



Article

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Abstract: The Pacific thread herring, *Opisthonema libertate*, is a fishery resource in the eastern tropical Pacific, yet its population dynamics are poorly understood. The aims of this work were to document the metazoan parasite species in *O. libertate* from the Gulf of California in Mexico, determine latitudinal changes in their infection levels, and assess their potential as biological tags. Six parasitic species were identified: *Myosaccium ecaude* and *Parahemiurus merus* digeneans, *Cribromazocraes* cf. *travassosi* and *Mazocraeoides georgei* monogeneans, *Pseudoterranova* sp. nematodes, and *Lepeophtheirus* sp. copepods. The monogenean and copepod species are reported for the first time in *O. libertate*. Many fish were infected with digeneans, and there was a rare occurrence of other parasites. While the prevalence and median intensity of *M. ecaude* and *P. merus* significantly varied among sampling localities, a multivariate analysis revealed a distinct separation between some localities; these results suggest that individual fish form several discrete populations. However, the utility of these parasites as biological tags will be further probed because they cannot satisfy all requirements for good biological tags. The present results might be helpful in complementing other techniques to determine the movement and stock structure of *O. libertate*, albeit with certain limitations.

Keywords: Platyhelminthes; Nematoda; Copepoda; marine fish; parasitic infections; Mexico

Key Contribution: Spatial changes in infection levels of adult digeneans suggest that individuals of Pacific thread herring remain resident in certain areas. However, the reliability of these parasites as biological tags is questioned.



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1. Introduction

The Pacific thread herring, *Opisthonema libertate* (Günther, 1867) (Clupeiformes, Dorosomatidae), is a small pelagic fish distributed from the Pacific coast of Baja California and the Gulf of California, in Mexico, to Peru [1]. Like other small pelagic fish species, *O. libertate* is ecologically essential due to its role in mediating energy transfer between trophic levels [2,3]. Additionally, this species substantially contributes to the small pelagic fishery in the Mexican Pacific, especially in the Gulf of California [4,5].

The Gulf of California is a marginal, semi-enclosed sea area exceeding 1100 km in length and is considered to be a tropical marine biodiversity hotspot that houses several small pelagic fish species hunted by commercial fishing fleets [6], all of which has resulted

in higher fishing pressure on *O. libertate* during the past decade [7]. This situation requires the structural population information of various species in order to achieve sustainable management. This information still needs to be improved for *O. libertate* despite the ecological and commercial importance thereof. Limited evidence on the morphometric study of the fish body and otoliths suggests a structured population of this species in the Gulf of California [8], which needs further investigation using a broad spectrum of techniques covering the multiple characteristics of this fish species [9].

Parasites are essential ecological organisms in oceans and can provide valuable information that enables a better understanding of all aspects of fish biology [10]. They also function as biological tags and help locate fish movement to improve the probability of correctly assigning a fish to its original stock, which are fundamental requirements for effective management [11–13]. The selection of parasites as tags requires careful screening; however, because not all parasites can be used as tags, with long-living parasites being recommended the most for this [14,15], this highlights the importance of the necessity of a knowledge of fish parasites and the ability to determine the spatial variability thereof across broad geographical areas. Concerning the parasites of *O. libertate*, a previous study reported *Kuhnia* sp. and *Polymicrocotyle manteri* Lamothe-Argumedo, 1967 monogeneans, *Myosaccium ecaude* Montgomery 1957 and *Parahemiurus merus* (Linton 1910) digeneans, *Proteocephalidea* gen. sp. cestodes, and *Pseudoterranova* sp. nematodes from fish collected in a locality of the Mexican Central Pacific [16], while no information is yet available regarding their distribution in the Gulf of California.

As such, the aims of this study were to investigate the distribution of the metazoan parasite species in *O. libertate* from the Gulf of California, determine latitudinal changes in their infection levels, and assess their potential as biological tags.

2. Materials and Methods

Fish samples were collected from fishing hauls in six localities of the eastern Gulf of California in June and July 2022 (Figure 1 and Table 1) during a research cruise onboard the R/V “Dr. Jorge Carranza Fraser” of the Instituto Nacional de Pesca y Acuicultura (IN-APESCA). The fishing hauls were made with a midwater net of four equal caps (i.e., top and bottom footrope length: 48.17 m). The trawls were towed at an average speed of 6.5 km h^{−1} for 45 min with an average depth of 25 m. The hauls were made by prior detection using echograms recorded 24 h d^{−1} with a Simrad EK60 scientific echo sounder (Simrad Kongsberg Maritime AS, Horten, Norway) equipped with five split-beam transducers (i.e., 18, 38, 70, 120, and 200 kHz). After the collected fish samples were sorted by hand, 257 fish specimens were isolated, identified to the genus level, and frozen at −4 °C pending further use.

