



## Low similarity between parasite communities of ten sympatric carangid species

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### ABSTRACT

Host phylogeny and ecological convergence are two factors thought to influence the structure of parasite communities. The aims of this study were to determine the diversity of metazoan parasites of 10 sympatric fish species of the family Carangidae from the southeastern Gulf of California, and to analyze their similarity at infracommunity and component community levels, in order to determine if the host species, particularly those congeneric with similar ecological characteristics, exhibit similar assemblages of parasites. In total, 874 fish specimens were examined and 40 parasite species were identified. The component community was composed by 21 parasite species in *Caranx caninus*, 20 in *C. caballus*, 11 in *C. vinctus*, five in *Chloroscombrus orqueta*, four in *Carangoides otrynter*, seven in *Hemicaranx leucurus*, eight in *Selene brevoortii*, 14 in *S. peruviana*, and 11 in *Trachinotus rhodopus*. The metazoan parasite communities of *C. vinctus*, *Ch. orqueta*, *H. leucurus*, and *S. brevoortii* are reported here for the first time. The parasite communities of the remaining six carangid species have been reported from regions other than the Gulf of California. All fish species differed significantly regarding the diversity of their parasite infracommunities. This possibly is due to different patterns of habitat use among fish species, and because of the differential host specificity among parasite taxa. Nonetheless, when the analysis was restricted to common parasite species, some fish showed similar parasite infracommunities, particularly congeners of the genus *Selene* as well as *C. caballus* and *C. vinctus*. The component communities of species of *Selene* were highly similar (>65%), but the three species of *Caranx* were not. This result supports the hypothesis that congeneric fish species with similar ecological filters harbor similar parasite communities. However, the difference observed between *C. caninus* and *C. caballus* suggests that these species, despite being evolutionary and ecologically related, have different physiological or immunological characteristics (compatibility filters) that may result in different parasite communities.

### 1. Introduction

Parasites are ubiquitous in biological communities, and play important roles in the functioning of ecosystems [1,2,3]. Host phylogeny and ecological convergence are two factors thought to influence the structure of parasite communities [4]. Indeed, phylogenetically related hosts might harbor similar parasite assemblages that were acquired through evolutionary events such as co-speciation or host-switching. In addition, such similarity can be promoted by common or generalist

parasite species encountered by hosts occurring in sympatry. In marine fish, it is expected that phylogenetically close hosts, living in sympatry with potential to access the same pool of local parasites, show high similarity in the structure and composition of their parasite communities [5]. Despite the evidence that host phylogeny has weak influence on parasite diversity and community structure [6,7], homogeneous parasite communities can be observed between fish species with similar ecological filters (e.g., size, habitat, trophic level, and depth distribution) [8].

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Carangidae (jacks and pompanos) is a family of ecologically and economically important fish, distributed mostly in marine tropical and subtropical waters, but also in temperate regions and in brackish waters. This family is highly diverse in terms of species, ecological niche, body shape, and size [9,10]. Carangidae is divided into four tribes or sub-families (Carangini, Naucratini, Trachinotini and Scomberoidini); however, their phylogenetic relationships are not fully understood [10]. They are abundant in coastal tropical waters forming shoals and feeding mostly on benthic invertebrates and small fish [11,12]. These habits favor the acquisition of both trophically and non-trophically transmitted parasites.

Studies on several carangid species have shown that they harbor rich communities of metazoan parasites (e.g., [13,14,15,16]). Of the 152 species of carangids currently known, 34 are distributed in the Mexican Pacific coast [17]. Of these, nine species (*Caranx caballus*, *C. caninus*, *C. sexfasciatus*, *Decapterus muroadsi*, *Oligoplites altus*, *O. saurus*, *O. refulgens*, *Selar crumenophthalmus*, and *Trachinotus rhodopus*) caught in the Mexican South Pacific coast have been investigated for the structure and composition of their metazoan parasite communities. These species can harbor from nine to 35 species of parasites [18,19,20,21–23]. Thus, from a parasitological perspective, carangids represent useful host models for testing ecological and evolutionary hypothesis.

Currently, no study has been conducted regarding the community of parasites of carangids from the Mexican North Pacific, which includes the Gulf of California. This gulf has a variety of habitats and oceanographic processes, which make it a megadiverse marine ecosystem and an important area for endemism [24,25]. Moreover, the Gulf of California supports about half of the Mexico fishery production. In its southeastern region, although carangids are not among the most valuable target species for fisheries, they are highly abundant and common in the landings of artisanal fishing fleets [26].

The present study was focused on parasites of 10 sympatric carangid species, original from the southeastern Gulf of California: *Carangoides otrynter*, *Caranx vinctus*, *C. caballus*, *C. caninus*, *Chloroscombrus orqueta*, *Hemicaranx leucurus*, *O. refulgens*, *Selene brevoortii*, *Selene peruviana*, and *T. rhodopus*. These species inhabit the coastal pelagic zone and have similar trophic levels (carnivores, tertiary consumers). However, some species, such as *C. caninus* and *C. caballus* achieve body lengths up to 100 cm and a depth distribution up to 100 m, whereas *H. leucurus* reaches 50 cm of body length and 30 m of depth. The aims of the present study were to determine the diversity of metazoan parasites from these 10 carangid species; and to analyze their similarity at infracommunity and component community levels. It is expected that congeneric fish species, with similar ecological characteristics, display similar assemblages of parasites.

