Research Article

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Interannual and spatial variation in the parasite communities of Pacific sierra *Scomberomorus sierra* (Jordan et Starks) on Mexico's Pacific coast

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Abstract: The parasite communities of predatory fish can be species rich and diverse, making them effective models for studying the factors influencing temporal and spatial variation in these communities. Over a ten-year period an initial study was done on the metazoan parasite communities of *Scomberomorus sierra* (Jordan et Starks) from four locations on the south-central Pacific coast of Mexico. Twenty-four metazoan parasite taxa were identified from 674 *S. sierra* specimens: three species of Monogenea, eight Digenea, one Cestoda, one Acanthocephala, four Nematoda, five Copepoda, and two Isopoda. The parasite communities were characterised by high ectoparasite species richness, with monogeneans and some didymozoid species being numerically dominant. Community structure and species composition varied between locations, seasons and sampling years. Similarity between the component parasite communities was generally low, despite the occurrence of a distinctive set of host-specialist parasites. Interannual or local variations in some biotic and abiotic environmental factors are possible causes of the observed variations in the structure and species composition of the parasite community of *S. sierra*. Ecological factors were therefore considered to have more influence than phylogenetic aspects (host phylogeny) on parasite community structure.

Keywords: Marine parasites, predatory fish, tropics, south-central Pacific, Mexico.

Marine metazoan parasite communities consist largely of ectoparasites (monogeneans, copepods and isopods) and endoparasites (digeneans, cestodes, nematodes and acanthocephalans) (Poulin and Rohde 1997, Rohde 2005). In each of these parasite groups species richness and diversity vary substantially between different host species (Poulin and Rohde 1997, Rohde 2005). For example, ectoparasite populations may be more abundant in fish with schooling behaviour than in solitary species because the probability of a transmission stage (e.g. eggs, larvae) contacting a host increases with greater host density (Sasal et al. 1997, Luque et al. 2004, Palacios-Fuentes et al. 2015). This has been reported in several tropical monogenean species such as *Pseudomazocraes selene* Hargis, 1957, *Parancylodiscoides chaetodipteri* Caballero et Bravo-Hollis, 1961, *Protomicrocotyle manteri* Bravo-Hollis, 1966 and *Neomicrocotyle pacifica* Meserve, 1938 (Gallegos-Navarro et al. 2018, Villalba-Vásquez et al. 2018, Violante-González et al. 2020), as well as several species of copepods of the genus *Caligus* Müller, 1785 (Palacios-Fuentes et al. 2015).

Understanding the factors that influence parasite community structure and organisation in marine fish populations is a primary focus in parasite ecology. Parasite communities can exhibit temporal and spatial changes in their species composition and structure due to seasonal and local variations in several biotic and abiotic environmental factors (Garcias et al. 2001, Henríquez and González 2012, Villalba-Vásquez et al. 2018). In the tropics, structural changes in these communities have been linked principally to host traits such as age, body size, feeding behaviour, host density and vagility. These traits can promote exposure to new parasite species, increase their colonisation rates, and are associated with parasite communities of greater diversity and species richness (Luque et al. 2004, Villalba-Vásquez et al. 2018).

Several studies indicate that trophic level and diet determine the prey range of a fish predator. Many parasite species, particularly endoparasites, have complex life cycles involving transmission through a trophic web of intermediate, paratenic and definitive hosts (Luque and Poulin 2008,

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Fig. 1. Geographic locations of the sample collections of *Scomberomorus sierra* (Jordan et Starks) alongside the Mexico's Pacific coast.

Timi et al. 2011). Over evolutionary time host species at higher trophic levels (i.e. carnivorous and piscivorous fish) would therefore be exposed through diet to greater numbers of infective endohelminth larvae from a broader range of parasite taxa than would those at lower levels (Luque and Poulin 2008, Timi et al. 2011).

The Pacific sierra, *Scomberomorus sierra* Jordan et Starks (Scombridae), is a pelagic-neritic fish that forms schools of similarly-aged individuals. It is widely distributed in the eastern Pacific from southern California, USA, to the Galapagos Islands and Paite, Peru. Adults feed mainly on small fish such as anchovies and sardines (Collette and Nauen 1983, Moreno-Sánchez et al. 2011), but it is considered an opportunistic predator (i.e. one able to feed on prey that is unusually abundant in its environment). Along the Pacific coast of Mexico *S. sierra* is a major fishery (Aguirre-Villaseñor et al. 2006, Moreno-Sánchez et al. 2011). Some parasites of *S. sierra* has been reported for at least two locations for this region (Pérez-Ponce de León et al. 1999, Bárcenas 2019), but spatial and temporal variation over long time periods (interannual scale) has not yet been studied in this species.

The present study addressed two main objectives: (1) to characterise the metazoan parasite communities of *S. sierra*, and (2) to evaluate spatial and temporal variability in its parasite communities.

MATERIALS AND METHODS

A total of 674 specimens of *Scomberomorus sierra* were obtained from commercial fishermen as twelve samples (March

2011; March and August 2012; November 2013; February and December 2017; January, April and December 2018; January and May 2019; February 2020) over a 10-year period from four locations along the Pacific coast of Mexico: Zapotalito, Oaxaca (15.9686N, 97.5380W, $n = 170$); Acapulco Bay (16.8524N, 99.8823W, $n = 391$), Puerto Vicente (17.2677N, 101.0519W, $n = 64$) in Guerrero; and Lázaro Cárdenas, Michoacán (17.9161N, 102.2033W, $n = 49$) (Fig. 1). Records of sea surface temperature per sampling date were obtained from other studies carried out in the same locations but not yet published. Multivariate El Niño index values (MEI) for each sampling date were obtained from the National Oceanic and Atmospheric Administration (NOAA: <https://www.esrl.noaa.gov/psd/enso/mei/table.html>). Fish sex, total length (fish body size) and total weight for each individual were measured at the time of collection.

Fish from each sampling location were pooled into three size-classes: immature (< 35 cm), pre-adults (36–40 cm) and adults (> 40 cm) (Aguirre-Villaseñor et al. 2006). The coefficient of variation (CV), i.e. the quotient between the standard deviation and the arithmetic mean, was used to assess the variability in the total length of fish populations in each location or sampling year. Possible differences in the fish body size between sexes, locations and sampling years were determined using a one-way ANOVA.

The Fulton's condition factor (CF) was calculated using the equation: $CF = W_t/L_t^3$, where W_t is total weight, and L_t = total length. A complete necropsy was done of all specimens and all parasites collected from the internal and external organs. Digestive tract contents were examined to identify prey items consumed by this species at each location. Dietary items were identified to the family level when possible. Prey item analysis was done using the frequency of occurrence method (Lima-Junior and Goitein 2001). Parasites were identified to the lowest possible taxonomic level; vouchers of the most abundant and best preserved specimens were deposited in the in the Colección de Morfología Animal (COMA 00098 to 00110), Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, México.

Infection levels for each parasite species were described using prevalence (percent of fish infected with a particular parasite species); mean abundance (mean number of individual parasites of a particular species per examined fish), expressed as the mean $\pm$ standard deviation (SD); and intensity (number of a particular parasite species per infected fish), expressed as range (minimum-maximum) (Bush et al. 1997). The total prevalence (i.e. the percentage of infected fish with at least one of the parasite species) and the total mean intensity (mean total number of parasites in each sample) were used to determine possible relationships between the fish total length and these infection parameters within and between locations or sampling years.

