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

Nataly G. Santos-Bustos¹, Juan Violante-González²*, Scott Monks¹, Princessa J. Villalba-Vásquez¹, Shirley S. Salas Villalobos², Monserrat S. Acosta-Hernández² and Aldo Díaz Gallegos²

¹Centro de Ciencias de Desarrollo Regional, Universidad Autónoma de Guerrero, Acapulco, México; ²Facultad de Ecología Marina, Universidad Autónoma de Guerrero, Acapulco, Guerrero, México; ³Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, México

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, *Paracycloidiscoides chaetodipteri* Caballero et Bravo-Hollis, 1961, *Protonemicrocotyle manteri* Bravo-Hollis, 1966 and *Neomicrocotyle pacifica* Meserve, 1938 (Galgles-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 (Garcías 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, 2009).
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: \( CF = \frac{W}{L^3} \), where \( W \) is total weight, and \( L \) = 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 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 ± 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) 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 χ² tests. Infracomunities 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, and one from Zapotalito 2017 were included in this analyses). 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 F1,24 = 102.69, p < 0.01). Of the total parasite species sample, ten were classified as host-specialists (three monogeneans, five digeneans and two cestodes; Table 1). Nine parasite species (Mexichelyte mexicana [Meserve, 1938], Thoracocotyle crocea [MacCallum, 1913], Didymociliindrus sp., Didymocystis sp., Lecithochirium microstomum [Chandler, 1935], Prosorhynchoides cybii [Park, 1939], Anisakid sp., Hysterolyacium sp. and Caligus omnisuus [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). ¹Number of fish examined, ²Total number of individual parasites collected, ³Number of parasites per fish (mean±SD), ⁴Minimum to maximum number of parasites present, ⁵Infracommunity index, ⁶New 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  | n²   | Prevalence (%) | Total³ | Abundance | Range of intensity⁴ | IC⁵ |
|----------------------------------|-------------------------|--------------|----------|-------|------|---------------|--------|-----------|---------------------|-----|
| **Digenea**                      |                         |              |          |       |      |               |        |           |                     |     |
| *Anacalathrubulum* sp.           | Specialist              | Acapulco     | 2012     | 19    | 1    | 2             | 0.03   | 1–2       | 0.004               |     |
|                                  |                         | Acapulco     | 2018     | 84    | 1    | 11            | 0.13   | 1–11      | 0.007               |     |
|                                  |                         | Acapulco     | 2019     | 59    | 15   | 19            | 0.32±1.27 | 1–4   | 0.062               |     |
|                                  |                         | Zapotalito   | 2017     | 48    | 19   | 22            | 0.46±2.35 | 1–7   | 0.054               |     |
|                                  |                         | Zapotalito   | 2017     | 28    | 7    | 4             | 0.14±1.41 | 1–3   | 0.059               |     |
|                                  |                         | Zapotalito   | 2019     | 40    | 48   | 59            | 1.48±3.23 | 1–4   | 0.123               |     |
|                                  |                         | Zapotalito   | 2020     | 54    | 72   | 564           | 10.44±22* | 1–109 | 0.122               |     |
| **Didymocilindrus sp.**          | Specialist              | Acapulco     | 2011     | 76    | 67   | 1025          | 13.49±14.61 | 5–101 | 0.216               |     |
|                                  |                         | Acapulco     | 2012     | 76    | 62   | 360          | 4.74±7.78 | 1–43  | 0.199               |     |
|                                  |                         | Acapulco     | 2018     | 84    | 29   | 100          | 1.19±4.37 | 1–17  | 0.172               |     |
|                                  |                         | Acapulco     | 2018     | 77    | 3    | 2            | 0.03     | 1–1      | 0.045               |     |
|                                  |                         | Acapulco     | 2019     | 59    | 56   | 154          | 2.61±4.65 | 1–22  | 0.226               |     |
|                                  |                         | Zapotalito   | 2017     | 48    | 17   | 52           | 1.08±5.40 | 1–13  | 0.048               |     |
|                                  |                         | Zapotalito   | 2017     | 28    | 21   | 25           | 0.89±3.37 | 2–9   | 0.177               |     |
|                                  |                         | Zapotalito   | 2019     | 40    | 68   | 180          | 4.50±7.65 | 1–27  | 0.175               |     |
|                                  |                         | Zapotalito   | 2020     | 54    | 80*  | 597          | 11.06±13.7* | 1–79  | 0.135               |     |
|                                  |                         | L. Cárdenas  | 2013     | 49    | 65   | 258          | 5.27±6.05 | 1–32  | 0.19                |     |
| **Didymocystis sp.**             | Specialist, Intestine,  | Acapulco     | 2011     | 76    | 67*  | 591          | 7.78±7.90* | 1–48  | 0.216               |     |
|                                  | Stomach,                | Acapulco     | 2012     | 76    | 74*  | 143          | 7.53±12.44* | 1–47  | 0.165               |     |
|                                  |                         | Acapulco     | 2012     | 76    | 8    | 30           | 0.39±3.79 | 2–12  | 0.025               |     |
|                                  |                         | Acapulco     | 2019     | 59    | 17   | 49           | 0.83±4.51 | 1–15  | 0.069               |     |
|                                  |                         | Zapotalito   | 2019     | 40    | 13   | 24           | 0.60±4.82 | 1–11  | 0.032               |     |
|                                  |                         | Zapotalito   | 2020     | 54    | 54   | 196          | 3.62±5.93 | 1–31  | 0.091               |     |
|                                  |                         | L. Cárdenas  | 2013     | 49    | 49   | 189          | 3.86±5.53 | 2–21  | 0.14                |     |
| **Didymozoon sp.**               | Specialist              | Intestine    | Zapotalito | 2020 | 54   | 4   | 4           | 0.07±1.41 | 1–3   | 0.006               |     |
| **Glomeritrema sp.**             | Specialist              | Intestine    | Zapotalito | 2020 | 54   | 4   | 4           | 0.07±1.41 | 1–3   | 0.006               |     |
| **Gonocercilla pacifica**        | Generalist              | Intestine    | Zapotalito | 2020 | 54   | 2   | 1           | 0.02     | 1–1   | 0.003               |     |
| *Manter, 1940*                   |                         |              |          |       |      |               |        |           |                     |     |
| *Lecithochirium microstomum*     | Generalist              | Intestine    | Acapulco   | 2011 | 76   | 1   | 1           | 0.01     | 1–1   | 0.004               |     |
| *Chandler, 1935*                 |                         |              |          |       |      |               |        |           |                     |     |
| *Prosohynchoides cybii*          | Generalist              | Intestine    | Acapulco   | 2011 | 76   | 21  | 50          | 0.66±3.79 | 1–14  | 0.068               |     |
| *Park, 1939*                     |                         |              |          |       |      |               |        |           |                     |     |
| *Monogenea*                     |                         |              | Acapulco   | 2011 | 76   | 28  | 38          | 0.50±1.60 | 1–8   | 0.089               |     |
| *Mexicotyle mexicana*            | Generalist              | Intestine    | Acapulco   | 2012 | 19   | 37  | 48          | 2.53±7.43 | 1–19  | 0.082               |     |
| *Lebedev, 1984*                  |                         |              |          |       |      |               |        |           |                     |     |
Table 1. Continued