At the laboratory, each frozen sample was thawed under ambient conditions and subjected to body weight (i.e., g), fork length (i.e., cm), and sex determination, and data were recorded. The fish were identified up to the species level using a previously published protocol [1]. The external surfaces, gills, cavities, internal organs, and musculature were examined for the presence of metazoan parasites using a stereomicroscope (Motic, Richmond, BC, Canada); all metazoan parasites were counted and preserved in 4% formalin. For morphological identification, platyhelminths were stained with Gomori’s trichrome reagent, dehydrated using graded ethanol series, cleared with methyl salicylate, and examined as permanent mounts in Canada balsam, while nematodes and crustaceans were cleared in lactic acid. All samples were examined using a compound microscope (Leica DMLB, Leica Microsystems, Wetzlar, Germany).

Fish length and weight were compared among the collected samples using one-way ANOVA. The prevalence and median intensity of parasitic infection was calculated for each parasite species [17,18], where the significant differences among the samples were determined by subjecting the prevalence values to Fisher’s exact test, and the intensity was compared with Mood’s median test (multiple comparisons) and bootstrap *t*-tests (pairwise comparisons), with 1000 replications using Qpweb software [18]. The mean intensity is

commonly provided in parasitological studies; however, in the present study, we preferred to use the median intensity because it is a suitable metric to describe the typical level of infection in a sample [18]. To display the geographical location of the parasites that infect fish in each sampling locality, maps were created with the geographical co-ordinates of localities using the PBSmapping [19] and mapplots [20] packages in R software [21].

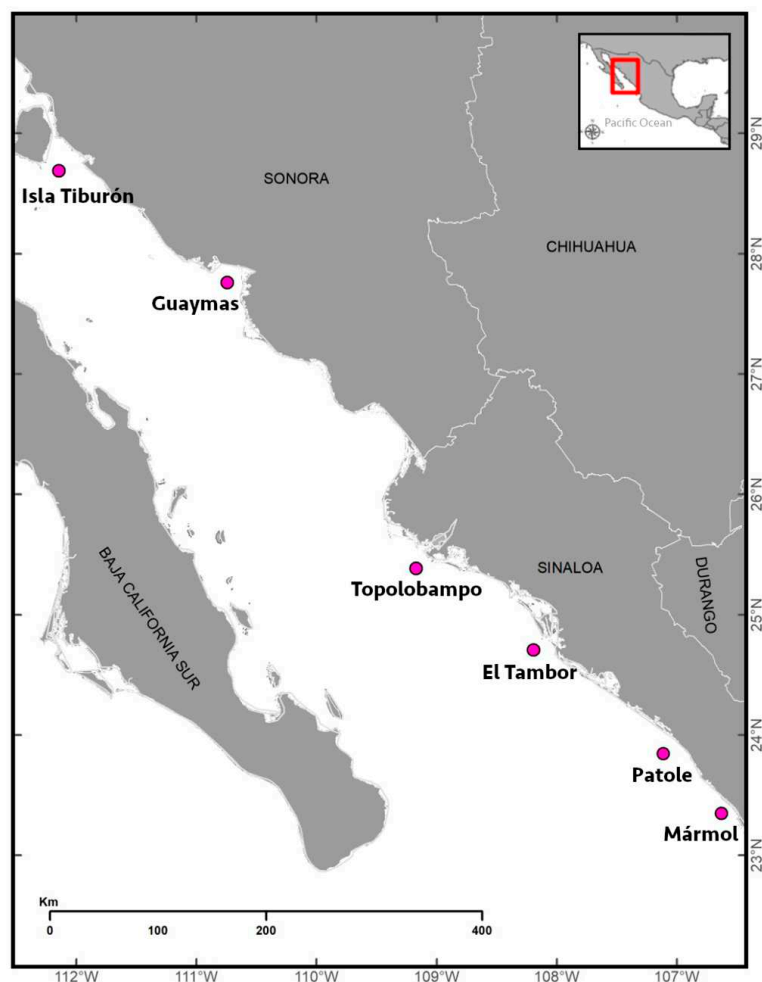


Figure 1. Study area and sampling localities (pink dots) in the Gulf of California in Mexico.

Table 1. Samples of Pacific thread herring, *Opisthonema libertate*, from six localities in the Gulf of California in Mexico.