2. Materials and methods

2.1. Fish and parasite collection

A total of 874 fish belonging to 10 carangid species (Table 1) were collected between February 2021 and May 2022 from the artisanal fishery that operates at a fishing area off Mazatlán in the southeastern Gulf of California (23°14'29" N; 106°24'35" W). Fish were collected in different months/seasons throughout the year for representativeness of the parasite fauna. Monthly sample size for each fish species are provided in Supplementary Table S1. Freshly caught hosts were transported to the laboratory for immediate parasitological examination. The total length (TL, cm) of each fish was measured. The external surface, gills, cavities, internal organs, and musculature were examined for the presence of metazoan parasites using a stereomicroscope. Parasites were fixed in 4% formalin, and preserved in 70% ethanol for morphological identification. In order to examine their morphological characteristics, crustaceans and nematodes were cleared in lactic acid, whereas monogeneans, digeneans, cestodes, and acanthocephalans were stained with Gomori's trichrome reagent, dehydrated in a graded ethanol series,

Table 1 Sample size and morphological and ecological characteristics of 10 species of Carangidae collected in the southeastern Gulf of California.

	<i>C. caninus</i>	<i>C. caballus</i>	<i>C. vinctus</i>	<i>Ca. otrynter</i>	<i>Ch. orqueta</i>	<i>H. leucurus</i>	<i>O. refulgens</i>	<i>S. brevoortii</i>	<i>S. peruviana</i>	<i>T. rhodopus</i>
n	244	129	79	64	40	32	31	57	111	87
Observed mean total length (cm)	28.34 ± 5.03	31.89 ± 3.81	29.16 ± 2.68	24.4 ± 4.08	22.54 ± 1.67	25.91 ± 2.72	23.9 ± 2.32	23.47 ± 4.27	25.26 ± 3.18	27.55 ± 4.67
Trophic level	3.9	4.1	3.3	4.4	2.5	3.8	4.2	3.8	4.3	4
Depth range (m)	100	100	50	100	53	30	30	50	50	30
Maximum length recorded (cm)	100	100	37	60	30	49.5	28.2	42	85	61
Environment type	Pelagic	Pelagic	Pelagic	Benthic–pelagic	Benthic–pelagic	Pelagic	Demersal	Pelagic	Pelagic	Benthic–pelagic
Habitat	Coastal	Coastal–oceanic	Coastal–oceanic	Coastal–oceanic	Coastal	Coastal	Coastal–oceanic	Coastal	Coastal	Coastal–oceanic
Water salinity	Freshwater, brackish, marine	Freshwater, brackish, marine	Brackish, marine	Brackish, marine	Brackish, marine	Marine	Brackish, marine	Freshwater, brackish, marine	Freshwater, brackish, marine	Brackish, marine
Body shape	Moderate	Moderate	Moderate	Compressed	Compressed	Moderate	Compressed	Compressed	Compressed	Compressed

Fish characteristics were obtained from the literature ([17]; [27]).

cleared with methyl salicylate, and mounted in Canada balsam. Observations were made using a compound microscope. All parasites were counted. Identification of parasites was based on specialized literature, including morphological descriptions of species.

## 2.2. Population and community descriptors

Parasitological parameters were calculated for each fish species. The prevalence and mean intensity of each parasite species in each host species were calculated according to Bush et al. [28]. Prevalence is the percentage of fish of a particular species infected with one or more individuals of a given parasite species. Mean intensity is the total number of a parasite of a particular species found in a sample divided by the number of hosts infected with that parasite. A parasite species was considered common if it occurred in at least two fish species, with prevalence  $\geq 10\%$  in at least one of them. Parasite communities were analyzed at both infracommunity (all the individuals of all parasite species in an individual fish) and component community (all the parasites in a sample of a given fish species) levels [28].

Infracommunities were described in terms of species richness ( $S$ ), which takes presence of a species into account, and Brillouin's diversity index ( $HB$ ), which takes into account the relative abundance of the species and it is recommended for fully censused communities [29]. While  $S$  was calculated for all individual fish,  $HB$  was calculated for each individual fish harboring two or more parasite species. At the infracommunity level, each fish is considered a sampling unit; it allows to compare statistically fish samples for determining whether there are differences in the central tendency. Thus,  $S$  and  $HB$  were compared between host species by Kruskal–Wallis testing and Dunn's pairwise comparisons with the Bonferroni correction to adjust the probability in the software R [30] using the package FSA [31].  $P$ -value  $< 0.05$  was considered statistically significant.

At the component community level, we evaluated the sample completeness for each fish species using the sample coverage estimator ( $\hat{C}_m$ ), which ranges from 0% to 100% [32]. Component communities were described by the Hill numbers  ${}^qD$  of order  $q = 0$  (species richness) and  $q = 1$  (the exponential of the Shannon's entropy index) [33,34]. As we had no replicates for component communities, comparisons through a statistical test were not possible. Nonetheless, the Hill numbers were compared using 95% confidence intervals among fish species with at least 90% of sample completeness. These confidence intervals were obtained by a bootstrap method based on 200 replications. Differences were considered significant if the 95% confidence intervals did not overlap [33]. These analyses were performed in the R package iNEXT [33,35].

## 2.3. Similarity analyses

The similarity in parasite composition among host species was determined based on Bray–Curtis distance matrix. For infracommunities, the matrix was constructed based on parasite abundance (number of individuals of a given parasite species in an individual fish). For component communities, the matrix was constructed based on mean parasite abundance (total number of individuals of a given parasite species in a sample of a particular host species divided by the total number of hosts of that species examined). The data were square-root transformed in order to down-weight the importance of highly abundant species, so that the less dominant species play some role in determining similarity among samples [36]. This was visualized through nonmetric multidimensional scaling (nMDS), which provides a graphical representation of the similarities between parasite communities; a shorter distance between two points on the nMDS graph indicates a greater similarity between the communities. Stress in nMDS indicates the distortion of the graphical representation from the positions of real data points, with low stress indicative of a better representation of the similarities. Parasite species with prevalence  $< 5\%$  (probably accidental)

were not included in the analysis.