| Species Name | Type | Location 1 | Year 1 | N 1 | Mean ± SD 1 | Reference 1 | Location 2 | Year 2 | N 2 | Mean ± SD 2 | Reference 2 | Location 3 | Year 3 | N 3 | Mean ± SD 3 | Reference 3 |
|--------------|------|------------|--------|-----|-------------|-------------|------------|--------|-----|-------------|-------------|------------|--------|-----|-------------|-------------|

Scomberocotyle scomberomori (Koratha, 1955) Hargis, 1956
Specialist Gillis
Acapulco 2011a 76 1 2 0.05 ± 0.01 1–2 0.004
Acapulco 2019a 59 2 1 0.02 ± 0.01 1–1 0.007
Zapotalito 2020a 54 13 12 0.22 ± 0.12 1–4 0.022

Thoracoctyloides crocea MacCallum, 1913
Specialist Gillis
Acapulco 2011a 76 62 240 3.16 ± 1.56 1–30 0.199
Acapulco 2012a 19 68 199 10.47 ± 1.16 1–55 0.153
Acapulco 2012a 76 82 345 4.54 ± 1.16 1–26 0.263
Acapulco 2018a 84 30 65 0.77 ± 0.11 1–14 0.179
Acapulco 2018a 77 9 11 0.14 ± 0.13 1–26 0.157
Acapulco 2019a 59 25 155 2.63 ± 0.36 1–73 0.103
Zapotalito 2017a 48 60 253 5.27 ± 1.71 1–41 0.174
Zapotalito 2017a 28 11 9 0.32 ± 0.36 1–73 0.089
Zapotalito 2019a 40 70 272 6.80 ± 1.71 1–72 0.182
Zapotalito 2020a 54 87 953 17.65 ± 1.71 1–186 0.148
L. Cárdenas 2013a 49 71 266 5.43 ± 1.22 1–50 0.20