Locality	Latitude, Longitude	Depth (m)	Temperature (°C)	n
Isla Tiburón	28°70'15.3" N, 112°12'46.9" W	45	30.2	38
Guaymas	27°77'20.9" N, 110°72'53.3" W	47	28.8	57
Topolobampo	25°23'89.6" N, 109°90'85.7" W	15	27.9	48
El Tambor	24°43'12.9" N, 108°10'42.3" W	15	27.7	34
Patole	23°51'49.6" N, 106°36'45.9" W	15	27.8	28
Mármol	23°21'46.1" N, 106°36'45.9" W	15	27.9	52

To study the effect of sampling locality differentiation based on parasite assemblages, non-metric multidimensional scaling (nMDS) was performed based on a Bray–Curtis similarity matrix of infection intensity data (i.e., excluding uninfected fish). The nMDS facilitates the creation of a points configuration in a specified number of dimensions in such a manner that the rank order agreement between the interpoint distances and the resemblance values is maximized. Distances to group centroids were visualized using bootstrap averaging (i.e., 50 iterations; correlation coefficient of $\rho = 0.99$; $m = 4$ dimensions) [22]. A one-way permutational multivariate analysis of the variance (PERMANOVA; 1×6 factorial design, “sampling locality” as a fixed factor) was used to test the differentiation of group centroids; “host size” was introduced as a covariable (ANCOVA model); and the main effects were tested for after 9999 permutations and subsequent post-hoc pair-wise comparisons [23]. The Bray–Curtis similarity matrix was computed on square-root-transformed data to reduce the influence of extreme values when determining similarity in infections among individual fish. These analyses were performed with the use of PRIMER 7 with PERMANOVA+ Add On package.

3. Results

Of the 257 individuals of *O. libertate* analyzed, 166 were females, and 91 were males. The mean fork length and body weight significantly varied between some localities ($p < 0.05$; Figure 2), with both weight and length being notably higher at Isla Tiburón— 21.6 ± 1 cm and 127 ± 18 g, respectively—compared to all other localities ($p < 0.05$), and the smallest fish were located in El Tambor; in this locality, while the fork length was significantly smaller (16.9 ± 1.5 cm) than in all the other localities, the body weight (85.5 ± 23.4 g) only differed from Isla Tiburón, Topolobampo, and Mármol. There was no significant difference in length between the females and males in each locality ($p > 0.05$); the weight of females in Topolobampo (104.2 g) was significantly higher than the males (89.4 g; $p < 0.05$).

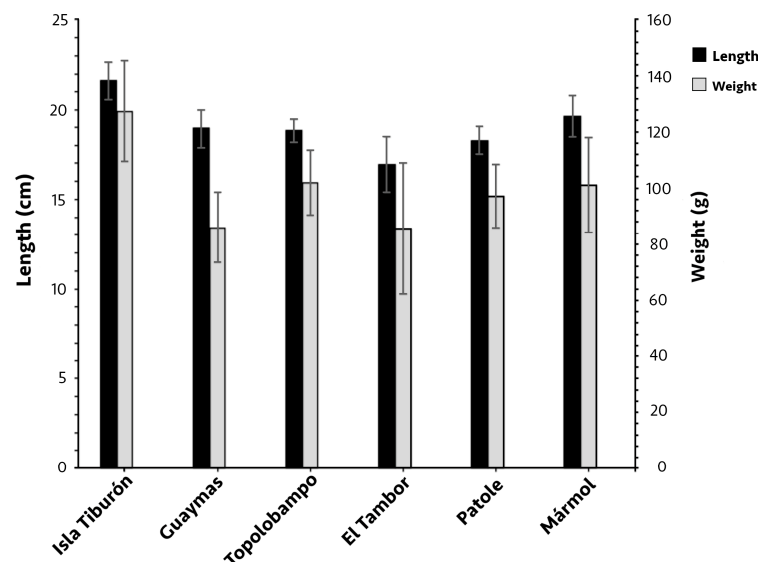


Figure 2. Mean fork length and body weight of Pacific thread herring, *Opisthonema libertate*, from six sampling localities in the eastern Gulf of California; error bars show the standard deviation.

