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Parasite communities of the gafftopsail pompano *Trachinotus rhodopus* (Carangiformes: Carangidae): examining the parasite species richness and diversity over time

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Abstract: In total 949 specimens of *Trachinotus rhodopus* (Gill) were collected over a 11-year period (from June 2013 to February 2024) from Acapulco Bay, Mexico. Parasite communities in *T. rhodopus* were quantified and analysed to explore two hypotheses related to their parasite species richness and diversity associated with the bentho-demersal and pelagic habits, and effects of the climatic fluctuations. Thirty-two metazoan parasite taxa/species were identified: three species of 'Monogenea', 14 Digenea, one Aspidogastrea, one Acanthocephala, two Cestoda, three Nematoda and eight Crustacea. The digeneans and copepods were the best represented groups. The component parasite communities were characterised by the numerical dominance of the acanthocephalan *Rhadinorhynchus* sp. Species richness (15–24 species) was similar to that reported for other species of carangid fish, but the richness of the digeneans was significantly higher. The parasite communities of *T. rhodopus* exhibited high variability in species composition, suggesting that each species of parasite may respond differently to environmental changes. However, the species richness and diversity were fairly stable over time. Climatic events of La Niña and El Niño probably generated notable changes in the structure of local food webs, thus indirectly influencing the transmission rates of several endoparasite species.

Keywords: Long-term studies, marine parasites, biotic and abiotic factors, determinants of species richness, tropical Pacific, Mexico

Understanding why some species of marine fish are infected by a greater number of parasite species compared to others is an important research topic in parasite ecology (Sasal et al. 1997, Luque et al. 2004, Luque and Poulin 2008). Some studies that tried to identify the main biotic factors influencing the species richness of parasite communities have pointed out that some host traits have a great influence. For example, species richness and diversity of endoparasites are generally positively correlated with the size of the host, because larger (older) hosts tend to ingest greater quantities of food, and thus have had more time to accumulate parasites than smaller individuals (Sasal et al. 1997, Luque et al. 2004, Villalba-Vasquez et al. 2018).

In populations of marine fish, body size has proved to be the main predictor of the presence of a particular parasite species, total abundance and species richness (Luque et al. 2004, Villalba-Vasquez et al. 2018). Feeding habits may also influence the endoparasite species richness. Host species of higher trophic levels (i.e., carnivorous and piscivorous fish) may be more exposed through diet to greater numbers of infective endohelminth larvae from a broader taxonomic range of parasites than would those of a lower trophic levels (Luque and Poulin 2008, Timi et al. 2011). Social behaviour is also considered an important determinant of species richness in parasites that infect populations of marine fish. Species with higher population densities can harbour more species of parasite, because higher population density can facilitate the transmission process, particularly of those with a direct transmission cycle, such 'as monogeneans' and copepods (Sasal et al. 1998, Luque et al. 2004, Violante-González et al. 2020). This gregarious behaviour in fish can cause the structuring of richer and more diverse communities than those in hosts with a low population density (Sasal et al. 1998, Morand et al. 2000, Luque et al. 2004).

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Other abiotic factors may also have important effects on species richness in parasite communities of marine fishes. Physical and biological characteristics of the habitat can indirectly influence the species richness of these communities. Parasite communities of benthic fishes are generally of greater species richness and diversity than fish of pelagic environments because the boundaries of the benthic zone are an important transition point for the exchange of parasites between the faunas that inhabit each different vertical layers in marine habitats (Marcogliese 2002, Luque and Poulin 2008). A greater sampling effort (e.g., long-term studies) can contribute to the detection of a greater number of rare species, which in turn contribute significantly to the species richness and diversity of parasite communities (Kennedy 1993, Schabuss et al. 2005, Villalba-Vasquez et al. 2022, Violante-González et al. 2023).

Finally, variations in abiotic factors such as local fluctuations in surface temperature, and large-scale climatic events such as El Níño and La Niña, which occur at intervals of several years (two to seven years), are known to affect many ecological processes, including the productivity of food webs, and the transmission rates of ectoparasites and trophically transmitted parasites, due to population increases or decreases in potential intermediate or definitive hosts. Therefore, these recurring climatic events can generate important changes in the structure and species composition of marine parasite communities (Oliva et al. 2008, Villalba-Vasquez et al. 2022, Violante-González et al. 2023).

Gafftopsail pompano *Trachinotus rhodopus* (Gill) is an important resource for artisanal fisheries of the Mexican Pacific coasts. It is distributed along the Pacific coast from the southern California, USA, to Peru including the islands of Cocos, Malpelo and Galapagos (Danemann 1993). Species of *Tachinotus* are opportunistic bentho-demersal predators, which feed mainly on benthic invertebrates, and present ontogenic and seasonal variations in feeding behaviour (Danemann 1993, Cruz-Escalona and Abitia-Cárdenas 2004).

The parasite communities of *T. rhodopus* recently have been studied in other locations from the Mexican Pacific. Martínez-Flores et al. (2023) registered nine species of parasites in 110 specimens of *T. rhodopus*, and Osuna-Cabanillas et al. (2024) reported 11 species from 87 fish of the same species. However, both studies were for short-term periods (one and two years, respectively), so possibly many rare species, or those that exhibit temporal variations in their abundance over time were not detected, which is reflected in the low species richness reported.

The objective of this study was to test two hypotheses: 1) due to the bentho-demersal habits of *T. rhodopus*, its parasite communities should present a greater species richness and diversity than that reported for other carangid species with pelagic habits that inhabit in the same study area; and 2) parasite species richness and composition should show interannual variations mainly during long-term periods, due to the effect of large-scale climatic fluctuations (El Niño and La Niña), which alter local environmental conditions for longer periods and would alter the parasite transmission processes.

MATERIALS AND METHODS

Study area

A total of 949 specimens of *Trachinotus rhodopus* were obtained from commercial fishermen as twelve samples over an 11-year period from Acapulco Bay, Mexico (16.8524N, 99.8823W). Aquatic productivity in this location is influenced by two climatic seasons: dry (December to May) and rainy (June to November). During the period covered by this study (June 2013–February 2024), two climatic events were recorded: a strong cooling phase of ENSO (La Niña 2020–2021), and a very strong warming phase (El Niño 2023–2024). Therefore, multivariate El Niño index values (MEI) for each sampling date were obtained from the National Oceanic and Atmospheric Administration (NOAA) database.

Fish collection and biometric data

Fish were measured (total length), weighed and sexed at the time of collection and later pooled into three size-classes: immature (< 20 cm), pre-adults (21–25 cm) and adults (> 25 cm). The Fulton's condition factor (CF) was calculated using the equation: $CF = W_t/L_t^3$, where W_t = total weight, and L_t = total length. Possible differences in body size of fish between sample dates were evaluated using a one-way Anova.

Parasite collection methods

A complete necropsy was carried out on all specimens and all parasites were collected from the external and internal organs. The helminths and crustaceans found were fixed in 4% formalin by 15 min and then stored in 70% ethanol. Helminths were stained with carmine or Gomori's trichrome, dehydrated using a graded alcohol series, cleared in methyl salicylate, and mounted whole on slides. Nematodes were cleared with glycerine for examination using light microscopy and then stored in 70% ethanol. Parasites were identified to the lowest possible taxonomic level using specialised literature, and vouchers of the most abundant and best preserved specimens deposited in the Colección Nacional de Helmintos (CNHE: 12165–12197), Universidad Nacional Autónoma de México, Mexico City.

Contents of the digestive tract were also examined to identify prey items that had been consumed by each fish. Prey item analysis was carried out using the frequency of occurrence method: FO = number of stomachs containing a specific prey item/total number of stomachs examined × 100 (Muñoz et al. 2006, Ñacari et al. 2022), and variety of fish diet was calculated as the diversity of items consumed by populations of fish in each sampling year through the use of the Shannon-Wiener index at the family level of prey items.