Possible differences in infection levels between sampling years and/or locations were identified using *G*-tests (Sokal and Rohlf 1998) for prevalence and a General Linear Model (GLM) for abundance. The normality of data was determined with the Kolmogorov-Smirnov test with the use of Lilliefors' approach (Sokal and Rohlf 1998). When important deviations from normality were found, data were log-transformed ($\ln [X + 1]$). The host range concept (Rohde 2005) was used to classify the parasite species as specialists or generalists. In the present study, host-specialist species were those previously reported from scombrid fish

Fig. 2. Box plot of species number of ectoparasites (monogenean, didymozoid and crustacean), and endoparasites (larvae and adults) in *Scomberomorus sierra* (Jordan et Starks) from the Pacific coast of Mexico. The bottom and top of the boxes represent the lower and upper quartiles respectively; the median is shown as a line through the centre of the boxes; outliers are indicated with circles for ectoparasites and asterisks for endoparasites.

(Scombridae), and generalists were those previously reported from species of fish of different families (Aguirre-Macedo et al. 2007). The infracommunity index (ICI) (Zander 2004), which describes the frequency of double and multiple infections by a single species of parasite in a distinct host (affinity level of a parasite species; i.e. parasite species with great tendency to join the infracommunity), was also calculated. Spearman's correlation coefficient (r_s) was used to determine possible relationships between host total length and the infection or infracommunity parameters.

Analyses were done at the levels of component community (i.e. total parasite species in all fish collected at a location) and infracommunity (i.e. total parasite species in each individual fish). Component community parameters included total species richness; total number of individuals of each parasite species; the Shannon-Wiener Index (H) as a measure of diversity; species evenness (equitability); and the Berger-Parker Index (BPI) as a measure of numerical dominance. The qualitative Sorensen's index and quantitative percentage of similarity (PS) index were used to evaluate similarity and difference in parasite community species composition between years and/or locations. Differences between component community parameters were identified with Student t and χ^2 tests.

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) was used to identify possible differences in infracommunity parameters (dependent variables) between locations and/or sampling years (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 $p < 0.05$, unless stated otherwise. A multivariate analyses (Principal Component Analy-

sis, PCA) was applied to identify biotic and abiotic factors that influenced parasite infracommunity species richness and diversity. To minimise the effect of host body size only fish > 35 cm (i.e. pre-adults and adults) were included in this analyses; so two samples of Acapulco 2018 (January, $n = 84$; and December, $n = 77$) and the Puerto Vicente 2018 (April, $n = 64$) were excluded.

The predictor variables used were Fulton's condition factor (CF); host diet diversity (calculated as the diversity of items consumed by host populations in each sampling location, through the use of the Shannon-Wiener index at the family level); number of didymozoid species; surface temperature; climate anomaly values (MEI); climatic season: (dry season, precipitation < 70 mm, and rainy season, precipitation ≈ 950 mm) (Violante-González et al. 2020); sampling year and collection location. The Kaiser-Meyer-Olkin (KMO) test of sampling adequacy for each variable in the model, as well as the Bartlett's test, which evaluates the possibility that there is redundancy among variables, were applied. The variance maximising rotation method was used to produce the two ordination axes. Discriminant function analyses (DFA) based on Mahalanobis distances were used to identify possible differences in parasite community structure between locations (to minimise temporal variation as a source of variability, only one sample from Acapulco 2018_{Jan} and one from Zapotalito 2017_{Feb} were included in this analysis). Only parasite species with a prevalence $> 10\%$ in at least one of the locations (a component species; *sensu* Bush et al. 1990) were included.

RESULTS

Species composition

Twenty-four taxa of metazoan parasites (17 helminths and seven crustaceans) were identified from a total sample of 10,573 individual parasites recovered from 674 *Scomberomorus sierra* specimens collected from four locations along the south-central Pacific coast of Mexico. Three of these species were Monogenea (adults), eight were Digenea (seven adults and one metacercaria), one was Cestoda (larvae), one was Acanthocephala (adult), four were Nematoda (three adults and one larva), five were Copepoda, and two were Isopoda (Table 1). Species richness was highest among the digeneans, representing 34% of total recovered species, followed by the copepods (29%). According to infection site, 13 parasite species were classified as ectoparasites and 11 as endoparasites. Ectoparasite species numbers (Fig. 2) varied widely from 0.05 ± 0.21 in hosts from Puerto Vicente to 3.06 ± 1.12 in those from Zapotalito (ANOVA $F_{3,244} = 102.69$, $p < 0.01$).

Of the total parasite species sample, ten were classified as host-specialists (three monogeneans, five digeneans and two copepods; Table 1). Nine parasite species (*Mexicotyle mexicana* [Meserve, 1938], *Thoracocotyle crocea* [MacCallum, 1913], *Didymocilindrus* sp., *Didymocystis* sp., *Lecithochirium microstomum* [Chandler, 1935], *Proisorhynchoides cybii* [Park, 1939], *Anisakis* sp., *Hysterothylacium* sp. and *Caligus omissus* [Cressey et Cressey, 1980]) were widely distributed and occurred in the *S. sierra* parasite communities at all or most of the sampled locations (Table 1).

Table 1. Parasite infection parameters for *Scomberomorus sierra* from Mexican Pacific coasts (Zapotalito, Oaxaca; Acapulco and Puerto Vicente, Guerrero; and Lázaro Cárdenas, Michoacán). ^aNumber of fish examined, ^bTotal number of individual parasites collected, ^cNumber of parasites per fish (mean±SD), ^dMinimum to maximum number of parasites present, ^eInfracommunity index, ^fNew geographical record. Subscripts to the right of the sampling year indicate the sampling month: J = January, F = February, Ma = March, Ap = April, M = May, A = August, N = November, D = December.