Among the six sampling localities, all collected specimens of *O. libertate* were infected with at least one species of parasite. The parasitofauna consisted of six species: two adult digeneans (i.e., *M. ecaude* and *P. merus*)- and one larval nematode (i.e., *Pseudoterranova* sp.)-infected stomach, and two adult monogeneans (i.e., *Cribromazocraes* cf. *travassosi* and *Mazocraeoides georgei* Price 1936)- and one juvenile copepod (i.e., *Lepeophtheirus* sp.)-infected gills (Figure 3). While the digeneans were highly prevalent at all sampling locations, the other species rarely appeared in some sampling localities with a prevalence and median

intensity of $\leq 12\%$ and ≤ 5 parasites/fish, respectively (Table 2). This was the only reason for applying comparative statistical tests to digenean prevalence and median intensity.

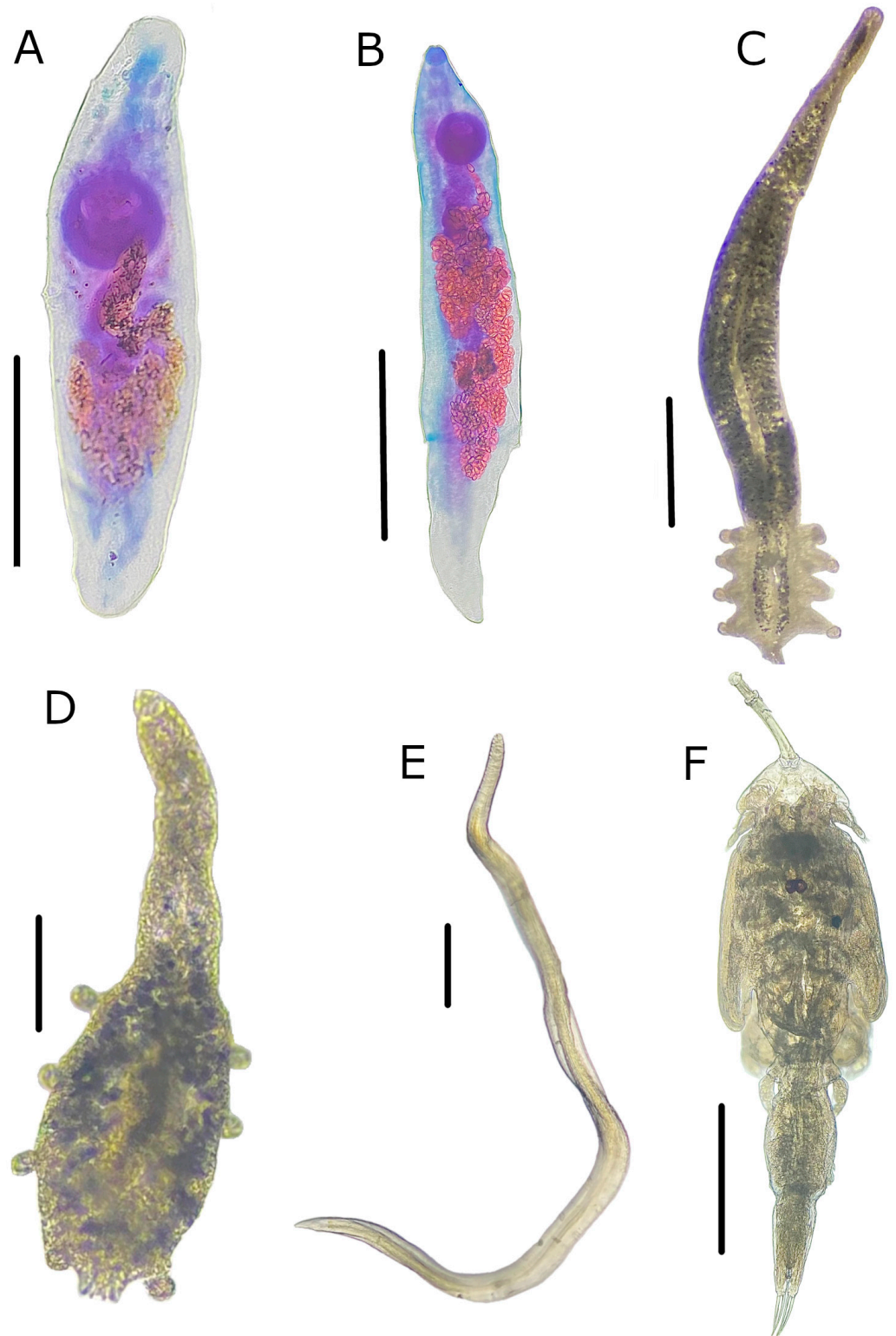


Figure 3. Parasite species found in Pacific thread herring, *Opisthonema libertate* (Günther, 1867), from the eastern Gulf of California in Mexico. (A) *Myosaccium ecaude* Montgomery 1957; (B) *Parahemiurus merus* (Linton 1910); (C) *Cribromazocraes cf. travassosi*; (D) *Mazocraeoides georgei* Price 1936; (E) *Pseudoterranova* sp.; (F) *Lepeophtheirus* sp. Scale bars: 250 μm for (A); 500 μm for (B,C,E); 100 μm for (D), and 1000 μm for (F).