Infection parameters

Infection levels for each species of parasite were described using prevalence, mean abundance and intensity (minimum–maximum) as indicated by Bush et al. (1997). Possible differences in infection levels between sampling dates were identified using likelihood ratio *G*-tests for prevalence, and Factorial Anovas (General Lineal Model, GLM) for abundance. Additionally, one-way permutational multivariate analysis of variance (PERMANOVA) with Bray-Curtis distances was used to examine the effects of biotic or abiotic factors on the abundance of component species (parasite species with a prevalence > 10%), and their

Table 1. Parasite infection parameters for *Trachinotus rhodopus* (Gill) from Acapulco Bay, Mexico. P = prevalence, (A) = number of parasites per infected fish, T = total number of individual parasites collected, [range] = minimum to maximum number of parasites present. Subscripts to the right of the sampling year indicate the sampling month. Significantly different measurements of prevalence (G-test) and abundance (Factorial Anova) ($p < 0.05$) are in bold.

Parasite	June 2013	Feb 2014	June 2017	Sept 2018	June 2019	May 2020b	July 2020c	June 2021	June 2022	July 2023	Dec 2023b	Feb 2024
'Monogenea'	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]	P(A)/ T[range]
Pyragraphorus hollisae Euzet et Ktari, 1970	77.8 (2.90) 183 [1–17]	56.9 (1.97) 142 [1–31]	52.9 (1.91) 130 [1–16]	53.5 (1.72) 122 [1–12]	76.0 (2.67) 256 [1–22]	74.7 (2.98) **435** [1–28]	**88.2** **(3.30)** 337 [1–15]	81.2 **(3.83)** 264 [1–19]	61.9 (1-75) 110 [1–12]	42.4 (0.73) 67 [1–9]	57.6 (1.61) 53 [1–12]	44.6 (1.65) 122 [1–23]
Pseudobicotylophora lopezochoterenai Lamothe-Argumedo et Pulido-Flores, 1997	31.7 (0.94) 59 [1–12]	15.3 (0.31) 22 [1–4]	44.1 (0.91) 62 [1–11]	8.4 (0.18) 13 [1–4]	28.1 (1.00) 96 [1–25]	28.8 (1.05) 153 [1–49]	17.6 (0.25) 25 [1–5]	**50.7** **(2.38)** **164** [1–20]	14.3 (0.49) 31 [1–18]	1.1 (0.01) 1 [0–1]	18.2 (0.21) 7 [1–2]	9.5 (0.14) 10 [1–2]
Pseudempleurosoma sp.	4.8 (0.08) 5 [1–2]	5.6 (0.06) 4 [0–1]	5.9 (0.07) 5 [1–2]		6.2 (0.11) 11 [1–4]	24.0 (0.66) 96 [1–7]		13.0 (0.28) 19 [1–5]	7.9 (0.11) 7 [1–2]			
Digenea												
Bucephalus margaritae Ozaki et Ishibashi, 1934											3.0 (0.06) 2 [0–2]	
Ectenurus virgula Linton, 1910	11.1 (0.19) 12 [1–3]	2.8 (0.03) 2 [0–1]	1.5 (0.01) 1 [0–1]	8.4 (0.13) 9 [1–3]	8.3 (0.09) 9 [1–2]	39.0 (1.39) 203 [1–18]	**55.9** **(3.35)** **342** [1–34]	1.4 (0.03) 2 [0–2]	7.9 (0.17) 11 [1–6]	1.1 (0.01) 1 [0–1]		4.0 (0.08) 6 [0–2]
Phyllodistomum carangis (MacCallum, 1913)	1.6 (0.02) 1 [0–1]	4.2 (0.04) 3 [0–1]										
Gonocercella pacifica Manter, 1940	62.0 (2.71) 171 [1–14]	62.5 (1.79) 129 [1–15]	61.8 (1.97) 134 [1–9]	16.9 (0.25) 18 [1–3]	52.1 (1.52) 146 [1–14]	47.9 (1.79) **262** [1–23]	10.8 (0.19) 19 [1–8]	**79.7** **(3.41)** 235 [1–14]	22.2 (0.44) 28 [1–9]	15.2 (0.25) 23 [1–3]	6.1 (0.06) 2 [0–1]	6.8 (0.07) 5 [0–1]
Lecithocladium angustiovum Yamaguti, 1953						5.5 (0.15) 22 [1–7]	2.0 (0.02) 2 [0–1]			7.6 8 [1–2]		
Lecithochirium microstomum Chandler, 1935	17.5 (0.40) 25 [1–3]	4.2 (0.08) 6 [1–3]	2.9 (0.03) 2 [0–1]	11.3 (0.15) 11 [1–3]	8.3 (0.18) 17 [1–4]	36.3 (0.89) 130 [1–10]	**61.8** **(2.96)** **302** [1–38]	2.9 (0.03) 2 [0–1]	7.9 (0.10) 6 [1–2]	2.2 (0.02) 2 [0–1]		17.6 (0.32) 24 [1–6]
Proctoeces sp.	68.2 (6.11) 381 [1–76]	11.1 (0.14) 10 [1–2]	23.5 (0.54) 37 [1–7]	15.5 (0.27) 19 [1–4]	14.6 (0.32) 31 [1–12]	**24.7** **(1.27)** **186** [1–57]	17.6 (0.35) 36 [1–5]	11.6 (1.14) 79 [1–51]	4.8 (0.14) 9 [1–6]	3.3 (0.03) 3 [0–1]	6.1 (0.12) 4 [1–3]	13.5 (0.42) 31 [1–6]
Phyllodistomum sp.		2.8 (0.03) 2 [0–1]	1.5 (0.01) 1 [0–1]		5.2 (0.06) 6 [1–2]	10.3 (0.24) 35 [1–7]	2.0 (0.02) 2 [0–1]	1.4 (0.01) 1 [0–1]	9.5 (0.38) 24 [1–10]	2.2 (0.02) 2 [0–1]	3.0 (0.03) 1 [0–1]	
Hirudinella ventricosa (Pallas, 1774)						2.0 (0.02) 3 [0–1]	2.0 (0.05) 5 [1–4]					
Opechona faryngodactyla Manter, 1940						3.4 (0.34) 49 [3–24]	7.8 (0.30) 31 [1–8]	2.9 (0.03) 2 [0–1]			6.1 (0.09) 3 [1–2]	16.2 (0.55) 41 [1–7]
Rhipidocotyle pentagonum (Ozaki, 1924)								7.2 (0.17) 12 [1–5]				
Stephanostomum casum (Linton, 1910)	15.9 (0.49) 31 [1–9]	6.9 (0.47) 34 [1–24]	7.3 (0.07) 5 [0–1]		4.2 (0.05) 5 [1–2]	6.2 (0.06) 9 [0–1]	2.9 (0.04) 4 [1–2]	7.2 (0.12) 8 [1–2]	6.3 (0.21) 13 [1–10]	4.3 (0.05) 5 [1–2]	9.1 (0.24) 8 [1–6]	23.0 (0.51) 38 [1–7]
Anacetabulum-type (larvae)	25.4 (0.37) 23 [1–3]	6.9 (0.08) 6 [1–2]		2.8 (0.03) 2 [0–1]	8.3 (0.13) 12 [1–2]	**24.0** **(0.44)** **64** [1–7]	21.6 (0.32) 33 [1–3]	13.0 (0.22) 15 [1–2]	6.3 (0.10) 6 [1–2]	3.3 (0.03) 3 [0–1]		5.4 (0.05) 4 [0–1]
Pseudopecoelus sp.						0.6 (0.03) 4 [0–4]					3.0 (0.06) 2 [0–2]	

Table 1. continued...