Parasite species	Parasite classification	Site on host	Location	Year	n ^a	Prevalence (%)	Total ^b	Abundance ^c	Range of intensity ^d	ICI ^e
Digenea										
<i>Anacetabulum</i> sp. (larvae)	Specialist	Gills	Acapulco	2012 _A	19	1	2	0.03	1–2	0.004
			Acapulco	2018 _J	84	1	11	0.13	1–11	0.007
			Acapulco	2019 _M	59	15	19	0.32±1.27	1–4	0.062
			Zapotalito	2017 _F	48	19	22	0.46±2.35	1–7	0.054
			Zapotalito	2017 _D	28	7	4	0.14±1.41	1–3	0.059
			Zapotalito	2019 _J	40	48	59	1.48±3.23	1–14	0.123
			Zapotalito	2020 _F	54	72*	564	10.44±22*	1–109	0.122
<i>Didymocilindrus</i> sp.	Specialist	Gills	Acapulco	2011 _{Ma}	76	67	1025	13.49±14.61	5–101	0.216
			Acapulco	2012 _{Ma}	19	53	87	4.58±4.72	2–15	0.118
			Acapulco	2012 _A	76	62	360	4.74±7.78	1–43	0.199
			Acapulco	2018 _J	84	29	100	1.19±4.37	1–17	0.172
			Acapulco	2018 _D	77	3	2	0.03	1–1	0.045
			Acapulco	2019 _M	59	56	154	2.61±4.65	1–22	0.226
			Zapotalito	2017 _F	48	17	52	1.08±4.50	1–13	0.048
			Zapotalito	2017 _D	28	21	25	0.89±3.37	2–9	0.177
			Zapotalito	2019 _J	40	68	180	4.50±7.65	1–27	0.175
			Zapotalito	2020 _F	54	80*	597	11.06±13.7*	1–79	0.135
			L. Cárdenas	2013 _N	49	65	258	5.27±6.05	1–32	0.19
			<i>Didymocystis</i> sp.	Specialist	Intestine, Stomach,	Acapulco	2011 _{Ma}	76	67*	591
Acapulco	2012 _{Ma}	19				74*	143	7.53±12.44*	1–47	0.165
Acapulco	2012 _A	76				8	30	0.39±3.79	2–12	0.025
Acapulco	2019 _M	59				17	49	0.83±4.51	1–15	0.069
Zapotalito	2019 _J	40				13	24	0.60±4.82	1–11	0.032
Zapotalito	2020 _F	54				54	196	3.63±5.93	1–31	0.091
L. Cárdenas	2013 _N	49				49	189	3.86±5.53	2–21	0.14
<i>Didymozoon</i> sp.	Specialist	Intestine	Zapotalito	2020 _F	54	4	4	0.07±1.41	1–3	0.006
<i>Glomeritrema</i> sp.	Specialist	Gills	Acapulco	2011 _{Ma}	76	11	55	0.72±10.84	1–30	0.034
			Acapulco	2018 _J	84	4	5	0.06±1.15	1–3	0.022
			Acapulco	2019 _M	59	15	18	0.31±0.71	1–3	0.062
			Zapotalito	2017 _F	48	79	395	8.23±11.29*	1–58	0.227
			Zapotalito	2019 _J	40	33	35	0.88±2.14	1–9	0.084
			Zapotalito	2020 _F	54	48	159	2.94±7.32	1–28	0.082
			<i>Gonocercella pacifica</i> Manter, 1940 ^f	Generalist	Intestine	Zapotalito	2020 _F	54	2	1
<i>Lecithochirium microstomum</i> Chandler, 1935 ^f	Generalist	Intestine	Acapulco	2011 _{Ma}	76	1	1	0.01	1–1	0.004
			Acapulco	2012 _A	76	1	3	0.04	1–3	0.004
			Acapulco	2018 _J	84	6	7	0.08±0.55	1–2	0.036
			Acapulco	2018 _D	77	7	7	0.09±0.55	1–2	0.112
			Acapulco	2019 _M	59	9	12	0.20±2.19	1–6	0.034
			Zapotalito	2017 _F	48	2	1	0.02	1–1	0.006
			Zapotalito	2017 _D	28	4	1	0.04	1–1	0.030
			Zapotalito	2019 _J	40	8	5	0.13±0.58	1–2	0.019
			Zapotalito	2020 _F	54	4	2	0.04	1–1	0.006
			L. Cárdenas	2013 _N	49	2	1	0.02	1–1	0.01
			P. Vicente	2018 _{Ap}	64	2	1	0.02	1–1	0.142
			<i>Proserhynchoides cybii</i> Park, 1939 ^f	Generalist	Intestine	Acapulco	2011 _{Ma}	76	21	50
Acapulco	2012 _{Ma}	19				37	48	2.53±7.43	1–19	0.082
Acapulco	2012 _A	76				7	7	0.09±0.89	1–3	0.021
Acapulco	2018 _J	84				2	12	0.14±7.07	1–11	0.014
Acapulco	2018 _D	77				1	1	0.01	1–1	0.022
Acapulco	2019 _M	59				3	3	0.05±0.71	1–2	0.014
Zapotalito	2017 _F	48				23	19	0.40±1.56	1–6	0.066
Zapotalito	2019 _J	40				20	19	0.48±2.07	1–6	0.052
Zapotalito	2020 _F	54				61*	173	3.20±5.68	1–21	0.104
L. Cárdenas	2013 _N	49				45	69	1.41±3.18	1–13	0.13
P. Vicente	2018 _{Ap}	64				5	3	0.05	1–1	0.426
Monogenea										
<i>Mexicotyle mexicana</i> (Meserve, 1938) Lebedev, 1984	Specialist	Gills	Acapulco	2011 _{Ma}	76	28	38	0.50±1.60	1–8	0.089
			Acapulco	2012 _{Ma}	19	63	52	2.74±2.84	1–9	0.141
			Acapulco	2012 _A	76	68	213	2.80±4.29	1–26	0.221
			Acapulco	2018 _J	84	31	51	0.61±1.40	1–8	0.186