Table 2. Parameters of parasite infection in Pacific thread herring, *Opisthonema libertate*, by six species of metazoan parasites in six localities in the Gulf of California in Mexico.

Parasite		Isla Tiburón	Guaymas	Topolobampo	El Tambor	Patole	Mármol
<i>Myosaccium ecaude</i>	P%	34(19–51) ^{a,c}	75(62–85) ^b	54(39–68) ^c	85(68–95) ^{b,d}	96(81–99) ^d	26(15–41) ^a
	MI	1(1–2) ^a	4(2–6) ^{a,d}	5.5(2–8) ^{c,d}	9(5–18) ^c	19(9–26) ^b	2(1–29) ^{a,b,c}
<i>Parahemiurus merus</i>	P%	84(68–94) ^{a,b}	93(83–98) ^{a,e}	33(20–48) ^c	100(89–100) ^e	96(81–99) ^{a,e}	78(65–88) ^{b,d}
	MI	3.5(2–5) ^{a,b}	7(5–9) ^{a,e}	3(1–8) ^{b,d}	14.5(10–23) ^f	20(15–41) ^{c,f}	6(5–10) ^e
<i>Pseudoterranova</i> sp.	P%	0	0	0	0	0	1(0–10)
	MI	0	0	0	0	0	1(0.9–1)
<i>Lepeophtheirus</i> sp.	P%	0	0	10(3–22)	8(1–23)	0	0
	MI	0	0	1(0.7–1.2)	1(0.9–1.1)	0	0
<i>Cribromazocraes</i> cf. <i>travassosi</i>	P%	0	10(4–21)	2(0–11)	11(3–27)	0	1(0–10)
	MI	0	1.8(1–3)	1(0.9–1.1)	1.75(1.5–1.9)	0	2(1.9–2)
<i>Mazocraeoides georgei</i>	P%	0	0	2(0–11)	11(3–27)	3(1–18)	5(1–15)
	MI	0	0	1(0.9–1.01)	1.25(1.1–1.3)	5(4.6–5.3)	2(1.8–2.1)

Note: statistical tests were only performed for *M. ecaude* and *P. merus*. P% = prevalence; MI = median intensity. Values within parenthesis represent 95% confidence intervals. Superscript letters within the same row indicate significant differences ($p < 0.05$) between localities.

The prevalence and intensity of infection of *M. ecaude* and *P. merus* did not differ significantly between the female and male fish ($p > 0.05$).

Regarding locality distribution, the significant prevalence and median intensity of digeneans were recorded in El Tambor and Patole (Table 2 and Figures 4 and 5). The prevalence of *P. merus* was 100% in El Tambor, which was significantly higher ($p < 0.05$) than in Isla Tiburón, Topolobampo, and Mármol. This was followed by *P. merus* with 96% prevalence in Patole, which was significantly higher ($p < 0.05$) than Topolobampo and Mármol. In contrast, the prevalence of *P. merus* was significantly lower (33%, $p < 0.05$) in Topolobampo compared to all other localities. Moreover, the median intensity of *P. merus* was also significantly higher in Patole (20 parasites/fish, $p < 0.05$) than in all other localities, except for El Tambor, while significantly lower in Topolobampo (3 parasites/fish, $p < 0.05$) than all other localities, except for Isla Tiburón.