Aspidogastrea												
Lobatostoma pacificum Manter, 1940	34.9 (1.70) 107 [1–17]							5.8 (0.06) 4 [0–1]				
Acanthocephala												
Rhadinorhynchus sp.	73.0 (3.08) 194 [1–13]	94.4 (5.38) 387 [1–27]	80.9 (8.43) 573 [1–105]	85.9 **(36.56)** 2596 [1–183]	66.7 (7.90) 758 [1–151]	76.7 (18.78) **2742** [1–166]	**96.1** (20.34) 2075 [1– 87]	91.3 (11.42) 788 [1–57]	82.5 (28.03) 1766 [1–450]	42.4 (2.04) 188 [1–41]	6.06 (0.09) 3 [1–2]	45.9 (4.26) 315 [1–90]
Cestoda												
'Tetraphyllidea' gen. sp. (larvae)		2.8 (0.03) 2 [0–1]	1.5 (0.01) 1 [0–1]	1.4 (0.01) 1 [0–1]		10.3 (0.18) 27 [1–6]	3.9 (0.04) 4 [0–1]			2.2 (0.04) 4 [0–2]		4.0 (0.16) 12 [2–8]
Trypanorhyncha gen. sp. (larvae)						6.2 (0.07) 10 [1–2]						
Nematoda												
Anisakis sp. (larvae)	9.5 (0.10) 6 [0–1]	1.4 (0.01) 1 [0–1]	17.6 (0.21) 14 [1–2]	26.8 **(0.66)** 47 [1–9]	12.5 (0.34) 33 [1–8]	26.7 **(0.64)** **94** [1–21]	29.4 (0.57) 58 [1–5]	18.8 (0.45) 31 [1–5]	9.5 (0.10) 6 [0–1]	**35.9** (1.09) 100 [1–16]	18.2 (0.18) 6 [0–1]	23.0 (0.61) 45 [1–9]
Hysterothylacium sp.	9.5 (0.14) 9 [1–3]	6.9 (0.07) 5 [0–1]		5.6 (0.08) 6 [1–2]	7.3 (0.08) 8 [1–2]	4.1 (0.05) 8 [1–3]	5.9 (0.07) 7 [1–2]		3.2 (0.03) 2 [0–1]		3.0 (0.03) 1 [0–1]	
Procamallanus sp.				1.4 (0.01) 1 [0–1]								
Copepoda												
Caligus asperimanus Pearse, 1951	77.8 (2.65) 167 [1–14]	75.0 (3.03) 218 [1–19]	48.5 (0.97) 66 [1–8]	43.7 (0.83) 59 [1–5]	54.2 (1.18) 113 [1–7]	85.6 (3.18) **464** [1–20]	**89.2** **(4.21)** **421** [1–23]	49.3 (1.39) 96 [1–10]	30.2 (0.46) 29 [1–6]	29.3 (0.33) 30 [1–2]	45.4 (0.67) 22 [1–3]	66.2 (1.18) 87 [1–7]
Caligus chorinemi Krøyer, 1863											6.1 (0.06) 2 [0–1]	
Caligus mutabilis Wilson, 1905											6.1 (0.06) 2 [0–1]	8.1 (0.08) 6 [0–1]
Bomolochus bellones Burmeister, 1835	39.7 (1.03) 65 [1–8]	32.0 (0.65) 47 [1–6]	25.0 (0.60) 41 [1–7]	35.2 (0.68) 48 [1–7]	43.7 (1.25) 120 [1–13]	42.5 (1.16) **169** [1–8]	**60.8** (1.46) 149 [1–9]	56.5 **(2.19)** 151 [1–14]	23.8 (0.59) 37 [1–8]	30.4 (0.64) 59 [1–6]	27.3 (0.42) 14 [1–3]	13.5 (0.14) 10 [0–1]
Hatschekia longibrachium Yamaguti, 1939						0.68 (0.01) 1 [0–1]						
Pentastomida												
Sebekia sp. (larvae)						0.68 (0.01) 2 [0–2]	0.98 (0.01) 1 [0–1]					
Isopoda												
Ancinus depressus (Say, 1818)	3.2 (0.03) 2 [0–1]	2.8 (0.03) 2 [0–1]			1.0 (0.01) 1 [0–1]	5.5 (0.05) 8 [0–1]	2.9 (0.03) 3 [0–1]					
Branchiura												
Argulus sp.			2.9 (0.03) 2 [0–1]									

interaction on species composition and the parasite community structure. Spearman's correlation coefficient (r_s) was used to determine possible relationships between total length of the fish and the abundance of each component species of parasite.

Study levels of parasite species

Analyses were made at the levels of component community (i.e., total species of parasite in all fish collected at a sampling date) and infracommunity (i.e., total species of parasite in each individual fish). Component community parameters included total species richness; total number of individuals of each species of parasite; the exponential of Shannon-Wiener Index (Hill number, ^{1}D) as a measure of parasite diversity; species evenness (equitability); and the Berger-Parker Index (BPI) as a measure of numerical dominance (Magurran 2004). Rank-abundance curves were used to visualise changes in the species composition between sampling dates.

Similarity analysis, based on Bray-Curtis similarity coefficients (square root transformed abundance data), was used to evaluate similarity and difference in species composition of parasite community between sampling dates. Non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity index was used to rank the component parasite communities according to their relative similarities and visualise possible differences in species composition. One-way analysis of similarity (ANOSIM) was used to determine the significance of possible grouping patterns in the nMDS ranking. When a Global R-value of the ANOSIM was > 0.75, the species composition of the parasite communities was considered to be different, and when a Global R value < 0.25, the communities exhibited high similarity in species composition. Differences between component community parameters were identified using the non-parametric Kruskal-Wallis test, or the Student *t* test, considering data of the total population of fish on each sampling date as a component community.

Infracommunities were described in terms of mean number of parasite species per host, mean number of individuals of each species and the mean Brillouin Diversity Index (H') value per host. The multivariate general linear model (GLM) and PERMANOVA analysis were used to identify possible differences in infracommunity parameters (dependent variables) between sampling years and climatic seasons (predictor variables); fish body size (total length) was used as a covariate to control for the influence of host body size. The significance of all statistical analyses was established at $\alpha = 0.05$, unless stated otherwise.

Additionally, possible variations in the parasite infracommunity structure over time were evaluated using the "nestedness temperature calculator" (T^o index, Atmar and Patterson 1995). This calculator considers a random matrix in terms of disorder, or entropy. The relationship between entropy and heat is used to quantify a randomness matrix in terms of temperature, with 0° representing minimum entropy (perfect nestedness) and 100° representing maximum entropy (randomness). The significance of a derived T^o value was estimated with a *t*-test, through the use of a normal distribution of 500 Monte Carlo simulated T^o values. Spearman rank correlation tests (r_s) between the fish total length and species richness of each infracommunity were applied to determine whether nestedness could result simply from a size-related accumulation of parasite species due to the increase in the fish feeding rate with the age (Poulin and Valtonen 2001).

Principal Component Analysis (PCA) was applied to identify factors that influenced parasite infracommunity species richness and diversity. The variables used were: Fulton's condition factor (CF) (Froese 2006), sex, host body size, diet diversity, MEI values and sampling date. Discriminant function analyses based on Mahalanobis distances were used to identify possible differences in parasite community structure between sampling dates. The probability of correct classification expected by chance alone of fish to any sampling year was calculated using the proportional chance criterion (Poulin and Kamiya 2015). Only species with a prevalence > 10% in at least one of the sampling years (a component species; *sensu* Bush et al. 1990) were included in these analyses. The statistical packages SPSS (IBM SPSS Statistics for Windows, Ver. 20.0), R package Ver. 2.5-7 and PRIMER v6. software were used for all statistical analyses.

RESULTS

Species composition

A total of thirty-two species/taxa of metazoan parasites (24 species of helminths and eight of crustaceans) were identified, and 22,497 individual parasites were recovered from 925 infected (97.5%) *Trachinotus rhodopus*, collected from Acapulco Bay, Mexico, during the 11-year period. These species included: three of 'Monogenea' (adults), 14 Digenea (13 adults and one metacercaria), one Aspidogastrea (adult), one Acanthocephala (adult), two Cestoda (larvae), three Nematoda (two adults and one larvae), and eight Crustacea (Table 1). Species richness was highest among digeneans, which represent 44% of total species, followed by copepods (16%).