Table 1. Continued

			Acapulco	2018 _D	77	7	29	0.38±6.57	1–13	0.112
			Acapulco	2019 _M	59	39	47	0.80±1.43	1–6	0.158
			Zapotalito	2017 _F	48	73	157	3.27±4.12	1–16	0.210
			Zapotalito	2017 _D	28	25	10	0.36±0.79	1–3	0.207
			Zapotalito	2019 _J	40	53	55	1.38±1.77	1–6	0.136
			Zapotalito	2020 _F	54	91*	420	7.78±8.46*	1–46	0.154
			L. Cárdenas	2013 _N	49	45	66	1.35±2.47	1–12	0.128
<i>Scomberocotyle scomberomori</i> (Koratha, 1955) Hargis, 1956	Specialist	Gills	Acapulco	2011 _{Ma}	76	1	2	0.03	1–2	0.004
			Acapulco	2019 _M	59	2	1	0.02	1–1	0.007
			Zapotalito	2020 _F	54	13	12	0.22±1.25	1–4	0.022
<i>Thoracocotyle crocea</i> MacCallum, 1913	Specialist	Gills	Acapulco	2011 _{Ma}	76	62	240	3.16±5.75	1–30	0.199
			Acapulco	2012 _{Ma}	19	68	199	10.47±17.16	1–55	0.153
			Acapulco	2012 _A	76	82	345	4.54±5.18	1–26	0.263
			Acapulco	2018 _J	84	30	65	0.77±3.11	1–14	0.179
			Acapulco	2018 _D	77	9	11	0.14±0.53	1–26	0.157
			Acapulco	2019 _M	59	25	155	2.63±20.36	1–73	0.103
			Zapotalito	2017 _F	48	60	253	5.27±10.71	1–41	0.174
			Zapotalito	2017 _D	28	11	9	0.32±3.46	1–73	0.089
			Zapotalito	2019 _J	40	70	272	6.80±17.01	1–72	0.182
			Zapotalito	2020 _F	54	87	953	17.65±31.7*	1–186	0.148
			L. Cárdenas	2013 _N	49	71	266	5.43±10.22	1–50	0.20
			Cestoda							
Tetrafilidae ^f (larvae)	Generalist	Intestine	Acapulco	2011 _{Ma}	76	1	10	0.13	1–10	0.004
Acanthocephala										
<i>Rhadinorhynchus</i> cf. <i>pristis</i> (Rudolphi, 1802) Lühe, 1911	Generalist	Intestine	Acapulco	2018 _J	84	2	3	0.04±0.71	1–2	0.014
			Acapulco	2019 _M	59	5	5	0.08±1.15	1–3	0.021
Nematoda										
<i>Anisakis</i> sp. (larvae)	Generalist	Intestine	Acapulco	2011 _{Ma}	76	15	41	0.54±6.10	1–21	0.047
			Acapulco	2012 _{Ma}	19	21*	34	1.79±12.40	1–27	0.047
			Acapulco	2012 _A	76	4	3	0.04	1–1	0.013
			Acapulco	2018 _J	84	2	2	0.02	1–1	0.014
			Acapulco	2018 _D	77	3	2	0.03	1–1	0.045
			Zapotalito	2017 _F	48	4	2	0.04	1–1	0.012
			Zapotalito	2020 _F	54	7	5	0.09±0.50	1–2	0.013
			L. Cárdenas	2013 _N	49	4	5	0.10±2.12	1–4	0.01
<i>Hysterothylacium</i> sp.	Generalist	Intestine	Acapulco	2011 _{Ma}	76	7	8	0.11±0.89	1–3	0.021
			Acapulco	2012 _{Ma}	19	21	10	0.53±1.73	1–5	0.047
			Acapulco	2012 _A	76	1	1	0.01	1–1	0.004
			Acapulco	2019 _M	59	12	18	0.31±1.62	1–6	0.048
			Zapotalito	2017 _F	48	10	6	0.13±0.45	1–2	0.030
			Zapotalito	2019 _J	40	40*	28	0.70±0.86	1–3	0.104
			Zapotalito	2020 _F	54	2	1	0.02	1–1	0.003
			L. Cárdenas	2013 _N	49	12	6	0.12	1–1	0.03
<i>Philometra</i> sp. ^f	Generalist	Gonad	Acapulco	2011 _{Ma}	76	1	6	0.08	1–6	0.004
			Acapulco	2012 _{Ma}	19	26	14	0.74±2.49	1–6	0.059
			Acapulco	2012 _A	76	1	1	0.01	1–1	0.004
			Zapotalito	2017 _F	48	2	1	0.02	1–1	0.006
			Zapotalito	2020 _F	54	2	4	0.07	1–4	0.003
			L. Cárdenas	2013 _N	49	2	1	0.02	1–1	0.01
<i>Procamallanus</i> sp. ^f	Generalist	Intestine	Acapulco	2012 _{Ma}	19	11	10	0.53±1.41	4–6	0.024
			Acapulco	2018 _D	84	1	1	0.01	1–1	0.007
			Zapotalito	2020 _F	54	6	3	0.06	1–1	0.009
Copepoda										
<i>Caligus omissus</i> Cressey et Cressey, 1980 ^f	Specialist	Gills	Acapulco	2011 _{Ma}	76	26	30	0.39±0.76	1–3	0.085
			Acapulco	2012 _{Ma}	19	74*	24	1.26±1.14	1–4	0.165
			Acapulco	2012 _A	76	72*	112	1.47±1.56	1–8	0.233
			Acapulco	2018 _J	84	55	70	0.83±0.62	1–3	0.330
			Acapulco	2018 _D	77	27	31	0.40±0.75	1–4	0.470
			Acapulco	2019 _M	59	37	31	0.53±0.73	1–3	0.151
			Zapotalito	2017 _F	48	58	82	1.71±4.14	1–22	0.168
			Zapotalito	2017 _D	28	54	32	1.14±2.10	1–9	0.443
			Zapotalito	2019 _J	40	25	17	0.43±0.82	1–3	0.065
			Zapotalito	2020 _F	54	60	62	1.15±1.83	1–10	0.100
			L. Cárdenas	2013 _N	49	51	43	0.88±1.70	1–9	0.15
			P. Vicente	2018	64	5	3	0.05	1–10	0.426
			L. Cárdenas	2013 _N	49	2	1	0.02	1–1	0.01
<i>Ergasilus</i> sp. ^f	Generalist	Gills	Acapulco	2011 _{Ma}	76	3	2	0.03	1–1	0.008
<i>Lernanthrophus</i> cf. <i>giganteus</i> Krøyer, 1863 ^f	Generalist	Gills	Acapulco	2011 _{Ma}	76	3	2	0.03	1–1	0.008
<i>Orbitacolax</i> cf. <i>aculeatus</i> ^g Pillai 1962	Generalist	Gills	Acapulco	2012 _A	76	3	3	0.04±0.71	1–2	0.008

Table 1. Continued

<i>Cybicola buccatus</i> (Wilson, 1922) ^f	Specialist	Gills	Acapulco	2018 _J	84	1	1	0.01	1–1	0.007
			Acapulco	2018 _D	77	1	1	0.01	1–1	0.022
			Acapulco	2018 _D	77	1	1	0.01	1–1	0.022
			Acapulco	2019 _M	59	12	7	0.12	1–1	0.048
			Zapotalito	2019 _J	40	5	3	0.08±0.71	1–2	0.013
			L. Cárdenas	2013 _N	49	2	1	0.02	1–1	0.01
Isopoda										
<i>Livoneca redmanii</i> Leach, 1818 ^f	Generalist	Gills	Acapulco	2018 _J	84	2	2	0.02	1–1	0.014
<i>Rocinela signata</i> ^f	Generalist	Gills	Zapotalito	2019 _J	40	5	2	0.05	1–1	0.013

Schioedte et Meinert, 1879^f*Significantly different measurements of prevalence (G-test) and abundance (two-way Anova) ($p < 0.05$).

Variation in infection level between locations and/or sampling years

In eight of these widely distributed species (except for *L. microstomum*) prevalence varied significantly between locations and/or sampling years. Infection percentages were highest for *M. mexicana* ($G = 129.87$, $p < 0.05$), *T. crocea* ($G = 152.6$, $p < 0.05$), *Didymocilindrus* sp. ($G = 136.46$, $p < 0.05$) and *P. cybii* ($G = 193.05$, $p < 0.05$) in the Zapotalito 2020_{Feb} sample, but were highest for *Hysterothylacium* sp. ($G = 83.87$, $p < 0.05$) in the Zapotalito 2019_{Jan} sample (Table 1). The three remaining parasite species (*Didymocystis* sp. [$G = 111.08$, $p < 0.05$], *Anisakis* sp. [$G = 42.32$, $p < 0.05$], and *C. omissus* [$G = 108.28$, $p < 0.05$]) were more prevalent in Acapulco, mainly in the Acapulco 2012_{Mar} sample (Table 1). In contrast to the infection percentage results, only two parasite species (*Hysterothylacium* sp. [GLM: $F_{2,674} = 7.75$, $p < 0.01$] and *C. omissus* [GLM: $F_{2,674} = 3.79$, $p < 0.05$]) exhibited significant variation in mean abundance between sampling locations. However, the abundance of most species (except *Anisakis* sp.) varied between sampling years within the same location (GLM: $F_{2,674}^* p < 0.01$).

Relationship between the host body size and the infection parameters

The abundance of at least three species of parasites showed a positive or negative relationship with the host body size. Positive correlations were registered for the monogenean *T. crocea* in the Acapulco 2012_{Mar} ($rs = 0.257$, $p < 0.05$) and L. Cárdenas 2013_{Nov} ($rs = 0.558$, $p < 0.05$) samples, and for the digenean *P. cybii* in the samples of Acapulco 2011_{Mar} ($rs = 0.574$, $p < 0.05$), and Acapulco 2012_{Mar} ($rs = 0.836$, $p < 0.05$). Whereas abundance of the copepod *C. omissus* was negatively correlated with the host body size in the Acapulco 2012_{Mar} ($rs = -0.648$, $p < 0.05$) and Zapotalito 2017_{Jan} ($rs = -0.686$, $p < 0.05$) samples.