In the case of infracommunities, for each fish species a centroid and its 95% confidence ellipse were generated by means of bootstrap averaging (50 interactions; rho coefficient = 0.99;  $m = 4$  dimensions). That represents the generalized position of the infracommunities in the nMDS space. Differentiation of group centroids was tested using a PERMANOVA test [37], introducing fish length as a covariable. Infracommunity structures between samples ( $1 \times 10$  factorial design, "fish species" as a fixed factor) were compared, testing for main effects after 9999 permutations and subsequent post hoc pairwise comparisons. A permutation of residuals under a reduced model was used as a method of permutation [37]. A sequential sum of squares (type I SS) was applied because fish length was used as a covariable and fish sample sizes were unequal. At the component community level, hierarchical agglomerative clustering was applied using group-average linking, and resemblance levels were overlaid on the nMDS plot.

In studies focused to analyze the similarity in parasite composition among fish samples, it is recommended to consider different parasite guilds (e.g., ectoparasites and endoparasites) as they can respond differently to the either environmental or host related variability [8]. In the present study, for infracommunities, analyses were first performed for all parasite species and then repeated for ectoparasites. In addition, analyses were restricted to common parasite species in order to avoid the effect, if any, of host identity on parasite communities (sensu [8]). The infracommunities included in the analyses were those composed of at least one parasite species. Endoparasite infracommunities were not analyzed separately because their richness was too low for a proper analysis.

## 2.4. Linkage between parasitological data and host/abiotic variables

Distance linear modeling (DISTLM routine) was performed using Bray–Curtis similarities as distance measures to determine which variable best explained the variation between fish parasite communities. The BEST procedure was used as the selection criteria based on the Akaike information criterion for finite samples (AICc). Eight fish characteristics were included as predictor variables (Table 1): observed total length, trophic level, depth range, maximum length recorded for each fish species, environment type, habitat type, water salinity, and body shape. Marginal tests for each variable were also conducted using the DISTLM routine. Statistical significance was tested based on 9999 permutations and an alpha level of 0.05.

All multivariate analyses were performed in PERMANOVA+ for PRIMER 7 [37].

## 3. Results

### 3.1. General results

In total, 40 species/taxa of metazoan parasites were identified from the 10 species of Carangidae collected: 10 monogeneans, 11 digeneans, one acanthocephalan, two nematodes, 14 copepods, and two isopods (Table 2). We observed a total of 110 host species–parasite species associations; in 93 cases the prevalence values were below 10%, and in 80 cases the mean intensity was below 5 parasites per infected fish (Table 2). Three monogeneans (*Allopyrgraphorus caballeroi*, *Pseudomazocraes selene*, and *Hargicola oligoplites*), one digenean (*Bucephalus margaritae*) and four copepods (*Caligus confusus*, *Caligus isonyx*, *Lernanthropus giganteus*, and *Lernaenicus longiventris*) were considered common as they occurred at least in two fish species, with prevalence  $\geq 10\%$  in at least one of them. *Pseudomazocraes selene* was the only parasite found in all fish species, reaching a prevalence of 74% in *S. brevoortii*, followed by that of *L. giganteus*, which was found in eight fish species.

Overall, the infracommunities with the highest  $S$  (3.3) and  $HB$  (0.88) values were observed in *O. refulgens*. Conversely, the lowest  $S$  (2.07) and

**Table 2**

Prevalence (P) and mean intensity (MI) of infection of metazoan parasite species in 10 carangid species from the southeastern Gulf of California. For each fish species the sample size (n) and total body length (LT, mean ± SD) are provided.