Based on the infection site, 10 species were ectoparasites and 22 were endoparasites. Eleven taxa occurred in all or most of samples (*Pyragraphorus hollisae* Euzet et Ktari, 1970; *Pseudobicotylophora lopezochoterenai* Lamothe-Argumedo et Pulido-Flores, 1997; *Ectenurus virgula* Linton, 1910; *Gonocercella pacifica* Manter, 1940; *Lecithochirium microstomum* Chandler, 1935; *Proctoeces* sp.; *Stephanostomum casum* (Linton, 1910); Anacetabulum-type, *Rhadinorhynchus* sp., *Caligus asperimanus* Pearse, 1951; and *Bomolochus bellones* Burmeister, 1835) (Table 1), and were considered to be component species (prevalence > 10%).

Variation in the parasite infection levels

The prevalence of the 11 component species varied significantly between sampling dates; however, no clear pattern of temporal variation could be identified. For example, only three endoparasite species: *E. virgula* (G = 247.1, $p < 0.01$), *L. microstomum* (G = 211.9, $p < 0.01$), and *Rhadinorhynchus* sp. (G = 110.5, $p < 0.01$), as well as the ectoparasites *Py. hollisae* (G = 39.1, $p < 0.01$), *C. asperimanus* (G = 79.9, $p < 0.01$), and *B. bellones* (G = 57.2, $p < 0.01$), exhibited higher prevalence values in July 2020 (Table 1), during a climatic event (La Niña). The remaining component species, were more prevalent on different sampling dates (Table 1).

All component species also exhibited significant variation in their mean abundance values. The mean abundance values of the ectoparasites *Py. hollisae* (GLM: $F_{11,924} = 6.37$, $p < 0.01$), *Ps. lopezochoterenai* (GLM: $F_{11,924} = 5.4$, $p<0.01$), *B. bellones* (GLM: $F_{11,924} = 7.1$, $p < 0.01$), and the endoparasite *G. pacifica* (GLM: $F_{11,924} = 18.5$, $p < 0.01$), were higher in June 2021 while those of the copepod *C. asperimanus* (GLM: $F_{11,924} = 18.6$, $p < 0.01$), and the digeneans *E. virgula* (GLM: $F_{11,924} = 18.4$, $p < 0.01$), *L. microstomum* (GLM: $F_{11,924} = 15.1$, $p < 0.01$), and Anacetabulum-type (GLM: $F_{11,924} = 6.7$, $p < 0.01$) were higher in July 2020 (Table 1).

Host body size was more negatively and significantly correlated with the abundance values of several parasite taxa: *Py. hollisae* (r_s = -0.130, $p < 0.01$), *E. virgula* (r_s = -0.221, $p < 0.01$), *G. pacifica* (r_s = -0.109, $p < 0.01$), *L. microstomum* (r_s = -0.215, $p < 0.01$), *Rhadinorhynchus*

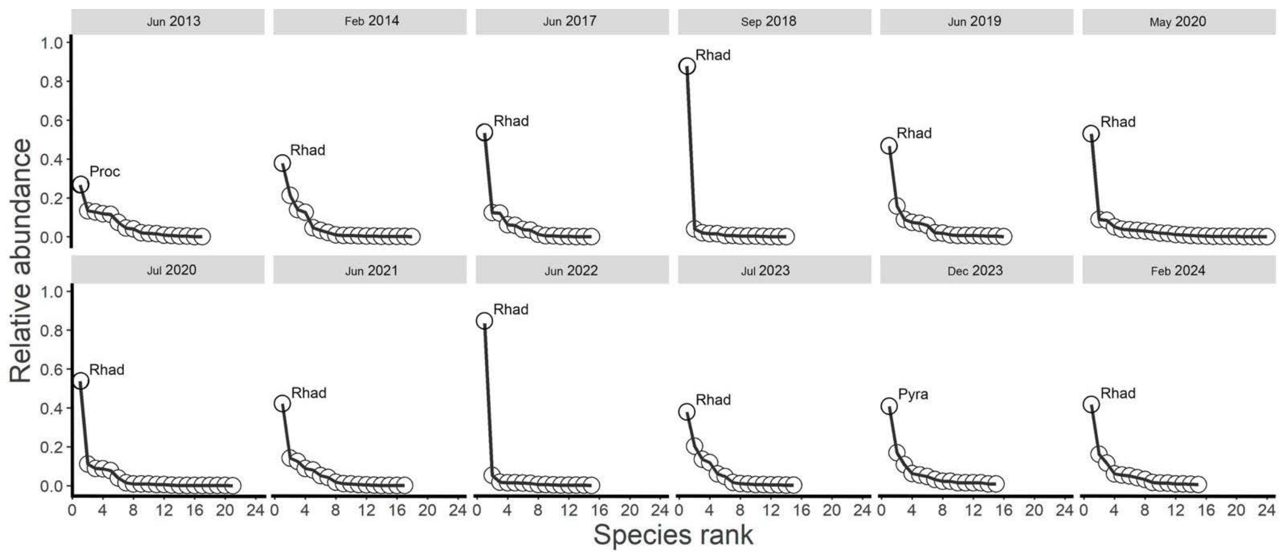

Fig. 1. Range-abundance curves for parasite component communities of *Trachinotus rhodopus* (Gill), from Acapulco Bay, Mexico. Proc – *Proctoeces* sp., Rhad – *Rhadinorhynchus* sp., Pyra – *Pyragraphorus hollisae.*

sp. (r_s = -0.357, $p<0.01$), *C. asperimanus* (r_s = -0.184, $p<0.01$), and *B. bellones* (r_s = -0.229, $p<0.01$).

Host diet composition

The alimentary spectrum of *Trachinotus rhodopus* included 15 prey items, of which snails (36.1%), crab larvae (26.5%) and amphipods (21.5%) represented the largest proportions. Additional prey items accounted for 15.8% of the diet and included: penneid larvae, isopods, small fish, clam larvae, etc. The diet composition varied through sampling dates (t = 3.92, $p<0.01$); for example, in May, July 2020, June 2021, and June 2022 the diet composition was more varied (H ≥ 0.900, Table 2). Feeding habits also changed with body size: immature fish (< 20 cm) and pre-adults (21–25 cm) had a more varied diet and consumed greater proportions of snails, amphipods and fish larvae than larger fish (adults: > 25 cm), in which the most common preys were crab larvae.

Component communities

Species richness of parasite at component community level (Table 2) varied significantly from 14 (September 2018) to 24 (May 2020) (Kruskal-Wallis test H = 342.30, d.f. = 9, $p<0.01$). The total number of individual parasites ranged from 215 (August 2016) to 4,222 (April 2021) (Kruskal-Wallis test H = 317.46, d.f. = 9, $p<0.01$). The acanthocephalan *Rhadinorhynchus* sp. numerically dominated the most parasite communities (Table 2). Diversity index values were generally high during ten sampling dates (^{1}D > 15). Rank-abundance curves indicated that the distribution of species abundance changed notably throughout the study period (Fig. 1). For example, in the June 2013, February 2014 and July 2020 samples the abundances of ≈ 32% of the species was more similar therefore these communities were more homogeneous in their species composition (Fig. 1). The abundance distribution in all samples was best described by the log-normal model. Significant nestedness occurred in all parasite communities,

Table 2. Characteristics of the parasite component communities in *Trachinotus rhodopus* (Gill) from Acapulco Bay, Mexico. MEI – multivariate El Niño index (positive values represent the warm phase, while negative values the cooling phase); length – total length; CF – condition factor; BPI – Berger-Parker index; Proc – *Proctoeces* sp.; Rhad – *Rhadinorhynchus* sp., Pyra – *Pyragraphorus hollisae*; ^{1}D – exponential of Shannon's entropy index; T^o – temperature index; *rs* – correlation coefficients. *Significant at $p<0.05$.