Analyses of host size-classes by location and sampling year (Table 2) indicated that mean species richness and mean total intensity tended to increase from the smallest to largest size-classes (< 30 cm = 1.92, 5.1; 36–40 cm = 3.57, 22.85; > 40 cm = 3.78, 24.08). Positive correlations registered between total fish length and these infection parameters within some samples from two locations confirmed this trend (Table 2). Considering the twenty host size-classes constructed, the mean total length of each size-class correlated positively with the mean species richness ($rs = 0.480$, $p < 0.05$) and mean total intensity ($rs = 0.639$, $p < 0.01$). No correlation was observed between the number

of examined fish in each size-class and mean species richness ($rs = -0.303$, $p > 0.05$), or mean total intensity ($rs = -0.045$, $p > 0.05$) indicating that the different sample sizes used in this analysis had no effect on the results.

Host diet composition

The dietary spectrum of *S. sierra* in the study area included nine items, with fish representing the highest proportion (88%). Additional prey items accounted only for 12% of the diet and included crab larvae, amphipods, penaeid shrimp larvae, mollusk larvae, isopods and stomatopods. Diet composition varied between locations and/or sampling years ($t = 6.62$, $p < 0.01$). For example, even though fish were the primary dietary component at all locations, diet composition was more variable at Zapotalito 2020_{Feb} ($H = 0.95$) and Acapulco 2011_{Mar} ($H = 0.87$) than at other locations such as Puerto Vicente 2018_{Apr} ($H = 0.20$). Feeding habits changed with fish body size; larger individuals (> 40 cm) consumed higher percentages of fish. The diet was slightly more varied between individuals of 36–40 cm (mean H values: < 30 cm = 0.47; 36–40 cm = 0.61; > 40 cm = 0.56), and it was positively correlated with the mean parasite species richness among the twenty size-classes considered ($rs = 0.480$, $p < 0.05$).

Component community

Parasite species richness recorded by location and/or sampling year (Table 3) varied widely from three (Puerto Vicente 2018_{Apr}) to 16 (Zapotitalito 2020_{Feb}) ($t = 7.71$, $p < 0.01$). No correlation was observed between sample size and species richness at this level ($rs = 0.293$, $p > 0.05$). Total number of individual parasites ranged from seven (P. Vicente 2018_{Apr}) to 3,156 (Zapotitalito 2020_{Feb}) ($t = 8.58$, $p < 0.05$). Different parasite species numerically dominated the communities, although the monogenean *T. crocea* dominated up to five of the twelve examined communities. Shannon-Wiener diversity index values varied significantly from 0.48 (P. Vicente 2018_{Apr}) to 1.20 (Zapotitalito 2020_{Feb}) ($t = 9.21$, $p < 0.01$). Similarity between component communities was slightly low overall ($< 70\%$, Fig. 3) and was higher at the qualitative level (mean = 65.6%) than at the quantitative level (mean = 32.5%).

Infracommunity

Body size of *S. sierra* varied from 24.1 ± 3.3 cm (Acapulco 2018_{Dec}) to 47.2 ± 4.3 cm (Acapulco 2012_{Mar}) (Table 3), and differed between locations (ANOVA $F_{3,618} = 99.56$, $p < 0.01$) and sampling years (ANOVA $F_{6,618} = 174.09$, p

Fig. 3. Similarity percentages (Bray-Curtis index) for parasite communities of *Scomberomorus sierra* (Jordan et Starks) between locations and sampling years.

< 0.01). No significant differences in size were observed between male and female fish ($p > 0.05$).

Mean parasite species richness ranged from 1.0 to 5.6 ± 1.5 and mean number of individual parasites from 1.0 to 43.9 ± 31.5 (Table 3). Brillouin diversity index (H') values varied from 0.13 ± 0.30 to 1.46 ± 0.50 . Values for all three parameters (mean number of species [GLM: $F_{2,618} = 37.62$, $p < 0.01$], mean number of parasite individuals [GLM: $F_{2,618} = 44.01$, $p < 0.01$] and mean diversity (H') [GLM: $F_{2,618} = 27.46$, $p < 0.01$]) were highest in the Zapotalito 2020_Feb sample (Table 3). Infracommunity index values (ICI) indicated that the monogeneans *M. mexicana* and *T. crocea*, the didymozoid *Didymocilindrus* sp. and the copepod *C. omissus* had the highest number of double or multiple infections with other parasite species (ICI mean > 0.15), at almost all locations or in nearly all sampling years (Table 1).

Multivariate analyses

The PCA applied to identify the influence of biotic and abiotic factors on parasite infracommunity structure (Fig. 4), the KMO (0.43) and the Bartlett's tests ($\chi^2 = 4,860.2$; d.f. = 66, $p < 0.001$), identified a sufficient relationship between the number of studied variables and the sample sizes, thus confirming the PCA's relevance. The first two component variables generated by the model explained 55% of total variance; they contributed 32% (eigenvalue = 3.78) and 24% (eigenvalue = 2.82), respectively. The first variable suggests that the richest and most diverse infracommunities among all the sampled locations were characterised by a significant number of didymozoid species. These infracommunities were mainly recorded in larger hosts. However, these infracommunities' richness and diversity varied between climatic seasons and locations. For example, a positive correlation for season and a negative one for sampling location variables (Table 4) suggested that the richest and most diverse infracommunities were collected from Zapotalito 2020_Feb during the dry season (Table 3).

Fig. 4. Scatter plot of Principal Component Analysis (PCA) of factors that influence the species richness and diversity of the parasite infracommunities in *Scomberomorus sierra* (Jordan et Starks) from Mexican Pacific coast. Predictor variables (●): Location = collection location, Season = climatic season (dry/rainy), Temp = surface temperature values, Enso = multivariate El Niño index, Diet = host diet variety, Size = host body size (total length), CF = Fulton's condition factor, Rldidy = number of didymozoid species. Infracommunity parameters (○): Richness = number of parasite species per infracommunity, Diversity = Brillouin diversity index values, Equitability = species evenness, Total = total number of parasites per infracommunity.

The model built to identify locations via differences in parasite community species composition showed the first two discriminant variables to explain 97% of total variance, contributing 54% (eigenvalue = 0.705) and 43% (eigenvalue = 0.563), respectively. A significant overall group effect was observed (Wilks' lambda = 0.361, $p < 0.001$). Individual fish were mainly distributed along the first axis (Fig. 5). Dimensionality tests showed that the four studied locations were significantly separate in both dimensions ($\chi^2 = 190.5$, d.f. = 24, $p < 0.001$) (Fig. 5). Each fish was correctly assigned to one of the four sampling locations at a 73% accuracy, more than twice the 26% produced by chance alone.