		Fish species									
		Ccan	Ccab	Trho	Cotr	Oref	Corq	Cvin	Sbre	Sper	Hleu
		n	244	129	87	64	31	40	79	57	111
	LT (cm)	28.34 ± 5.03	31.89 ± 3.81	27.55 ± 4.67	24.4 ± 4.08	23.9 ± 2.32	22.54 ± 1.67	29.16 ± 2.68	23.47 ± 4.27	25.26 ± 3.18	25.91 ± 2.72
<b>Parasite species</b>											
<b>Monogenea</b>											
<i>Allopyragraphorus caballeri</i>	P (%)	12.7	4.8	1.1				2.5			
	MI	6.7	3	1				5.5			
<i>Amphipolycotyle chloroscombrus</i>	P (%)						53.8				
	MI						6.3				
<i>Hargicola oligoplites</i>	P (%)					6.5					34.4
	MI					1					17.7
<i>Heteromicrocotyla carangis</i>	P (%)	4.1	4								
	MI	18.5	1.2								
<i>Neobenedenia melleni</i>	P (%)	5.7									
	MI	11.4									
<i>Polymicrocotyle manteri</i>	P (%)	59.8									
	MI	27.4									
<i>Pseudaxine trachuri</i>	P (%)							49.4			
	MI							9.5			
<i>Pseudobicotylophora lopezochoterenai</i>	P (%)			26.4							
	MI			11.8							
<i>Pseudomazocraes selene</i>	P (%)	11.1	16.1	19.8	56.2	22.6	28.2	41	74.5	43	34.4
	MI	5.5	2.9	8.2	6.8	3.2	14	9.4	10.7	7.2	6.9
<i>Pyragraphorus hollisiae</i>	P (%)	41	0.8				5.1	3.8	1.8	2.8	
	MI	7.6	2				20	9.3	1	1.3	
<b>Digenea</b>											
<i>Bucephalus margaritae</i>	P (%)	4.1	4	3.4				3.8			6.2
	MI	127	89.2	2.3				1.6			1.5
<i>Dactylostomum winteri</i>	P (%)		1.6								
	MI		4								
<i>Didymozoid larvae</i>	P (%)	0.8	0.8							1.9	
	MI	1.5	1							1	
<i>Ectenurus carangis</i>	P (%)		1.6								
	MI		1.5								
<i>Ectenurus virgula</i>	P (%)	0.4		2.3				1.3			
	MI	1		4.5				1			
<i>Lecithochirium microstomum</i>	P (%)								1.8	1.9	
	MI								1	1	
<i>Manteria brachyderus</i>	P (%)					3.2					
	MI					1					
<i>Phyllodistomum carangis</i>	P (%)	0.4									
	MI	1									
<i>Pseudopecoeloides carangis</i>	P (%)	1.6	0.8					1.3	3.6	2.8	
	MI	2.2	1					1	1	2	
<i>Stephanostomum carangis</i>	P (%)	0.4	4								
	MI	1	1.2								
<i>Stephanostomum megacephalum</i>	P (%)					3.2					
	MI					1					
<b>Nematoda</b>											
<i>Anisakis sp.</i>	P (%)	2.9	7.9	1.1	1.6	3.2			1.8	1.9	3.1
	MI	1.2	1.6	1	1	5		1	2.8	2.8	1
<i>Procamallanus sp.</i>	P (%)	0.8	3.2			3.2				2.8	
	MI	1.5	1			3				1	
<b>Acantocephala</b>											
<i>Radinorhynchus sp.</i>	P (%)										
	MI			32.2							
				12.2							
<b>Copepoda</b>											
<i>Acanthocolax extilipes</i>	P (%)		2.4	9.2						1.9	
	MI		1	1						1	
<i>Caligus asperimanus</i>	P (%)							15.2			
	MI							1.8			
<i>Caligus chorinemi</i>	P (%)	5.3									
	MI	3.8									
<i>Caligus confusus</i>	P (%)	35.7	1.6								3.1
	MI	26	1.5								1
<i>Caligus isonyx</i>	P (%)			8	23.4					2.8	
	MI			1.8	1.2					1	
<i>Caligus latigenitalis</i>	P (%)									8.4	

(continued on next page)

Table 2 (continued)

		Fish species									
		Ccan	Ccab	Trho	Cotr	Oref	Corq	Cvin	Sbre	Sper	Hleu
	n	244	129	87	64	31	40	79	57	111	32
	LT (cm)	28.34 ± 5.03	31.89 ± 3.81	27.55 ± 4.67	24.4 ± 4.08	23.9 ± 2.32	22.54 ± 1.67	29.16 ± 2.68	23.47 ± 4.27	25.26 ± 3.18	25.91 ± 2.72
<i>Caligus mutabilis</i>	MI									1.1	
	P (%)		0.8								
<i>Caligus robustus</i>	MI		1								
	P (%)	4.5	9.5	1.1						2.8	
<i>Caligus selenecola</i>	MI	1.1	1.5	1						1	
	P (%)								20		
<i>Lepeophtheirus bifurcatus</i>	MI								1.2		
	P (%)					3.2					
<i>Lepeophtheirus mondacola</i>	MI					5					
	P (%)					16.1					
<i>Lernaenicus longiventris</i>	MI					1.8					
	P (%)	16	1.6								
<i>Lernanthropus giganteus</i>	MI	2.7	2								
	P (%)	0.4	10.3	1.1	6.2	6.5	33.3	22.8			3.1
<i>Lernanthropus ilishae</i>	MI	7	1.3	1	6	9	3	2.8			1
	P (%)								3.6	8.4	
<b>Isopoda</b>	MI								1	1.8	
	P (%)	0.8	0.8					1.3	1.8	1.9	
<i>Gnathia</i> sp.	MI	1	1					3	25	4	
	P (%)	7.4	3.2				3.8	7.6		2.8	3.1
<i>Rocinela signata</i>	MI	1.9	2.5				2	5		1.3	1
	P (%)										

Ccan = *Caranx caninus*, Ccab = *Caranx caballus*, Trho = *Trachinotus rhodopus*, Cotr = *Carangoides otrynter*, Oref = *Oligoplites refulgens*, Corq = *Chloroscombrus orqueta*, Cvin = *Caranx vinctus*, Sbre = *Selene brevoortii*, Sper = *Selene peruviana*, Hleu = *Hemicaranx leucurus*.

HB (0.35) values were observed in *Ca. otrynter* (Table 3). However, the Kruskal–Wallis tests followed by the Dunn’s pairwise comparisons with Bonferroni correction indicated that these differences were not significant (pBonf.Corr >0.005). At the component community level, sampling coverage was >90% for each fish species, except for *O. refulgens* (76%) and *H. leucurus* (85%). The component community was composed of 21 parasite species in *C. caninus*, 20 in *C. caballus*, 14 in *S. peruviana*, 11 in *C. vinctus*, 11 in *T. rhodopus*, eight in *S. brevoortii*, seven in *H. leucurus*, five in *Ch. orqueta*, and four in *Ca. otrynter*. According to the Hill numbers ( $q = 0$  and  $q = 1$ ), the diversity of parasites was significantly higher in *C. caninus* and *C. caballus* than in *S. brevoortii*, *Ch. orqueta*, and *Ca. otrynter* (Fig. 1). The values of sampling coverage and Hill numbers for each fish species are provided in Supplementary Table S2.