Cestoda Tetrafilidae (larvae)
Generalist Intestine Acapulco 2011a 76 1 10 0.13 ± 0.15 1–10 0.004

Acanthocephala Rhadinorhynchus cf. primitis (Rudolphi, 1802) Lühe, 1911
Generalist Intestine Acapulco 2018a 84 2 3 0.04 ± 0.01 1–2 0.014
Acapulco 2019a 59 5 5 0.08 ± 0.15 1–3 0.021

Nematoda Anisakis sp. (larvae)
Generalist Intestine Acapulco 2011a 76 15 41 0.54 ± 0.10 1–21 0.047
Acapulco 2012a 19 21* 34 1.79 ± 1.24 1–27 0.047
Acapulco 2012a 76 4 3 0.04 ± 0.1 1–1 0.013
Acapulco 2018a 84 2 2 0.02 ± 0.1 1–1 0.014
Acapulco 2018a 77 3 2 0.03 ± 0.1 1–1 0.045
Zapotalito 2017a 48 4 2 0.04 ± 0.1 1–1 0.012
Zapotalito 2020a 54 7 5 0.09 ± 0.50 ± 0.1 1–2 0.013
L. Cárdenas 2013a 49 4 5 0.10 ± 0.12 1–4 0.01

Hysterothyacum sp.
Generalist Intestine Acapulco 2011a 76 7 8 0.11 ± 0.89 1–3 0.021
Acapulco 2012a 19 21 10 0.53 ± 1.73 1–5 0.047
Acapulco 2012a 76 1 1 0.01 ± 0.1 1–1 0.004
Acapulco 2019a 59 12 18 0.31 ± 1.62 1–6 0.048
Zapotalito 2017a 48 10 6 0.13 ± 0.45 1–2 0.030
Zapotalito 2019a 40 40* 28 0.76 ± 0.86 1–3 0.104
Zapotalito 2020a 54 2 1 0.02 ± 0.1 1–1 0.003
L. Cárdenas 2013a 49 12 6 0.12 ± 0.1 1–1 0.003

Philometra sp.
Generalist Gonad Acapulco 2011a 76 1 6 0.08 ± 0.1 1–6 0.004
Acapulco 2012a 19 26 14 0.74 ± 2.49 1–6 0.059
Acapulco 2012a 76 1 1 0.01 ± 0.1 1–1 0.004
Zapotalito 2017a 48 2 1 0.02 ± 0.1 1–1 0.006
Zapotalito 2020a 54 2 4 0.07 ± 1–4 0.003
L. Cárdenas 2013a 49 2 1 0.02 ± 1–1 0.01

Procamallanus sp.
Generalist Intestine Acapulco 2012a 19 11 10 0.53 ± 1.41 4–6 0.024
Acapulco 2018a 84 1 1 0.01 ± 0.1 1–1 0.003
Zapotalito 2020a 54 6 3 0.06 ± 1–1 0.009

Copepoda Caligus omnissus
Specialist Gillis
Acapulco 2011a 76 26 30 0.39 ± 0.76 1–3 0.085
Acapulco 2012a 19 74* 24 1.26 ± 1.14 1–4 0.165
Acapulco 2012a 76 72* 112 1.47 ± 1.56 1–8 0.233
Acapulco 2018a 84 55 70 0.83 ± 0.62 1–3 0.330
Acapulco 2018a 77 27 31 0.40 ± 0.75 1–4 0.470
Acapulco 2019a 59 37 31 0.53 ± 0.73 1–3 0.151
Zapotalito 2017a 48 58 82 1.71 ± 1.14 1–22 0.168
Zapotalito 2017a 28 54 32 1.14 ± 2.10 1–9 0.443
Zapotalito 2019a 40 25 17 0.43 ± 0.82 1–3 0.065
Zapotalito 2020a 54 60 62 1.15 ± 1.83 1–10 0.100
L. Cárdenas 2013a 49 51 43 0.88 ± 1.70 1–9 0.15
P. Vicente 2018a 64 5 3 0.05 ± 1–10 0.426

Ergasilus sp.
Lernanthrophas cf. giganteus Kroyer, 1863
Generalist Gillis
L. Cárdenas 2013a 49 2 1 0.02 ± 1–1 0.01