Of the 14 selected component species (i.e. prevalence > 10%), only six were accepted by the model based on their lower Wilks' lambda values. The high prevalences of the monogenean *M. mexicana*, the didymozoid *Glomeritrema* sp. and the copepod *C. omissus* effectively assigned their hosts to Zapotalito (Table 5). The higher abundances observed for the digeneans *P. cybii*, *Didymocilindrus* sp. and *Didymocystis* sp. were characteristic of hosts from Lázaro Cárdenas. High prevalence for *C. omissus* also helped to separate out most (68%) of the hosts from Acapulco. None of the component species was effective at assigning fish hosts to Puerto Vicente (Table 5).

DISCUSSION

The parasite communities of *Scomberomorus sierra* were characterised by numerical dominance of ectoparasites. Parasite community structure and species composition varied between locations, seasons and sampling years. Despite the presence of a distinctive set of host-specialist parasites (monogeneans, didymozoids and copepods), sim-

Table 2. Relationships between host body size and the infection parameters of metazoan parasites communities in *Scomberomorus sierra* (Jordan et Starks) from Mexican Pacific coasts (Zapotalito, Oaxaca; Acapulco and Puerto Vicente, Guerrero; and Lázaro Cárdenas, Michoacán).

Location	Sample/ size-class	Examined fish	No. infected	CV ^a %	Diet	Mean richness	Total prevalence	Mean total intensity	Fish length vs. richness ^b	Fish length vs. intensity ^b
Acapulco	Mar 2011 > 40 cm	76	75	7.6	0.87	3.1 ± 1.5	98.6	28.0 ± 24.5	0.467*	-0.021
	Mar 2012 > 40 cm	19	19	10.7	0.53	4.5 ± 1.9	100	32.9 ± 23.9	0.003	-0.151
	Aug 2012 < 35 cm	11	11	8.4	0.46	3.4 ± 0.8	100	11.9 ± 8.2	-0.094	-0.545
	36–40 cm	28	28	3.9	0.59	3.3 ± 1.1	100	14.6 ± 9.8	-0.142	-0.001
	> 40 cm	37	37	6.3	0.50	2.9 ± 0.7	100	14.6 ± 10.4	0.405*	0.247
	Jan 2018 < 35 cm	84	73	10.1	0.79	1.9 ± 1.0	86.9	4.5 ± 5.3	0.100	0.001
	Dec 2018 < 35 cm	77	35	13.8	0.42	1.3 ± 0.7	45.4	2.9 ± 5.0	0.439*	0.419*
	May 2019 < 35 cm	29	24	4.5	0.50	2.0 ± 1.0	82.8	5.2 ± 5.7	0.328	0.454*
	36–40 cm	15	14	4.1	0.53	4.5 ± 1.9	93.3	17.0 ± 17.0	-0.222	-0.116
	> 40 cm	15	11	4.8	0.68	3.2 ± 2.0	73.3	14.1 ± 23.6	-0.349	-0.468
Zapotalito	Feb 2017 36–40 cm	10	10	13.6		3.4 ± 1.3	100	10.7 ± 6.4	0.484*	0.142
	> 40 cm	38	38	6.46		3.5 ± 1.3	100	23.2 ± 21.73	0.116	0.123
	Dec 2017 36–40 cm	17	12	8.7		1.7 ± 0.6	70.6	5.1 ± 3.2	-0.085	-0.115
	> 40 cm	11	9	2.2		1.6 ± 0.7	81.8	2.2 ± 1.6	0.038	0.139
	Jan 2019 > 40 cm	40	40	4.6	0.61	3.8 ± 1.6	100	17.5 ± 18.9	-0.086	0.019
	Feb 2020 36–40 cm	11	11	4.3		5.9 ± 1.0	100	77.5 ± 48.4	-0.389	-0.355
	> 40 cm	43	43	4.4		5.9 ± 1.6	100	55.6 ± 43.1	0.028	-0.292
Lázaro Cárdenas	Nov 2013 36–40 cm	21	19	5.1		3.9 ± 1.3	90.5	19.6 ± 19.5	-0.370	-0.376
	> 40 cm	28	27	14.8		3.6 ± 1.8	96.4	17.6 ± 16.0	0.041	0.009
Puerto Vicente	Apr 2018 < 35 cm	64	7	5.2	0.20	1	10.9	1		

^a Coefficient of variation in fish length (%). ^b Spearman rank correlation coefficient. *Significant at $p < 0.05$. Letters as superscripts represent codes of climatic seasons (d = dry, r = rainy).

Fig. 5. Graphic of multivariate discriminant analyses for parasite communities of *Scomberomorus sierra* from four locations. The symbols represent each one of the sampling locations. Centroid = mean group.

ilarity between the component parasite communities was generally low. Interannual or local variations in some biotic and abiotic environmental factors are possible causes

of the observed variations in *S. sierra* parasite community structure and species composition. Ecological factors were therefore considered more important than phylogenetic aspects (host phylogeny) in structuring parasite communities.

Parasite community species composition

The overall dominance pattern of the main metazoan parasite taxa recorded in *S. sierra* was Digenea > Copepoda > Nematoda > Monogenea > Isopoda > Cestoda = Acanthocephala. Fourteen (seven helminths and seven crustaceans) of the 24 recorded parasite taxa are new geographical records for *S. sierra* on Mexico's Pacific coast (Table 1). Ectoparasites (three monogeneans, three didymozoids, five copepods and two isopods) numerically dominated the parasite communities, accounting for 82% of the total number of individual parasites recovered. Monogeneans are often transmitted directly between individual hosts through contact, exhibit high host-specificity, have a direct life cycle and can reproduce in a wide range of temperatures (Mendllová and Šimková 2014). The monogenean *Thoracocotyle crocea* was the dominant parasite in as many as five of the 12 examined parasite communities. This species has been recorded in all 18 species of *Scomberomorus* Lacepède,

Table 3. Characteristics of the parasite component communities and infracommunities in *Scomberomorus sierra* (Jordan et Starks) from Mexican Pacific coasts (Zapotalito, Oaxaca; Acapulco and Puerto Vicente, Guerrero; and Lázaro Cárdenas, Michoacán).