3.2. Similarity analyses

At the infracommunity level, if all parasites were included, except for those with prevalence <5%, the two-dimensional nMDS with a 0.17 level of stress showed close relatedness of all parasite infracommunities according to fish species (Fig. 2), which was also observed in the three-dimensional nMDS (Supplementary Fig. S1). A clear separation among the three species of *Caranx* was observed, whereas the two species of *Selene* and *Ca. otrynter* were apparently overlapped. PERMANOVA

Table 3

Mean values of species richness (S) and Brillouin’s diversity index (HB) of metazoan parasite infracommunities of 10 carangid species.

Fish species	S	HB
<i>C. caninus</i>	2.86 ± 1.12	0.50 ± 0.25
<i>C. caballus</i>	2.5 ± 0.62	0.44 ± 0.19
<i>C. vinctus</i>	2.30 ± 0.52	0.46 ± 0.18
<i>Ca. otrynter</i>	2.07 ± 0.26	0.35 ± 0.15
<i>Ch. orqueta</i>	2.16 ± 0.51	0.44 ± 0.25
<i>H. leucurus</i>	2.2 ± 0.42	0.40 ± 0.12
<i>O. refulgens</i>	3.33 ± 0.57	0.88 ± 0.03
<i>S. brevoortii</i>	2.25 ± 0.62	0.35 ± 0.13
<i>S. peruviana</i>	2.4 ± 1.21	0.37 ± 0.24
<i>T. rhodopus</i>	2.23 ± 0.42	0.37 ± 0.16

testing on all parasite species showed a significant effect of fish total length on the response variables, and an interaction between fish length and fish species (Table 4). According to this analysis, the parasite composition varied significantly among fish species. In agreement with the nMDS, all pairwise comparisons resulted in significant differences ( $P < 0.05$ ; Table 5).

Similar results were obtained when analysis was repeated for ectoparasites (Supplementary Fig. S2; Table S3), with all pairwise comparisons being significantly different ( $P < 0.05$ ). When analysis was restricted to common parasite species (Fig. 3, Table 4), fish species overlapped more than previous analyses, but *C. caninus* appeared still segregated, as shown by the pairwise comparisons (Table 5). In this latter analysis, there were no differences between the two species of *Selene*, nor between *C. caballus* and *C. vinctus*.

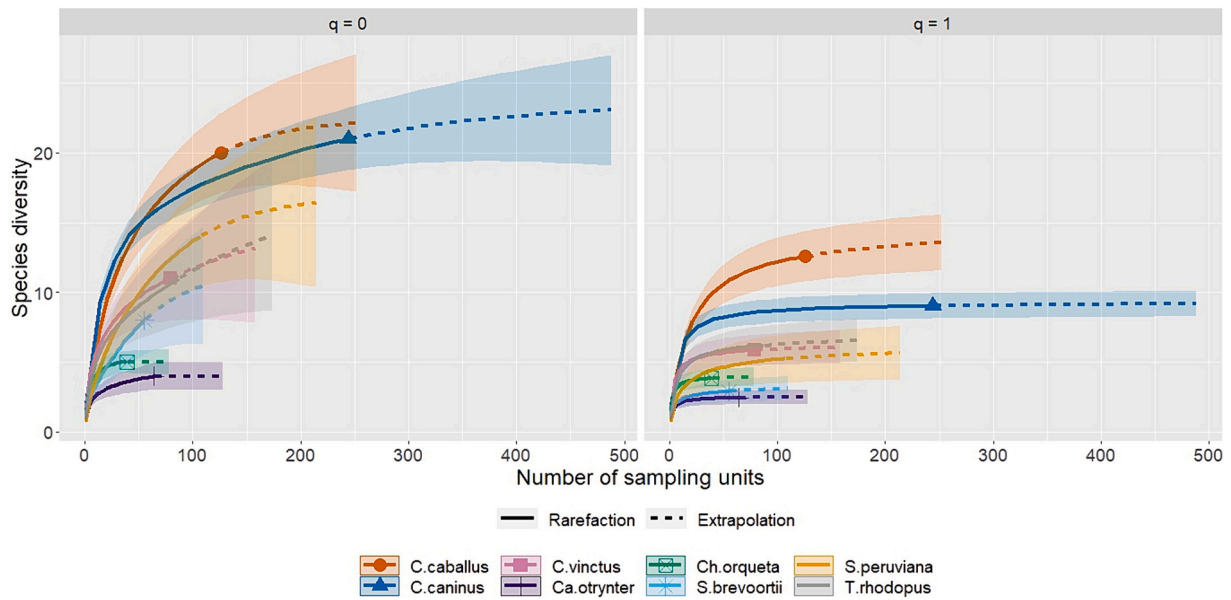
At the component community level, the two-dimensional nMDS showed that at the 50% threshold, five fish species had similar compositions of parasite species; the only pair of fish species with a higher similarity (65%) were *S. brevoortii* and *S. peruviana* (Fig. 4). The three species of *Caranx* were clearly separated from each other and from other fish species.