Year	Date	Season	MEI	No. of fish	Length (cm)	CF	Diet variety	Species richness	No. of parasites	BPI	Dominant species	^{1}D	T^o	Size vs richness rs
2013	Jun	rainy	-1.2	63	21.8 ± 2.5	1.10	0.851	17	1445	0.266	Proc	34.23	19.59	-0.322*
2014	Feb	dry	-0.4	72	23.4 ± 1.8	0.90	0.869	18	1022	0.379	Rhad	19.26	8.30	0.251*
2017	Jun	rainy	-0.7	68	26.5 ± 2.5	1.02	0.872	15	1074	0.534	Rhad	14.03	14.35	-0.139
2018	Sep	rainy	0.5	71	25.0 ± 3.9	1.01	0.731	14	2952	0.879	Rhad	3.45	12.64	-0.141
2019	Jun	rainy	0.2	96	27.4 ± 5.9	0.98	0.844	16	1622	0.467	Rhad	18.82	15.90	-0.243*
2020	May	dry	-0.7	146	25.4 ± 5.2	1.01	1.30	24	5176	0.530	Rhad	20.94	19.91	0.038
2020	Jul	rainy	-1.0	102	22.4 ± 3.3	0.95	0.950	21	3866	0.537	Rhad	15.11	14.42	-0.174
2021	Jun	rainy	-1.5	69	23.7 ± 1.2	1.05	0.903	17	1873	0.421	Rhad	20.83	12.31	-0.045
2022	Jun	rainy	-2.2	63	25.0 ± 2.6	0.96	0.954	15	2085	0.847	Rhad	4.31	11.65	0.069
2023	Jul	rainy	0.5	92	26.2 ± 3.1	0.97	0.823	15	496	0.379	Rhad	19.63	11.93	-0.226*
2023	Dec	dry	0.9	33	28.7 ± 1.9	0.87	0.815	15	130	0.408	Pyra	25.47	7.19	-0.009
2024	Feb	dry	0.7	74	27.6 ± 4.1	0.89	0.792	15	756	0.417	Rhad	23.79	18.27	0.131

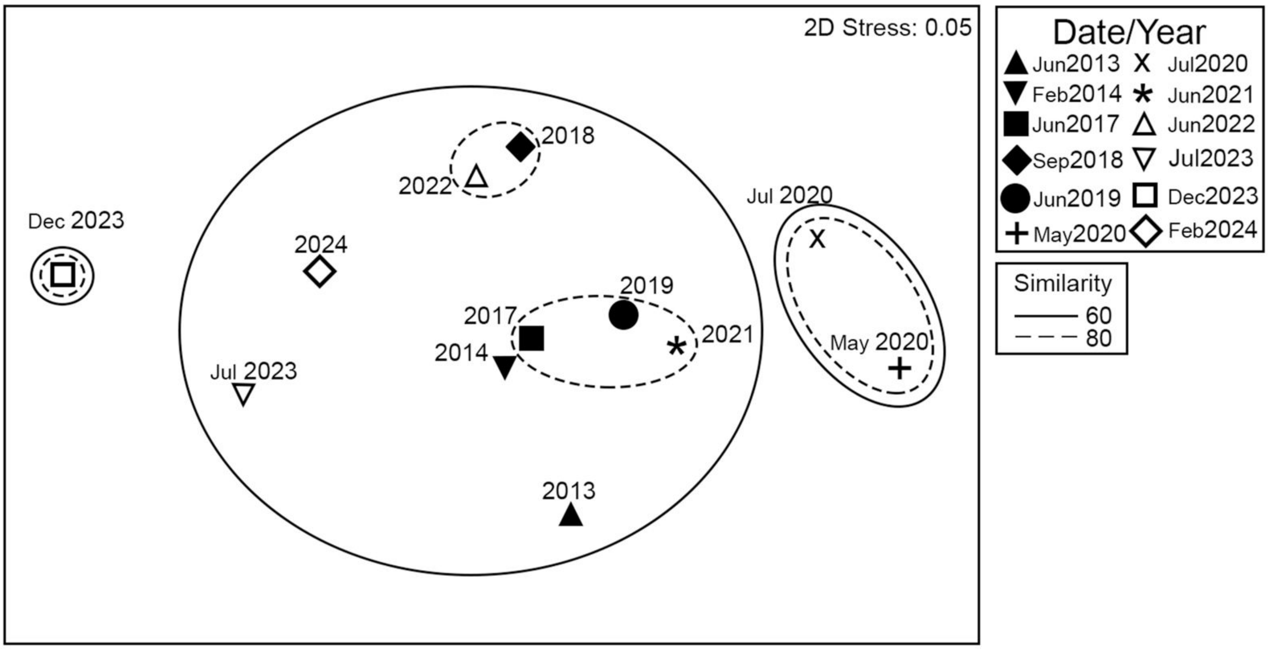

Fig. 2. Non-metric multidimensional scaling (nMDS) plot for parasite communities of *Trachinotus rhodopus* (Gill), from Acapulco Bay, Mexico. Ellipses represent similarity levels between sampling year.

but the intensity varied significantly (t = 5.69, p<0.01, n = 10) from T^{p} = 7.19 (December 2023) to T^{p} = 19.59 (June 2013), during the study period (Table 2). Negative correlation between parasite species richness and host body size observed only in some communities. Similarity between component communities varied widely from 4.7% (May 2020–December 2023) to 89.7% (June 2019–June 2021) (mean = 43.4%). The nMDS ranking of the component communities showed a strong clustering (9/12 communities) at a similarity level of 60% but there was a clear separation of three parasite communities (May 2020, July 2020 and December 2023, Fig. 2).

The ANOSIM did not show significant differences in the similarity of parasite communities between sample dates (global R = 0.186, p<0.01), suggesting high similarity in species composition. However, the results of the PERMANOVA analysis indicated that abundance of component parasite species varied significantly between sample dates. The interactions between year/date × size and year/date × CF explained the highest percentage of the variability in the abundance of these parasite species over the study period (Table 3).

Infracommunities

The body size of the fish ranged from 22.4 ± ± 3.3 cm (July 2020) to 28.7 ± 1.9 cm (December 2023) (Table 2), and differed between sample dates (Anova $F_{9,924}$ = 20.62, p<0.01). Females were significantly larger than males (Anova $F_{1,676}$ = 7.90, p<0.01). All infracommunity parameters varied significantly between sampling dates. Mean species richness of parasites varied from 2.5 ± 1 to 5.86 ± 1.9 (GLM: Anova $F_{9,924}$ = 50.33, p<0.01), the mean number of individual parasites from 4.48 ± 3.42 to 43.41 ± 39.5 (GLM: Anova $F_{9,924}$ = 16.87, p<0.01), and the Brillouin diversity

Table 3. Results of the PERMANOVA analysis based on Bray-Curtis dissimilarities, on biotic and abiotic factors that explain variation in the abundance of component species and infracommunity parameters for parasites of *Trachinotus rhodopus* (Gill) from Acapulco Bay, Mexico. Size – host body size (total length); CF – condition factor; Richness – number of parasite species per host; Load = total number of parasites per infracommunity; Diversity – Brillouin diversity index values. Only significant effects are listed. df – degrees of freedom; SS – sums of squares; MS – mean squares.