Location	Date	SST °C	MEI	Examined fish	Length (cm)	C.V. %	Diet	Component communities			Infracommunities				
								Species richness	No. of para- sites	BPI	Dominant species	H	Mean number of species	Mean number of parasites	Mean value of Brillouin Index
Acapulco	Mar 2011 ^d	26.2	-1.8	76	44.9 ± 3.42	7.62	0.87	14	2,099	0.488	Dici	1.15	3.1 ± 1.5	28.0 ± 24.5	0.97 ± 0.5
	Mar 2012 ^d	27.6	-0.6	19	47.2 ± 4.3	10.7	0.53	10	621	0.320	Thor	1.00	4.5 ± 1.9	32.9 ± 23.9	1.22 ± 0.6
	Aug 2012 ^r	29.8	-0.1	76	40.2 ± 4.6	11.4	0.63	12	1,080	0.333	Dici	1.08	3.1 ± 0.9	14.2 ± 9.8	0.95 ± 0.4
	Jan 2018 ^d	27.1	-0.8	84	28.5 ± 2.9	10.1	0.79	13	330	0.303	Dici	1.11	1.9 ± 1.0	4.5 ± 5.3	0.43 ± 0.4
	Dec 2018 ^d	27.4	0.1	77	24.1 ± 3.3	13.8	0.42	9	85	0.365	Mexi	0.95	1.3 ± 0.7	2.9 ± 5.0	0.13 ± 0.3
	May 2019 ^d	29.6	0.3	59	35.7 ± 6.7	18.9	0.78	13	519	0.299	Thor	1.11	3.4 ± 2.0	11.6 ± 17.1	0.76 ± 0.7
Zapotalito	Feb 2017 ^d	27.5	-0.4	48	44.0 ± 4.7	10.8	0.56	11	990	0.399	Glom	1.04	3.5 ± 1.3	20.9 ± 20.2	1.06 ± 0.4
	Dec 2017 ^d	27.0	-0.7	28	38.9 ± 3.6	9.3	0.37	6	81	0.395	Cali	0.78	1.6 ± 0.7	3.9 ± 3.0	0.32 ± 0.3
	Jan 2019 ^d	28.3	0.1	40	46.4 ± 2.1	4.6	0.61	12	699	0.389	Thor	1.08	3.8 ± 1.6	17.5 ± 18.9	1.03 ± 0.5
	Feb 2020 ^d	29.0	0.3	54	43.4 ± 3.1	7.0	0.95	16*	3,156*	0.302	Thor	1.20*	5.9 ± 1.5*	58.4 ± 44.8*	1.6 ± 0.5*
L. Cárdenas	Nov 2013 ^r	29.0	-0.2	49	43.2 ± 6.4	14.7	0.64	12	906	0.294	Thor	1.08	3.8 ± 1.6	18.5 ± 17.4	1.11 ± 0.5
P. Vicente	Apr 2018 ^d	25.5.	-1.3	64	32.0 ± 1.6	5.2	0.20	3	7	0.429		0.48	1.0	1.0	

SST = sea surface temperature, MEI = climate anomaly values, Length = total length, Diet = diet variety, BPI = Berger-Parker Index; H = Shannon-Wiener diversity index, Cali = *Caligus omissus*, Dici = *Didymocilindrus* sp., Glom = *Glomeritrema* sp., Mexi = *Mexicotrypa crocea*. *Significant at p < 0.05. Letters as superscripts represent codes of climatic seasons (d = dry, r = rainy) used in the multivariate statistical analysis.

SST = sea surface temperature, MEI = climate anomaly values, Length = total length, Diet = diet variety, BPI = Berger-Parker Index; H = Shannon-Wiener diversity index. Cali = *Caligus omissus*, Dici = *Didymocilindrus* sp., Glom = *Glomeritrema* sp., Mexi = *Mexicotyle mexicana*, Thor = *Thoracotyle crocea*. *Significant at $p < 0.05$. Letters as superscripts represent codes of climatic seasons (d = dry, r = rainy) used in the multivariate statistical analysis.

from both the Pacific and Atlantic coasts of the Americas (Hayward and Rohde 1999).

Didymozoids are also considered to be highly host-specific; this parasite group mainly parasitises tropical and subtropical scombrids and is rarely found in freshwater fish species (Madhavi and Ram 2000, Mele et al. 2012). Five didymozoid species have been reported in *S. japonicus* from Peru (Cruces et al. 2014) and six species (including the five didymozoid species reported here) have been reported in *S. sierra* from another location on Mexico's Pacific coast (Bárcenas 2019).

Variation in parasite infection levels between sampling years and/or locations

Temporal and spatial variation in infection levels were identified in as many as eight (33% of the total number of species) of the parasite species collected from *S. sierra*. This is a common pattern in many marine parasite species (Poulin 2006, Villalba-Vásquez et al. 2018, Miranda-Delgado et al. 2019, Violante-González et al. 2020). Five of these eight were intestinal helminths, suggesting that these variations may be explained by changes in host diet between locations and/or sampling years, and the consequent availability of prey harbouring infective stages (Luque et al. 2004, Alves and Luque 2006). Although *S. sierra* is considered to have a specialised piscivorous diet (Collette and Nauen 1983), feeding mainly on small forage fish, dietary analysis has shown that along the Pacific coast of Mexico it is an opportunistic predator (Moreno-Sánchez et al. 2011). It can feed on prey that is abundant during a specific season or at a specific location. The present results showed it to have a more variable diet at some locations and/or in different sampling years. For example, the digeneans *Didymocilindrus* sp. and *Proserhynchoides cybii* were most prevalent in the Zapotalito 2020_{Feb} sample (Table 1).

Host diet is an important factor in the structuring of intestinal parasite communities in marine fish (Sasal et al. 1997, Luque et al. 2004, Villalba-Vásquez et al. 2018). However, the population density and gregarious behaviour (school training) of *S. sierra* (see Collette and Nauen 1983) may better explain the temporal and spatial variation observed in three ectoparasite species: *Mexicotyle mexicana*, *T. crocea* and *Caligus omissus*. Formation of large schools, as occurs in *S. sierra*, facilitates parasite transmission, particularly of those with a direct transmission cycle such as monogeneans and copepods (Sasal et al. 1997, Luque et al. 2004).

Variations in abiotic factors such as local fluctuations in surface temperature are known to affect many ecological processes, including the productivity of food webs, and the transmission rates of many trophically transmitted parasites due to population increase or decreases in potential intermediate or final hosts (Oliva et al. 2008, Miranda-Delgado et al. 2019). Trophically-transmitted parasites have free-living stages that are affected by the same oceanographic physical conditions (e.g. temperature, salinity, currents) that affect the larval stages of other marine organisms, including those of their hosts (Lohmus and Bjorklund 2015).

Table 4. Summary of the Principal Component Analysis (PCA) on biotic and abiotic factors that influence the diversity and species richness of the infracommunities of *Scomberomorus sierra* (Jordan et Starks). The first and second principal component axes are indicated by PC1 and PC2, respectively. Variables that contribute to the total explained variance in each PC are indicated by an asterisk. Eigenvalues, percentage of variance and accumulative 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. MSA = Measure of Sampling Adequacy.

Variables	PC1	PC2	MSA	Communality R ²	Uniqueness % not predicted
Richness	0.934*	0.135	0.781	0.891	0.109
Diversity	0.923*	0.110	0.822	0.864	0.136
Total	0.861*	-0.066	0.705	0.746	0.254
Rdidy	0.831*	-0.055	0.891	0.694	0.306
Equitability	0.568*	0.341	0.652	0.333	0.667
Diet	0.403*	-0.295	0.190	0.249	0.751
Size	0.330*	-0.066	0.419	0.113	0.887
Temp	-0.032	0.898*	0.289	0.807	0.193
Enso	0.007	0.885*	0.280	0.783	0.217
CF	-0.107	0.812*	0.958	0.672	0.328
Season	-0.059	0.565*	0.133	0.322	0.678
Location	0.122	-0.353*	0.094	0.140	0.860
Eigenvalue	3.78	2.82			
% total variance	31.50	23.60			
Accumulative variance	31.50	55.10			

Predictor variables: Location = collection location, Season = climatic season (dry/rainy), Temp = surface temperature values, Enso = Multivariate El Niño index values, Diet = host diet variety, Size = host body size (total length), CF = condition factor, Rdidy = number of didymozoid species. Infracommunity parameters: Richness = number of parasite species per infracommunity, Diversity = Brillouin diversity index values, Equitability = species evenness, Total = total number of parasites per infracommunity.