3.3. Links between parasitological data and host/abiotic variables

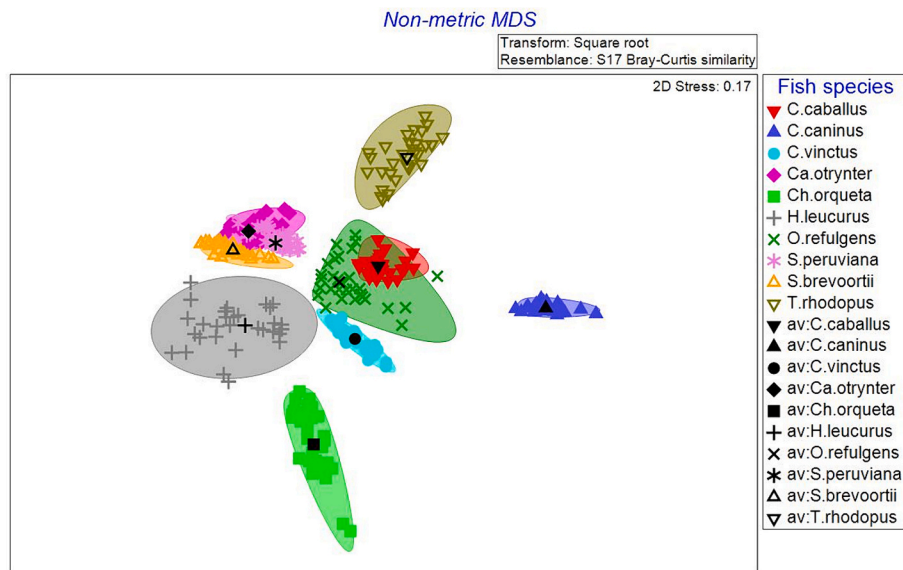
When all parasite species were included, the DISTLM marginal test showed that all the variables tested could explain differences in the infracommunities (all  $P < 0.01$ ). However, body shape, followed by depth range and maximum length were the variables that explained the main variability (24%) to Bray–Curtis similarity patterns among fish species infracommunity structure (Table 6). Similar results were obtained if the analysis was restricted to common parasite species.

4. Discussion

Currently, there is no record of parasites in *C. vinctus* and *H. leucurus*, whereas for *Ch. orqueta* and *S. brevoortii*, only a few ectoparasites have been reported and not the entire community of metazoan parasites [38,39,40]. Regarding the other six carangid species, in the case of *Ca.*



**Fig. 1.** Comparisons of the diversity values ( $q = 0$  and  $1$ ) among the component communities of metazoan parasites of carangid species. Shaded areas represent  $\pm 95\%$  confidence intervals.



**Fig. 2.** Two-dimensional nMDS plot of bootstrap averages of all metazoan parasite infracommunities in 10 carangid fish species based on Bray–Curtis similarity of square-root-transformed data. Individual repetitions are based on random draw and replacement of samples from the original dataset. Av = bootstrap average of infracommunities.

*otrynter*, *C. caballus*, *C. caninus*, and *O. refulgens*, the number of parasite species reported here was generally lower and the species composition somewhat different compared to previous studies in the Mexican South Pacific [20,41,21,22]. Violante-González et al. [22] reported 35 parasite species in *C. caninus* from the Mexican South Pacific, whereas in the Gulf of California (present study), 21 parasite species were found in this host, with only 13 matches with those reported by the previous authors. However, the contrary was observed for *T. rhodopus* and *S. peruviana*; that is, we recorded more parasite species than in other studies carried out in southern regions [42,19]. This difference on parasite communities possibly is consequence of environmental conditions discontinuity among localities geographically distant [43]. Since the southeastern Gulf of California is influenced by the California Current, the North Equatorial Current, and the Gulf of California Waters, the oceanographic

conditions might be different from other parts of the Eastern Tropical Pacific.

Based on phylogenetic and ecological convergence, it is expected that closely related host species, with similar ecological characteristics and living in sympatry, may harbor similar parasite faunas, and that the similarity decays with host phylogenetic distance [8,44,5,45]. However, in the present study, the phylogenetic relatedness and sympatry seem to be weak determinants of the structure and composition of parasite communities in these carangids. According to the similarity analysis based on all parasites or only on ectoparasites, infracommunities were significantly different among all the species of carangids studied. Such results agree with those by Poulin [44], who observed that, within a single fish family, the decay in similarity of parasite communities between fish species is not explained by phylogenetic relationships. The

**Table 4**  
PERMANOVA results of square-root-transformed infracommunity abundance data of parasites of 10 fish species, based on measured Bray–Curtis similarity.

Data	Source	d.f.	SS	MS	Pseudo F	Pperm
All parasite species*	Total length	1	50,156	50,156	18.027	0.001
	Fish species	9	7.13E+05	79,174	28.457	0.001
	Total length x fish species	9	37,468	4163.1	1.4963	0.004
	Residual	570	1.59E+06	2782.2		
	Total	589	2.39E+06			
Common parasite species	Total length	1	86,807	86,807	38.622	0.001
	Fish species	9	3.74E+05	41,557	18.489	0.001
	Total length x fish species	9	24,565	2729.5	1.2144	0.163
	Residual	402	9.04E+05	2247.6		
	Total	421	1.39E+06			

\* Excluding parasite species with prevalence <5%.

observed differences were influenced by non-common parasites, because when the analysis was restricted to common parasites some fish species showed homogeneous parasite infracommunities. This may