Source	df	SS	MS	Pseudo-F	*p*-value	Variation components (%)
Abundance of component species						
Year/date	11	460300	41846	29.44	0.001	23.03
Size	924	450200	2473.6	1.40	0.001	11.89
CF	924	1715700	1921.3	1.42	0.002	23.36
Year/date × size	924	539140	1485.2	1.21	0.001	12.60
Year/date × CF	924	7293.3	2431.1	2.41	0.002	37.72
Infracommunity parameters						
Richness	924	270550	24595	15.10	0.001	17.80
Load	924	534890	4952.7	3.30	0.001	20.32
Diversity	924	1125200	2250.5	1.51	0.001	20.35
Year/date × load	924	395770	1256.4	1.08	0.015	6.72

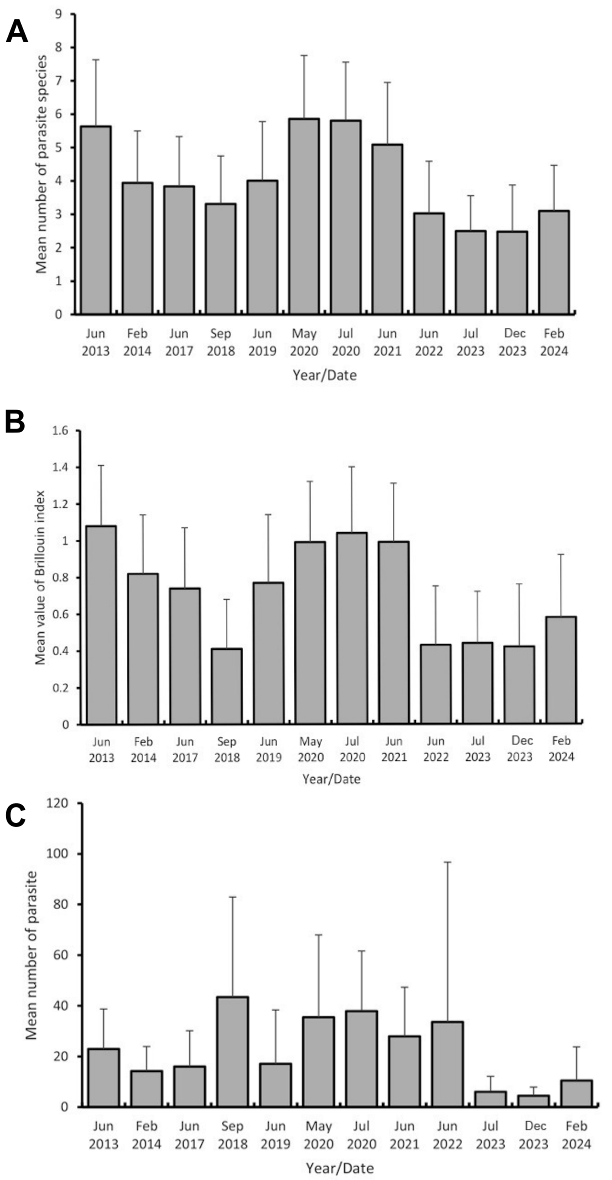

Fig. 3. Mean values of the infracommunity parameters (± standard deviation) of *Trachinotus rhodopus* (Gill), from Acapulco Bay, Mexico. **A** – Mean number of parasite species; **B** – Mean value of Brillouin index; **C** – Mean number of parasite.

index (H') values varied from 0.42 ± 0.34 to 1.08 ± 0.33 (GLM: Anova $F_{9,924}$ = 54.28, p<0.01). The mean species richness and mean diversity, were significantly higher between 2020 and 2021 (Fig. 3). Considering all the sampling dates, mean species richness (r_s = -0.284, p<0.01), mean number of parasite individuals (r_s = -0.473, p<0.01), and mean diversity (r_s = -0.173, p<0.01) exhibited negative correlations with host body size.

Multivariate analyses

In the PCA used to identify the possible influence of biotic and abiotic factors on parasite infracommunity structure (Fig. 4), the host sex and Fulton's condition factor (CF) were eliminated as "predictor" variables, because of the low contribution to total explained variance. The first two principal component axes explained 53.46% of total variance:

Table 4. Summary of the Principal Component Analysis results (PCA) on biotic and abiotic factors that influence the diversity and species richness of the infracommunities of *Trachinotus Rhodopus* (Gill). The first and second principal component axes are indicated by PC 1 and PC 2, respectively. Variables that contribute more to the total explained variance in each PC are indicated by an asterisk. Eigenvalues, percentage of variance and cumulative variance are shown at the end of the table. Communality – total influence of the variable with respect to all other associated variables. Uniqueness – percentage of variability that is not predicted by the variable in the model.

			Communality	Uniqueness
Variables	PC 1	PC 2	R^2	% not predicted
Diversity	0.945*	0.186	0.928	0.072
Richness	0.934*	-0.156	0.897	0.103
REcto	0.769*	-0.111	0.604	0.396
REndo	0.747*	-0.138	0.578	0.422
TEcto	0.656*	-0.144	0.451	0.549
Diet	0.478*	-0.095	0.237	0.763
MEI	-0.420*	0.277	0.254	0.746
Year	-0.297*	0.122	0.103	0.897
TEndo	0.124	-0.823*	0.694	0.306
Load	0.260	-0.810*	0.724	0.276
Size	-0.201	0.657*	0.474	0.526
Evenness	0.464	0.629*	0.611	0.389
Weight	-0.126	0.617*	0.397	0.603
Eigenvalue	4.46	2.48		
% total variance	32.26	21.21		
Cumulative variance	32.26	53.47		

Diversity – Brillouin diversity index values; Richness – number of parasite species per host; REcto – number of ectoparasite species; REndo – number of endoparasite species; TEcto – total number of ectoparasites; Diet – host diet variety; MEI – Multivariate El Niño index values; Year – sampling year; TEndo – total number of endoparasites; Load – total number of parasites per infracommunity; Size – host body size (total length); Evenness – species evenness; Weight – total weight of the host.

they contributed 32.26% (eigenvalue = 4.46) and 21.21% (eigenvalue = 2.48), respectively. The first component variable was associated with the host diet, sample year, and climatic anomalies (multivariate El Niño index), along with the parasite species richness, and diversity parameters (Table 4). This variable suggested that fish with a more varied diet, had parasite infracommunities with a greater species richness and diversity. These fish were collected mainly between 2020 and 2021, when the surface temperature of the sea was slightly cooler (Table 2). The second variable negatively associated the parasite load and the total number of endoparasites with the size and weight of the hosts (Table 4).

In the model constructed to identify possible inter annual differences in parasite community structure, the first two discriminant variables explained 70% of total variance, contributing 48.1% (eigenvalue = 0.969) and 21.8% (eigenvalue = 0.439), respectively. Individual fish were distributed mainly along the first axis (Fig. 5). Dimensionality tests indicated that all annual samples were significantly different in both dimensions (χ^2 = 250.56, d.f. = 99, p<0.001). Each fish was correctly classified to one of the ten sample years with a 40% accuracy, more than triple that achieved by chance alone (11%). Based on their lower Wilks' lambda values, 11 component species (i.e. prevalence>10 %) were accepted by the model (Table 5). High abundances of the digeneans *E. virgula*, *G. pacifica*, and *Proctoeces*

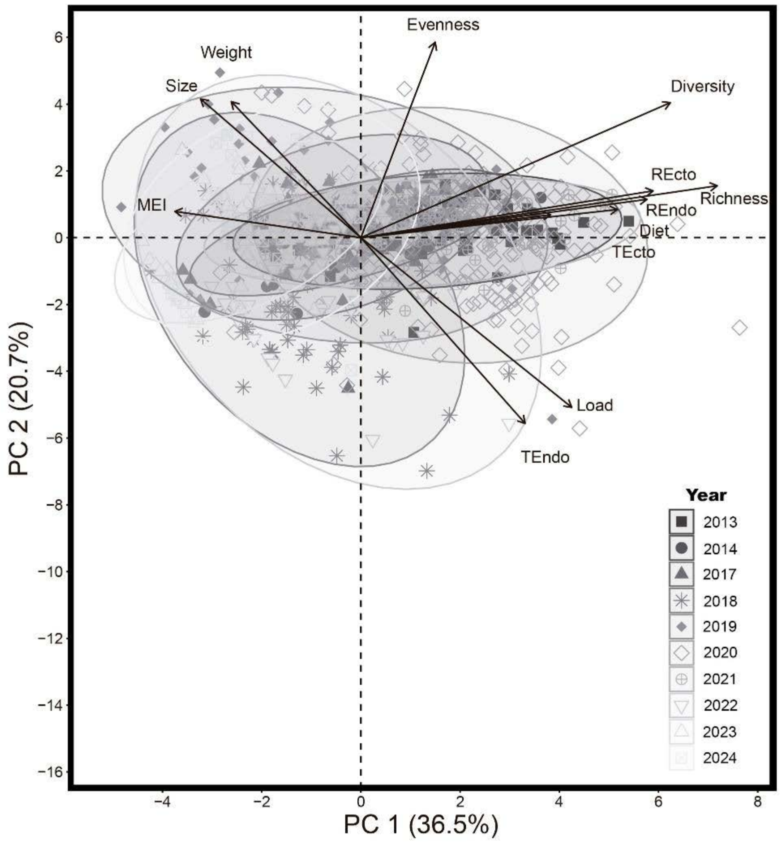

Fig. 4. Scatter plot of Principal Component Analysis (PCA) of factors that influence the species richness and diversity of the parasite infracommunities of *Trachinotus rhodopus* (Gill), from Acapulco Bay, Mexico. Richness – number of parasite species per host; Diversity – Brillouin diversity index values; REndo – number of endoparasite species; Diet – host diet variety; Year – sampling year; MEI – multivariate El Niño index values; REcto – number of ectoparasite species; Size – host body size (total length); Season – climatic season; Load – total number of parasites per infracommunity; TEndo – total number of endoparasites; Evenness – species evenness; TEcto – total number of ectoparasites. Ellipses represent sampling dates.