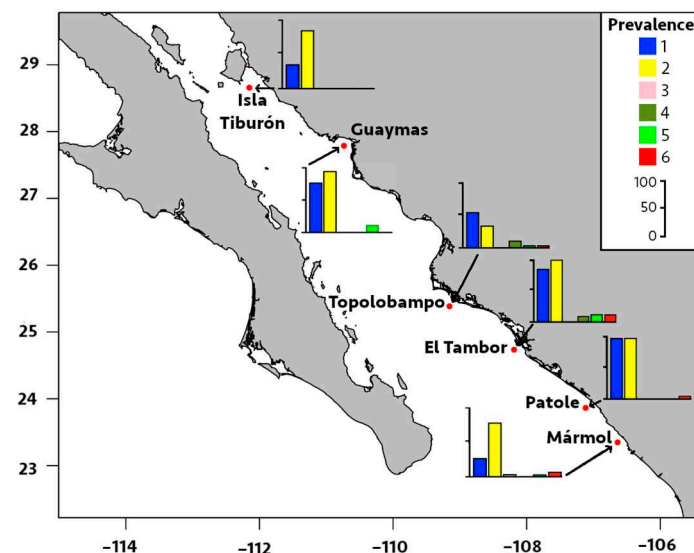


Figure 4. Prevalence of infection by six metazoan parasites in Pacific thread herring, *Opisthonema libertate*, from six localities in the eastern Gulf of California in Mexico. The bar chart represents the prevalence of infection in each locality; each bar corresponds to a parasite species, and the parasites are represented by the following numbers: 1 = *M. ecaude*; 2 = *P. merus*; 3 = *Pseudoterranova* sp.; 4 = *Lepeophtheirus* sp.; 5 = *Cribromazocraes* cf. *travassosi*; 6 = *M. georgei*.

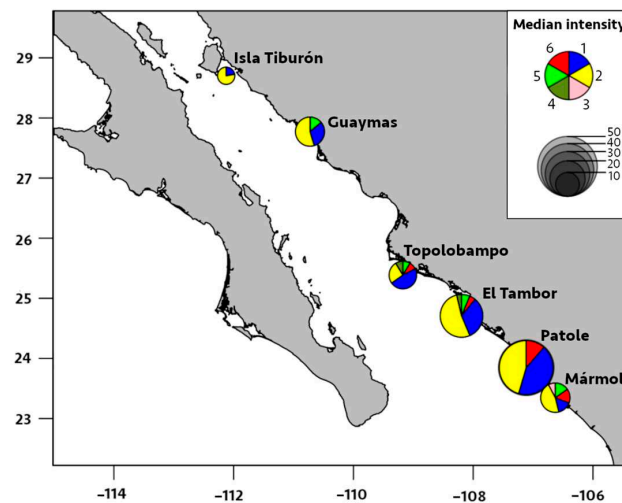


Figure 5. Median intensity of infection by six species of metazoan parasites in Pacific thread herring, *Opisthonema libertate*, from six localities in the eastern Gulf of California in Mexico. The radius of each pie chart represents the total intensity of parasites of all species found in a locality; each slice corresponds to a parasite species, and the parasites are represented by the following numbers: 1 = *M. ecaude*; 2 = *P. merus*; 3 = *Pseudoterranova* sp.; 4 = *Lepeophtheirus* sp.; 5 = *Cribromazocraes* cf. *travassosi*; 6 = *M. georgei*.

The prevalence of *M. ecaude* reached 96% in Patole and was significantly higher ($p < 0.05$) than all other localities, except for El Tambor (85%), with the median intensity reaching 19 parasites/fish in Patole, which was significantly higher than all other areas, except for Mármol ($p < 0.05$). This was followed by *M. ecaude* with the second highest median intensity of 10 parasites/fish in El Tambor, being only significantly higher than in Isla Tiburón and Guaymas ($p < 0.05$).

A Bray–Curtis similarity matrix was computed for the intensity of *P. merus* and *M. ecaude* infection, followed by bootstrap-average-based nMDS ordination generation, which showed an apparent separation between some sampling localities, with clear separation observed for Topolobampo, in addition to El Tambor and Patole separated from Isla Tiburón, Guaymas, and Mármol (Figure 6). According to the PERMANOVA, there was significant variability in the intensity of *P. merus* and *M. ecaude* infection between localities (Table 3). Furthermore, pairwise tests indicated significant differences in all cases ($P_{perm} < 0.01$), except between Isla Tiburón and Mármol and between El Tambor and Patole ($P_{perm} > 0.05$).

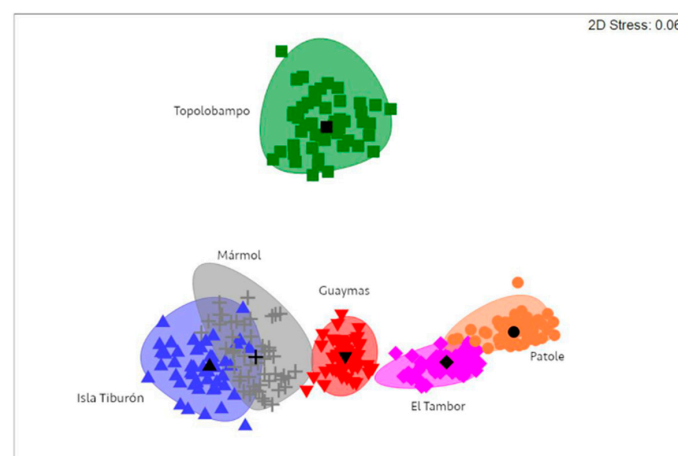


Figure 6. Non-metric multidimensional scaling representation showing separation of sampling localities based on infection intensity of *P. merus* and *M. ecaude* in Pacific thread herring, *Opisthonema libertate*, from the eastern Gulf of California using a Bray–Curtis similarity index.