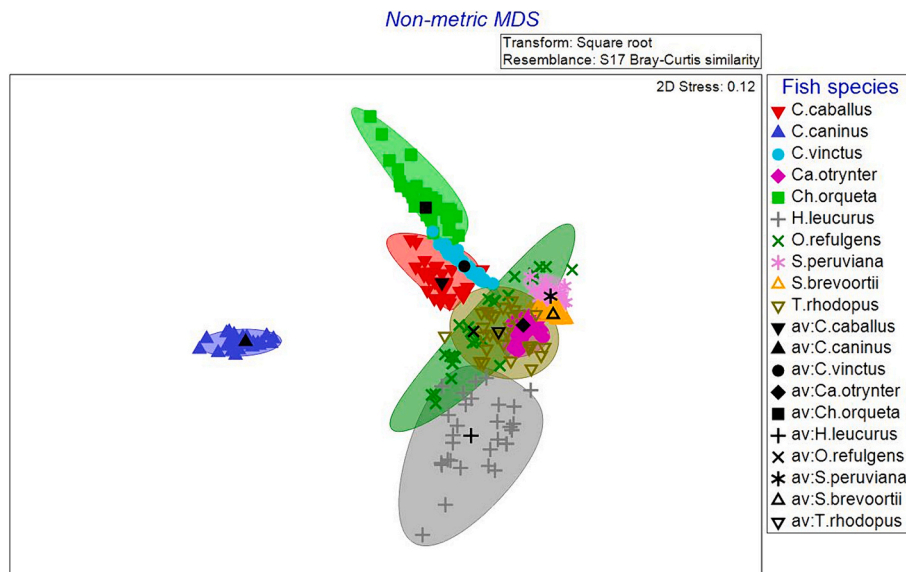
**Table 5**  
Values of t-scores of one-factor PERMANOVA post hoc pair-wise comparisons of square-root-transformed abundance of parasites of 10 fish species, based on the Bray–Curtis similarity measure with host length as covariable. P-values obtained after 9999 permutations. Results of analyses based on all non-accidental parasites and common parasites species above and below the diagonal, respectively. Nonsignificant differences in bold.

	<i>C. caninus</i>	<i>C. caballus</i>	<i>C. vinctus</i>	<i>Ca. Otrynter</i>	<i>Ch. orqueta</i>	<i>H. leucurus</i>	<i>O. refulgens</i>	<i>S. brevoortii</i>	<i>S. peruviana</i>	<i>T. rhodopus</i>
<i>C. caninus</i>	–	5.95	7.93	7.48	6.16	4.74	3.69	7.79	7.75	6.89
<i>C. caballus</i>	5.57	–	3.6	2.39	2.51	2.09	1.49	2.39	2.24	3.71
<i>C. vinctus</i>	6.31	<b>1.2</b>	–	3.72	3.15	2.88	2.65	3.6	3.78	5.18
<i>Ca. Otrynter</i>	5.7	1.84	2.26	–	5.68	3.66	2	2.11	2.51	4.38
<i>Ch. orqueta</i>	3.9	<b>1.59</b>	<b>1</b>	3.97	–	4.16	2.23	6.11	5.15	4.02
<i>H. leucurus</i>	4.01	2.45	2.6	3.87	2.94	–	1.51	3.64	3.24	3.3
<i>O. refulgens</i>	3	<b>0.96</b>	<b>1.83</b>	<b>1.61</b>	<b>1.5</b>	<b>1.61</b>	–	1.58	1.58	2.72
<i>S. brevoortii</i>	6	2.37	2.62	2.68	4.86	4.4	2.14	–	1.57	4.39
<i>S. peruviana</i>	6.46	1.98	2.84	2.58	4.76	4.58	1.71	<b>1.59</b>	–	2.54
<i>T. rhodopus</i>	3.88	<b>1.49</b>	1.75	<b>0.93</b>	2.46	<b>2.74</b>	1.32	2.41	2.56	–

happen because common, non-specific parasites are not inherited from a common ancestor and they are potentially available for all host species [46]. Yet, *C. caninus* was separated from all other carangid species, which is discussed below.

Some studies have also observed lack of similarity between sympatric marine fish species belonging to a particular family. For instance, Tavares and Luque [47] observed two distinct parasite infracommunities from two fish species of the family Ariidae inhabiting the coastal zone of Brazil. In other example, Lablack et al. [7], who examined two fish species of the family Sparidae from the Mediterranean, observed that each fish species harbored distinct parasite communities. Reverter et al. [48] found that 34 sympatric butterflyfish species (family Chaetodontidae) in the Indo-West Pacific were typically parasitized by different combinations of monogenean species. These results might reflect different use of the habitat by fish species and possible influence of different host specificity of parasites [7,49].

Differences on habitat use contributes to the stability of sympatric fish species [50], and may explain the observed heterogeneity in the present parasite communities among carangid species. Indeed, the 10 carangids examined in the present study inhabit the same geographical area, and they have some differences regarding morphology, bathymetric distribution, and trophic level. These characteristics possibly determined the differences observed in the parasite communities of each host species as indicated by DISTLM marginal test. According to this test, body shape, depth range, and maximum length recorded were the most



**Fig. 3.** Two-dimensional nMDS plot of bootstrap averages of common metazoan parasite infracommunities in 10 carangid fish species based on Bray–Curtis similarity of square-root-transformed data. Individual repetitions are based on random draw and replacement of samples from the original dataset. Av = bootstrap average of infracommunities.

