ecosystem monitoring under future global change scenarios.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315425100623>.

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Competing interests. The authors declare none.

Ethics statement. This study did not involve endangered or protected species. No living animals were captured specifically for this project. The specimens examined were collected during a research cruise. The fishing permit was issued by the National Commission for Aquaculture and Fisheries (PPF/DGOPA-090/23).

Data availability. Data will be made available on request.

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