Table 3. PERMANOVA results of comparisons of infection intensity of *Parahemiurus merus* and *Myosaccium ecaude* in Pacific thread herring, *Opisthonema libertate*, across six localities in the Gulf of California.

Data	Source	d.f.	SS	MS	Pseudo F	P_{perm}
Both parasites (Bray–Curtis similarity)	Host size	1	26,768	26,768	14.23	<0.01
	Locality	5	85,006	17,001	9.03	<0.01
	Host size $\times$ Locality	5	8686.60	1737.3	0.92	>0.05
	Residual	245	4.60 e^5	1880.9		
	Total	256	5.81 e^5			

4. Discussion

4.1. Parasite Species

The novelty of this study lies in reporting the parasitofauna in *O. libertate* from the Gulf of California in Mexico. While six fish parasitic species—including *P. merus*, *M. ecaude*, and *Pseudoterranova* sp.—were previously documented for *O. libertate* from Chamela Bay on the central Pacific coast of Mexico [16]; *Cribromazocraes* cf. *travassosi*, *M. georgei*, and *Lepeophtheirus* sp. have not been previously recorded in this fish species.

Cribromazocraes cf. *travassosi* reported herein morphologically resembles *Cribromazocraes travassosi*, which was originally described by Santos and Kohn [24]; however, our collected specimens were insufficient for correct identification. Moreover, *C. travassosi* has only been found on clupeiform fishes from Brazil, specifically on the *Sardinella brasiliensis*, *Opisthonema oglinum*, *Cetengraulis edentulus*, and *Harengula clupeiola* [25–28]. Similarly, *M. georgei* has been reported in at least seven clupeiform species from the western Atlantic [25,28–32]. It should be noted that some of these records referred to either *Mazocraeoides opisthonema*, *Mazocraeoides hargisi*, or *Mazocraeoides olentangiensis*, all of which are synonymously used for *M. georgei* [31,33]. According to Sailaja et al., only 13 of the 25 species described under the *Mazocraeoides* genus were valid [33]. Moreover, *M. georgei* has only been reported in *Opisthonema oglinum* in the Atlantic but not in any Pacific species of *Opisthonema* [29]. The *Lepeophtheirus* copepods were also never identified at the species level, as they were found at the juvenile (i.e., chalimus) stage. In this study, the copepods were assigned to *Lepeophtheirus* based on body shape, appendage structure, and the absence of lunules in the frontal plate, and no literature is yet available on *Lepeophtheirus* in any *Opisthonema* species. The findings of *C. cf. travassosi*, *M. georgei*, and *Lepeophtheirus* sp., therefore, constitute new host and geographical records.

4.2. Infection-Level Changes

Changes in the prevalence and intensity of infection with *P. merus* and *M. ecaude*, being significantly lower in Topolobampo than in El Tambor and Patole, as well as the separation of the localities indicated by the nMDS and PERMANOVA, suggest a discontinuous distribution of both digenean species; this is possibly due to the latitudinal variability in oceanographic conditions (e.g., water temperature) and the availability of intermediate hosts. Topolobampo is located on the border of the central and southern regions of the gulf, where the abundance of zooplankton is known to be lower than the southern area comprised of El Tambor and Patole [34]. The zooplankton communities are largely formed by copepods [34], which typically act as second intermediate hosts of hemiurid digeneans [35]. The copepod community structure between the southern and central regions differs in response to contrasting environmental conditions [34,36]. The southern region (i.e., the entrance of the gulf) covers the California Current, the Mexican Coastal Current, and the Gulf of California waters and results in particular oceanographic conditions, such as relatively higher seawater temperatures and species assemblages, which facilitate tropical species domination [36–40]. Some studies have reported that increased temperature positively affects the transmission of digeneans, which could be the reason for higher infection levels [41,42]. As such, the relatively higher abundance of intermediary hosts and higher

seawater temperature could have caused the highest parasite infection levels in *O. libertate* caught in El Tambor and Patole to some extent.