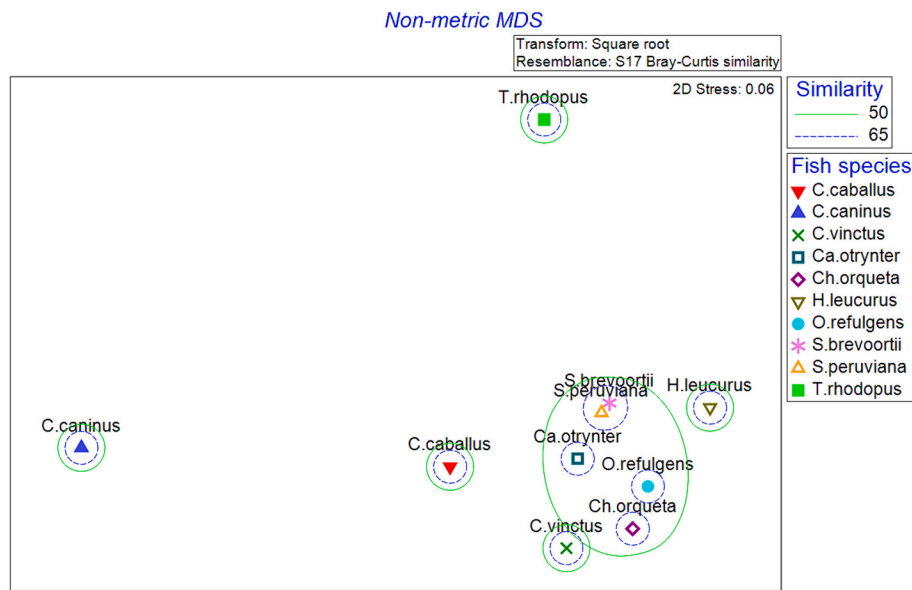


Fig. 4. Two-dimensional nMDS plots of the component communities with superimposed clusters from group-average clustering. Similarity levels represent 50% (continuous line) and 65% (dashed line).

Table 6  
Marginal test for biotic and biotic variables included in the DISTLM routine.

Variable	Sum of squares (trace)	Pseudo-F	P (permutation significance test)	Proportion of variation explained
Observed total length	50,156	12.625	0.0001	0.02102
Trophic level	69,480	17.635	0.0001	0.029119
Depth range	190,420	50.995	0.0001	0.079805
Maximum length recorded	179,970	47.968	0.0001	0.075425
Environment type	82,668	21.103	0.0001	0.034646
Habitat	75,365	19.178	0.0001	0.031586
Water salinity	140,040	36.663	0.0001	0.058692
Body shape	219,730	59.641	0.0001	0.092089

explicative variables for the structure of parasite communities. In this sense, larger fish and those exploring wider depth ranges have higher dispersion capacity, which may expose them to a diversity of parasite forms, possibly resulting in a richer parasite community; on the other hand, smaller fish restricted to narrow depth ranges, will be less exposed to parasites and possibly more depauperate parasite communities [51,52,53]. Moreover, the variability in fish body shape suggests different ecological niche [54] and, consequently, exposition to different parasite faunas.

In addition to differences in habitat use by hosts, the low values of similarity among the present parasite communities may be also explained by different host specificity among the parasite species. It is known that some parasite species are highly host-specific, infecting a single or a few closely related host species [55]. Others, with low specificity, are able to infect phylogenetically distant hosts [55]. Furthermore, a parasite with low host specificity may have preference for a particular one, which can be indicated by higher infection levels [56]. Specificity is determined by both encounter and compatibility filters [57]. Compatibility refers to the morphological, physiological, and immunological processes of the host that allow the success of parasite infection [55]. In the present study, some carangid species encountered the same parasites, but the compatibility was variable. Such as the monogenean *P. selene*, found in all the fish species studied

but more prevalent and, therefore, more compatible with *S. brevoortii* and *Ca. otrynter*. Likewise, the copepod *L. giganteus* was more compatible with *Ch. orqueta*. This pattern influenced the differences in similarity between most fish species based on common parasite data. As observed in other fish families ([58]; [59,60]), the defense mechanisms against parasites possibly vary between carangid species despite being closely related, that is, the molecular strategies that enable a parasite to infect one fish species perhaps do not work for another. These host–parasite co-evolutionary associations that lead to compatibility are thought to be one of the major factors limiting the parasite distribution among host species [61].

Also, Alarcos and Timi [8] pointed out that fish phylogeny have weak influence on parasite diversity, whereas congeneric fish species with similar ecological filters can harbor homogeneous parasite communities. Such patterns could be observed in the present study, since both species belonging to *Selene* showed homogeneous parasite communities. However, the parasite fauna of *C. caninus* was markedly different from that of the other two *Caranx* species. This was unexpected because from a phylogenetic perspective *C. caninus* is closer to *C. vinctus* than to *C. caballus* [10], and from an ecological perspective, *C. caninus* appears more similar to *C. caballus* than to *C. vinctus*. Therefore, it is possible that the difference between *C. caballus* and *C. caninus* could be explained by their phylogenetic distance, whereas *C. caninus* and *C. vinctus* impose different compatibility filters to parasites.

The present analyses of parasite infracommunities and component communities revealed significant differences among the fish hosts. This result suggests that phylogenetic relatedness and sympatry of different fish species, not necessarily result in similar parasite communities, or at least, similar proportions of them. The differences observed in these parasite communities most likely are related to different habitat used by fish species, and/or different degrees of host specificity by parasites that may depend upon compatibility (e.g., host physiology and immunology).

**CRedit authorship contribution statement**

**Juan M. Osuna-Cabanillas:** Writing – original draft, Visualization, Investigation, Formal analysis. **Emigdio Marín-Enríquez:** Resources, Methodology. **Ana P. Martínez-Falcón:** Supervision, Methodology. **Juan T. Timi:** Writing – original draft, Methodology. **Francisco N. Morales-Serna:** Writing – original draft, Supervision, Methodology,



Funding acquisition, Conceptualization.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.parint.2024.102885>.

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