The PCA results (Fig. 4, Table 4) suggest that interannual variations in local environmental factors (i.e. temperature, climate season and ENSO index) had a substantial effect on parasite infracommunity structure. Some studies carried out in Acapulco Bay indicate that slight changes in the temperature and salinity parameters can be enough to generate notable changes in species composition of copepod communities throughout the year (Rojas-Herrera et al. 2016). For example, decreases in water temperature in this Bay during the first months of the year have been associated with increases in the cyclopoid and harpacticoid copepods population (Rojas-Herrera et al. 2016), both important intermediate hosts for intestinal helminths (Rohde 2005, Miranda-Delgado et al. 2019).

Component communities

Parasite species richness at the component level in *S. sierra* (3 to 16 parasite taxa; Table 3) was similar to the thirteen species reported for this host species at another location on Mexico's Pacific coast (Bárcenas 2019). It was also similar to the species richness in other species of *Scomberomorus*, such as *S. commerson* (Lacepède) (14 species), *S. brasiliensis* (Collette, Russo et Zavala-Camin) (7 species) and *S. maculatus* (Mitchill) (5 species) (Lester et al. 2001, Alves and Luque 2006, Aguirre-Macedo et al. 2007). Hosts with a broad geographical distribution are exposed to large numbers of parasite species because they interact with myriad intermediate host species throughout their distribution (Sasal et al. 1997). The present data support this hypothesis since a combined total of 24 parasite species taxa were recorded in *S. sierra* at the four sampled locations during the study period (Table 1).

Similarity in species composition between the parasite communities (Fig. 3) was generally low (< 70%) at both the qualitative and quantitative levels compared to parasite community similarity values reported for other marine fish from the Pacific coast of Mexico, namely 76% in *Parapsettus panamensis* (Steindachner) (Villalba-Vásquez et al. 2018), 79% in *Caranx caballus* (Günther) (Gallegos-Navarro et al. 2018) and 85% in *Oligoplites altus* (Günther) (Santos-Bustos et al. 2018). Perhaps the low similarity values observed in *S. sierra* were due to the fact that 50% of the identified parasite taxa (12 species: seven helminths and five crustaceans) were recorded in only one or two locations or in very few sampling years (Table 1). Local and interannual variations in biotic (e.g. diet, body size, availability of larva-infected prey) and/or abiotic environmental factors (Luque et al. 2004, Timi et al. 2010), may have caused the low similarity between the studied parasite communities of *S. sierra*.

Infracommunities

At the infracommunity level mean species richness and diversity values in *S. sierra* (mean number of species = 1 to 5.6, mean diversity = 0.13 to 1.46; Table 3) were also similar to those reported for other parasite infracommunities of predatory marine fish on the Pacific coast of Mexico (Gallegos-Navarro et al. 2018, Violante-González et al. 2020). However, they were lower than those reported in another scombrid fish, *Euthynnus lineatus* (mean number of species = 4.7 to 8.2, mean diversity = 1.31 to 1.94) (Miranda-Delgado et al. 2019).

Several biotic and abiotic factors are known to be important determinants of species richness and diversity in the parasite communities of marine fish (Luque et al. 2004,

Table 5. Discriminant analysis classification showing the numbers and percentages of the *Scomberomorus sierra* (Jordan et Starks) classified in each sampling location (rows correspond to group memberships). The bottom of the table shows the matrix of classification coefficient values for parasites that allowed differentiation between sampling locations; asterisks indicate the importance of each parasite species in distinguishing among locations.

Location	Acapulco	Zapotalito	L. Cárdenas	P. Vicente	Percent
Acapulco	57	1	3	23	67.9
Zapotalito	13	30	1	4	62.5
L. Cárdenas	12	0	28	9	57.1
P. Vicente	3	0	0	61	95.3
Parasite					
<i>Mexicotyle mexicana</i>	0.136	0.538*	0.261	0.000	
<i>Proisorhynchoides cybii</i>	0.029	0.114	0.527*	0.022	
<i>Didymocilindrus</i> sp.	0.094	0.054	0.273*	-0.001	
<i>Glomeritrema</i> sp.	-0.017	0.287*	-0.040	0.000	
<i>Didymocystis</i> sp.	-0.063	-0.077	0.457*	-0.001	
<i>Caligus omissus</i>	0.257*	0.518*	0.174	0.014	

Miranda-Delgado et al. 2019). The PCA results (Fig. 4) and ICI values (Table 1) indicated that infracommunity species richness and diversity in *S. sierra* depend heavily on the occurrence of a distinctive set of specialist parasite species (*M. mexicana*, *T. crocea*, *Didymocilindrus* sp., *Didymocystis* sp., *Glomeritrema* sp. and *C. omissus*). Host phylogeny (i.e. phylogenetic affinities) should therefore be considered as a crucial determinant of parasite infracommunity structure (Poulin et al. 2011, Krasnov et al. 2012) in *S. sierra*.

However, species frequency varied between sampling years and locations (Table 1). Several studies indicate that temporal variations in parasite infracommunity species composition can be attributed to variations in the prevalence and/or abundance of dominant taxa (Garcias et al. 2001, Villalba-Vásquez et al. 2018). As suggested above, fluctuations in the infection levels of some specialist parasites (such as didymozoid species) can be attributed mainly to changes in *S. sierra* feeding behaviour or foraging habitat over time and between locations.

Host body size was also an important structuring factor in the studied parasite infracommunities (Table 2, Fig. 4). Positive correlations between the total length and abundance of some parasite species, as well as the mean species richness and mean total intensity within each sample and across the locations or sampling year (Table 2), showed that this host trait was also an important factor in the structuring of parasite infracommunities of *S. sierra*. In the PCA results this variable made also a sizable contribution to the final built model (Table 4). In marine fish populations, the body size has proved to be the main predictor of the presence of a particular parasite species, of total abundance, and of species richness (Timi and Poulin 2003, Luque et al. 2004, Luque and Poulin 2008, Villalba-Vásquez et al. 2018). A large body size can facilitate the ectoparasite attachment; in addition,

larger individuals tend to ingest greater quantities of food and are older and thus have had more time to accumulate parasites than smaller individuals (Timi and Poulin 2003, Luque et al. 2004, Luque and Poulin 2008).

The predatory habits of *S. sierra* promote accumulation of trophically-transmitted parasite species throughout this host's long life span. Predatory fish such as *S. sierra* are larger than their prey (Collette and Nauen 1983) and thus offer larger target areas for contact-transmitted parasites such as ectoparasites.

The discriminant analysis (Fig. 5, Table 5) identified at least six parasite species (*M. mexicana*, *Didymocilindrus* sp., *Didymocystis* sp., *Glomeritrema* sp., *P. cybii* and *C. omissus*) as biological tags useful in differentiating between *S. sierra* stocks along Mexico's southern Pacific coast. Parasites are well established as biological tags for distinguishing between stocks of the same fish species (Timi 2007, Poulin and Kamiya 2015), but the parasite fauna method has received only limited use in Mexico's fisheries (Violante-González et al. 2016).

Overall, the parasite communities of *S. sierra* were characterised by high ectoparasite species richness, with monogeneans and some didymozoids being numerically dominant. Parasite community structure and species composition varied between locations, seasons and sampling years. These variations were probably due to factors such as host traits (e.g. feeding behaviour and body size), presence of a set of distinctive parasite species (i.e. specialist parasite species), and possible interlocation differences in environmental factors and infected prey availability.

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