Based on the above findings, it is envisaged that the parasite-infection levels in Mármol are comparable to El Tambor and Patole; these levels were lower in Mármol, however, and were highly similar to Isla Tiburón and to Guaymas to a limited extent. While increased temperature positively affects digenean transmission, other local factors may be more critical, so latitudinal gradients in infection levels may not be observed [43]. The eastern coast of the Gulf of California has spatially distinct environmental conditions influenced by agriculture, mariculture, upwellings, seasonal currents, river discharges, and hypoxia [44,45]; these environmental factors along the shallow coastal waters might influence host–parasite interactions differently, thereby making noticeable spatial patterns that are challenging to observe.

4.3. Potential Biological Tags

Parasites are generally reliable biological tags that can improve the understanding of many marine fish stocks [12,14]. The principle underlying this approach is that fish harboring a given parasite species come from geographical areas where this parasite is endemic [12,14]. Parasites can also be used as a tag within their endemic areas, where differences in the behavior and feeding habits of different host populations or the abundance of intermediate hosts can translate into significantly different infection levels in different geographical areas [46]. One prerequisite selection criterion is based on significant levels of parasitic infections in different parts of the study area [14], making *P. merus* and *M. ecaude* digeneans well-suited candidates. Weston et al. employed this criterion to identify different stocks of South African sardine, *Sardinops sagax* (Clupeiformes, Alosidae), using a larval-stage (metacercariae) digenean [47]. Unlike metacercariae, adult digeneans are thought to have short life spans, which hinders their use as biological tags [14,15]; according to Hemmingsen and MacKenzie, however, some adult digeneans might serve as potential indicators for fish movements [48]. Moreover, Jacobson et al. clarified Pacific sardine migration using *M. ecaude* abundance data, pointing out that this parasite has a sufficiently long life span to evaluate the movement of its fish host [13].

Based on the observed differences in *P. merus* and *M. ecaude* infection, it is possible to hypothesize that the individuals of *O. libertate* could have limited movement between certain geographical areas within the Gulf of California. The collected fish specimens in this study were mostly < 20 cm in length, and they could be regarded as non-migrant based on their size. While the clupeiforms' movements throughout the life cycle are not well understood [49]; according to Lo et al., fish < 20 cm in length appear to be unable to migrate due to insufficient energy resources to swim long distances [50].

The overlap between El Tambor and Patole shown by nMDS suggests that fish were moving between these locations or that the environmental and ecological conditions affecting parasite infection were similar, owing to the contiguous nature of the localities [11]; in contrast, the overlap between Isla Tiburón and Mármol may be confusing, since these localities represented the northern and southern extremes of the studied area and might be due to the similarity of infection with *P. merus* and *M. ecaude*. It is worth noting, however, that fish in Isla Tiburón were not infected with the other parasite species found in *O. libertate* from other localities. Nematodes and monogeneans were found in Mármol fish but not in Isla Tiburón; as such, from an ecological perspective, these could be considered different populations based on parasite assemblage differences [12]. A possible structured population of *O. libertate* was also described by Pérez-Quiñonez et al. based on fish morphometrics [8]; they determined that specimens from the central region of the gulf (i.e., Guaymas) represent a different morphotype than specimens from the southern region (i.e., Mazatlán). Similarly, Jacob–Cervantes et al. differentiated southern and northern stocks based on body size [51]. Thus, integrating parasites using other techniques might bring better support when delineating movement patterns and identifying stocks of

thread herrings in the future, which might then provide helpful information to improve the management and sustainable use of marine resources in the context of fisheries.

4.4. Limitations

The limitations of the study might be the differences in host sizes among fishing areas because this can influence parasite burdens. As suggested by Braicovich et al., however, fish length was incorporated as a covariate in the PERMANOVA to “correct” the effect of this variable [52]. The parasitic burden of fish typically increases with age or size, possibly due to large hosts having more surface area for parasite attachment and consuming more food, thereby resulting in higher exposure to infective stages as they grow and leading to cumulative patterns of parasite abundance [53]. Interestingly, in the present study, the smallest fish caught in El Tambor presented a high parasite burden.

5. Conclusions

In this study, the observed changes in parasite infection in *O. libertate* suggest a discontinuous distribution of *P. merus* and *M. ecaude* among localities in the Gulf of California in Mexico. While these changes may indicate that fish—particularly those measuring < 20 cm in length—form discrete populations across the gulf, this is not a solid conclusion because these parasites satisfy some—but not all—of the selection criteria to be used as good biological tags [14]. In the future, it is necessary to continue parasite surveys of *O. libertate* in more locations across the Gulf of California while considering possible drivers such as seasonality and host traits (e.g., diet and ontogeny).

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