Table 5. Discriminant analysis classification showing the numbers and percentages of *Trachinotus rhodopus* (Gill) classified in each sampling year (rows correspond to group memberships). The bottom of the table, shows the matrix of classification coefficient values for parasites that allowed differentiation between sampling dates; asterisks indicate the importance of each parasite species in distinguishing among years.

Year	**Jun 2013**	**Feb 2014**	**Jun 2017**	**Sep 2018**	**Jun 2019**	**May 2020**	**Jun 2021**	**Jun 2022**	**Jul 2023**	**Feb 2024**	**Percent**
Jun 2013	27	9	6	0	2	3	8	0	1	7	42.9
Feb 2014	1	29	11	0	8	1	5	1	1	15	40.3
Jun 2017	1	8	23	0	5	0	8	4	8	10	34.3
Sep 2018	0	3	3	44	3	0	1	0	4	10	64.7
Jun 2019	1	11	17	0	9	5	15	6	10	21	9.5
May 2020	6	22	6	0	10	57	15	11	5	14	39.0
Jun 2021	3	5	14	0	10	4	25	2	2	2	37.3
Jun 2022	0	0	3	0	9	2	2	22	8	16	35.5
Jul 2023	0	0	8	0	5	0	1	2	38	28	46.3
Feb 2024	1	8	2	0	0	1	1	7	11	41	56.9
Parasite taxa											
Pyragraphorus hollisae	0.256	0.159	0.174	0.0180	0.241	0.251	0.355*	0.171	0.062	0.147	
Ectenurus virgula	-0.152*	-0.140	-0.069	0.024	-0.059	0.655	-0.124	0.134	-0.028	-0.075	
Gonocercella pacifica	0.480*	0.350	0.345	0.074	0.226	0.196	0.557*	-0.032	0.033	0.002	
Lecithochirium microstomum	0.348	-0.006	-0.073	0.107	0.164	0.767*	-0.110	0.085	0.029	0.429	
Proctoeces sp.	0.305*	0.009	0.034	0.022	0.020	0.063	0.069	0.017	0.001	0.020	
Stephanostomum casum	0.006	0.005	0.009	0.292*	-0.004	-0.004	-0.005	0.000	-0.010	0.001	
Anacetabulum-type	0.957	0.049	-0.224	0.195	0.227	1.174*	0.317	0.048	0.121	0.203	
Rhadinorhynchus sp.	-0.005	0.002	0.010	-0.002	0.008	0.029	0.007	0.053*	0.004	0.009	
Anisakis sp.	-0.007	-0.047	0.078	0.030	0.131	0.249*	0.182	0.059	0.537	0.249*	
Caligus asperimanus	0.514	0.613*	0.200	0.135	0.196	0.542*	0.246	0.047	0.028	0.207	
Bomolochus bellones	0.165	0.063	0.100	0.047	0.334	0.197	0.598*	0.116	0.221	-0.007	

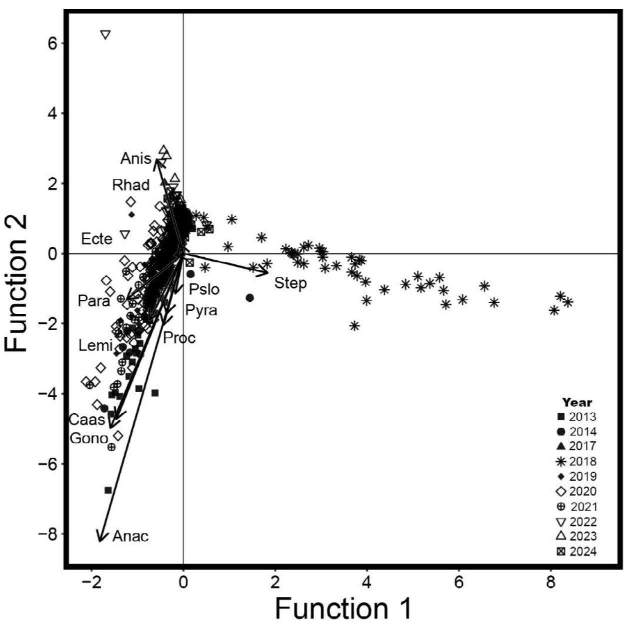

Fig. 5. Graphic of multivariate discriminant analyses for parasite infracommunities of *Trachinotus rhodopus* (Gill), from Acapulco Bay, Mexico. The symbols represent each one of the fish examined during each sampling year. Centroid – mean group.

sp. were characteristic of fish collected in June 2013. The digeneans *L. microstomum* and Anacetabulum-type, the nematode *Anisakis* sp. and the copepod *C. asperimanus* effectively functioned to assign fish to May 2020 (Table 5).

DISCUSSION

Parasite community species composition

Parasite communities of *Trachinotus rhodopus* were characterised by a greater species richness of digeneans and copepods (14 and five species, respectively). In tropical regions, digeneans are usually the most diverse group of helminths in fish from all environments (fresh, marine and brackish water) (Luque and Poulin 2007). Copepods are also a highly diverse group and mainly parasitise marine fish (Luque and Tavares 2007). Carangid fish are frequently parasitised by copepods, mainly Caligidae (Gallegos-Navarro et al. 2018, Violante-González et al. 2019, 2020). In the current study, *Caligus* was the best represented (3 species, Table 1). Endoparasites comprised 75% of the total parasite fauna in this host.

Predatory fish species such as *T. rhodopus* tend to have a greater species richness of endoparasites that are acquired by ingesting of infected prey (Luque et al. 2004, Gallegos-Navarro et al. 2018, Violante-González et al. 2019, 2020). In particular, the diet of *T. rhodopus*, which is based mainly on benthic mollusks (36.1%), predisposes it to be infected by a greater variety of digenean parasites, which use mollusks as first intermediate hosts (Rohde 2005).

Variation in parasite infection levels

Seven of the 11 component species that exhibited significant differences in infection levels between sampling years, were intestinal helminths (Table 1). Many species of endoparasites are transmitted through predation on infected prey with parasite larvae, so variations in their infection levels can be attributed to inter annual changes in the diet of *T. rhodopus*, and/or availability of infected prey (Luque et al. 2004, Gallegos-Navarro et al. 2018, Violante-González et al. 2019, 2020). Variations in abiotic factors, such as local fluctuations in sea surface temperature, and large-scale climatic events, such as El Niño and La Niña, are known to affect many ecological processes, including the productivity of local food webs, and the transmission rates of endoparasites, due to increases or decreases in populations of potential intermediate or definitive hosts (Oliva et al. 2008, Lohmus and Björklund 2015, Villalba-Vasquez et al. 2022).

The sampling period of the current study included, a strong cooling phase of the ENSO (La Niña 2020–2022), and a very strong warming phase (El Niño 2023–2024). Four species of endoparasites (*Ectenurus virgula*, *Lecithochirium microstomum*, *Gonocercella pacifica* and *Rhadinorhynchus* sp.), as well as the ectoparasites *Pyragraphorus hollisae*, *Caligus asperimanus* and *Bomolochus bellones* exhibited higher infection prevalence values between July 2020 and June 2022 (La Niña event, Table 1). In contrast, the infection percentages of these same parasite species were low during the years 2023–2024 (El Niño event, Table 1).

Component communities

Species richness at the component community level (15–24 species, Table 2), was similar to that reported for other Carangidae of the Mexican Pacific such as *Caranx caballus* Günther (12–18 parasite species), *C. caninus* Günther (16–22 species), and *C. sexfasciatus* Quoy et Gaimard (8–25 species) (Gallegos-Navarro et al. 2018, Violante-González et al. 2019, 2020). However, the total parasite fauna for *T. rhodopus* was 32 species even though the highest species richness at the component level was 24 species (Table 2).

Unlike other species of pelagic carangids that have been studied on the Mexican Pacific coast (*C. caballus*, *C. caninus*, C. *sexfasciatus*), *T. rhodopus* remains near to the sea floor in coastal areas, for which it acquires more parasites from prey that inhabit the benthic or demersal zones. For example, the species richness of digeneans, which are transmitted mainly by predation on infected mollusks, was higher in *T. rhodopus* (14 species) than in other pelagic carangids (9 to 11 species; Gallegos-Navarro et al. 2018, Violante-González et al. 2019, 2020). Therefore, the greater richness of this group of parasites may be related to the bentho-demersal habits of *T. rhodopus*.

The rank-abundance curves constructed for each parasite community (Fig. 1) suggest that relative abundance of the numerically dominant species changed remarkably between sampling years. However, although most parasite communities were primarily dominated by the acanthocephalan *Rhadinorhynchus* sp., they exhibited greater homogeneity in parasite abundances during some sampling periods (June 2013, February 2014, and July 2023) (Fig. 1).

Therefore these communities presented a greater diversity of species (Table 2).

The presence of significant nestedness in all parasite communities (Table 2) suggests that a certain degree of structure exists in the species composition over time, i.e., a certain order existed in the species composition. Several processes have been suggested as generators of nestedness within parasite communities, including the host body size, which is linked to changes in feeding rates, passive sampling and sequential colonisation of parasite species (Poulin and Valtonen 2001, Zelmer 2014).

The hypothesis of the variation in the size of fish, as a factor that can generate nestedness in parasite communities was not fully supported by our results, because there was also a negative correlation between the total length of fish and the species richness of parasite only in four of 12 nested communities (Table 2). Conversely, because the dominant species, and the degree of dominance changed over time (Table 2), a sequential colonisation process may explain the variation in the intensity of nestedness observed during some years. Similarity in species composition between component parasite communities was generally low (mean = 43.4%), which can be attributed to that 37% of the species (eight endoparasites and four ectoparasites) were rare or accidental species, since they occurred in only one or two sampling dates (Table 1). This result suggests that species composition of these parasite communities, can be unstable and may vary due to the addition of some rare species over time.

However, the species richness and diversity were high in most sampling dates (Table 2), indicating low aggregate variability (Micheli et al. 1999). This means there was more stability, or repeatability, in these structural parameters. Therefore, the possible variability scenario for the parasite community of *T. rhodopus* could be in compensation phase (Micheli et al. 1999), in which the community exhibits high compositional variability, but low aggregate variability. This same ecological pattern has been observed in other marine fish, such as some lutjanids (Villalba-Vasquez et al. 2022, Violante-González et al. 2023, 2024), so it may be a trait of the parasite communities of several marine fish in this same location and the same ecological conditions.

Infracommunites

Several biotic and abiotic factors are known to strongly influence species richness and diversity over time in the parasite communities of marine fish (Timi and Poulin 2003, Luque et al. 2004). The PCA results (Table 4) indicate that inter annual variations in feeding habits and differences in the host body size were important factors that generated changes in the structure of parasite infracommunities. Inter annual variations in the diet of *T. rhodopus* were possibly amplified by the occurrence of climatic events such as La Niña and El Niño, which have opposite effects on the productivity of the marine environment (Checkley and Barth 2009). These events may have cascade effects on the transmission processes of many endoparasite species due to the reduction or population increase of potential intermediate, paratenic or definitive hosts (Oliva et al. 2008, Violante-González et al. 2023).

During May 2020–June 2021 samples (La Niña), the fish diet was more varied (Table 2), and the mean species richness of parasite, and mean diversity were higher during this period, compared to other sampling dates (Fig. 3A,C). Although La Niña event occurred between 2020, 2021, the MEI values indicate that effects of the cooling phase of the ENSO lasted until 2022. Therefore, these slightly cooler temperatures (negative MEI values, Table 2) could have indirectly influenced (due a more varied fish diet) the greater species richness and diversity of the parasite infracommunities during these sampling years. Body size of the fish also was an important factor in the structuring of parasite infracommunities mainly of smaller fish (Table 4). In marine fish, body size has proved to be the main predictor of the presence of a particular species of parasite, total abundance and species richness (Sasal et al. 1997, Luque et al. 2004, Luque and Poulin 2008).

However, in *T. rhodopus* small body size was associated with greater structuring of parasite infracommunities, as indicated by the results of the PCA (Table 4). Negative correlations between host body size and the abundance of the endoparasites *E. virgula*, *G. pacifica*, *L. microstomum* and *Rhadinorhynchus* sp., and the ectoparasites *Py. hollisae*, *C. asperimanus* and *B. bellones* also indicated that smaller fish had higher abundances of these species. These results therefore suggest that parasites are not gradually accumulated in larger or older fish due to a longer exposure time to infections, as has been suggested for other marine fish species. Higher infection levels of some parasites in small fish can be the result of several factors: younger fish may acquire parasites that are later eliminated once the fish become adults; younger fish may also differ from older fish in preying on some forage species that act as intermediate hosts (Luque and Chaves 1999, Campos et al. 2009, Villalba-Vasquez et al. 2018). The degree to which fish aggregate in shoals may also be reduced as fish get larger (Hemelrijk and Kunz 2004).

In *T. rhodopus*, differences in the diet of smaller (immature and subadults) and large fish (adults) may explain the greater abundance of some endoparasitic species among the smaller fish. For example, immature and subadult fishes fed mainly on snails, and amphipods that act as first intermediate hosts of digeneans or acanthocephalans such as *Rhadinorhynchus* sp. Schoals of smaller fish of *T. rhodopus* are more frequent (unpublished data), which can also increase the infection levels of some ectoparasites that are transmitted by contact between infected and non-infected fish (Luque et al. 2004, Violante-González et al. 2020).

Parasites are known to be useful as biological tags in distinguishing between fish stocks of the same species (Timi 2007, Poulin and Kamiya 2015, Violante-González et al. 2020), but they have only rarely been used to determine changes in community structure and species composition over time. The results of the discriminant analysis (Table 5) indicated that the high variation in infection levels of component species may generate important inter annual changes in the parasite community structure of *T. rhodopus* in Acapulco Bay, Mexico. In other words, even though community species composition remains relatively stable, its structure may be less predictable mainly between multi-year periods.

In conclusion, the hypotheses tested in this study were supported by the results. The parasite communities of *T. rhodopus* had a greater richness (mainly of digenean species) and species diversity than that reported for other carangid fish that live in the same location. The diet variety and the bentho-demersal habits of *T. rhodopus* may explain the greater richness of some groups of parasites in this host. As in other species of carangid fish, the parasite communities of *T. rhodopus* were generally dominated by a single species. However, the constant dominance of an acanthocephalan (*Rhadinorhynchus* sp.) is a pattern that had not been reported for other parasite communities of carangids on the Mexican Pacific coast.

Although the species composition was quite stable, the species richness and diversity exhibited significant inter annual variations, mainly over long-term periods. Changes in these structural parameters could be attributed to variations in feeding behaviour and differences in the body size of fish. Climatic episodes such as La Niña and El Niño that occurred during the study period, possibly generated notable changes in the structure of local food webs, thus indirectly influencing the transmission rates of intestinal parasites due to the reduction or population increase of potential intermediate, paratenic or definitive hosts.

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