Larina sp.
Generalist Gillis
Acapulco 2011a 76 3 2 0.03 ± 1–1 0.008

Orbitococylus sp. aculeatus Pillai, 1962
Generalist Gillis
Acapulco 2012a 76 3 3 0.04 ± 0.71 1–2 0.008

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Table 1. Continued

| Species                        | Type     | Location | Year | Sample Size | Sample Size | Sample Size | Sample Size | Sample Size | Sample Size |
|--------------------------------|----------|----------|------|-------------|-------------|-------------|-------------|-------------|-------------|
| Cymbiola buccata               | Specialist| Acapulco | 2018 | 84          | 1           | 1           | 0.01        | 1–1         | 0.007       |
| (Wilson, 1922)                 | Gills     | Acapulco | 2018 | 77          | 1           | 1           | 0.01        | 1–1         | 0.022       |
| C. buccata sp.                 | Specialist| Acapulco | 2018 | 77          | 1           | 1           | 0.01        | 1–1         | 0.022       |
| (Wilson, 1922)                 | Gills     | Acapulco | 2018 | 59          | 12          | 7           | 0.12        | 1–1         | 0.048       |
| C. buccata sp.                 | Specialist| Acapulco | 2019 | 40          | 5           | 3           | 0.08±0.71   | 1–2         | 0.013       |
| (Wilson, 1922)                 | Gills     | Zapotalo | 2019 | 40          | 2           | 1           | 0.02        | 1–1         | 0.01        |
| Isopoda                        |          |          |      |             |             |             |             |             |             |
| Livoneca redmani               | Leach, 1818 |         | Generalist | Gills     | Acapulco | 2018 | 84 | 2 | 2 | 0.02 | 1–1 | 0.014 |
| Racinella signata              | Leach, 1818 |         | Generalist | Gills     | Zapotalo | 2019 | 40 | 5 | 2 | 0.05 | 1–1 | 0.013 |

*S*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 Zapotalo 2020 sample, but were highest for *Hysterothyaculum* sp. (*G = 83.87, p < 0.05*) in the Zapotalo 2019 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 sample (Table 1). In contrast to the infection percentage results, only two parasite species (*Hysterothyaculum* sp. [*GLM: F = 7.75, p < 0.01*] and *C. omissus* [*GLM: F = 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. 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, naeaid 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 Zapotalo 2020 (*H = 0.95*) and Acapulco 2011 (*H = 0.87*) than at other locations such as Puerto Vicente 2018 (*H = 0.20*).

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 sample (*rs = 0.257, p < 0.05*), and *L. Cárdenas 2013* sample (*rs = 0.558, p < 0.05*) samples, and for the digenean *P. cybii* in the samples of Acapulco 2012 (*rs = 0.574, p < 0.05*), and Acapulco 2012 (*rs = 0.836, p < 0.05*) samples. Whereas abundance of the copepod *C. omissus* was negatively correlated with the host body size in the Acapulco 2012 (*rs = -0.648, p < 0.05*) and Zapotalo 2017 (*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

Component community

Parasite species richness recorded by location and/or sampling year (Table 3) varied widely from three (Puerto Vicente 2018) to 16 (Zapotalo 2020) with no correlation 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) to 3,156 (Zapotalo 2020) with no correlation observed between sample size and species richness at this level (*rs = 0.293, 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) to 1.20 (Zapotalo 2020) indicating that the different sample sizes used in this analysis had no effect on the results.
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 < 0.001]) were highest in the Zapotalito 2020 sample (Table 3). Infracommunity index values (ICI) indicated that the richest and most diverse infracommunities were collected from Zapotalito 2020\_feb during the dry season (Table 3).

**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).

**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 site-class | Examed fish | No. infected | CV % | Diet | Mean richness | Total prevalence | Mean total intensity | Fish length vs. richness | Fish length vs. intensity |
|---------------------|-------------------|-------------|--------------|------|------|---------------|-------------------|-----------------------|--------------------------|--------------------------|
| Acapulco Mar 2011   | > 40 cm           | 76          | 75           | 7.6  | 0.87 | 3.1 ± 1.5     | 98.6              | 28.0 ± 24.5           | 0.467*                   | 0.467*                   |
| Mar 2012            | > 40 cm           | 19          | 11           | 10.7 | 0.53 | 4.5 ± 1.9     | 100               | 32.9 ± 23.9           | 0.003                    | 0.151                    |
| Aug 2012            | < 35 cm           | 11          | 28           | 8.4  | 0.46 | 3.4 ± 0.8     | 100               | 11.9 ± 8.2            | -0.094                   | -0.545                   |
| 36-40 cm            | > 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            | > 40 cm           | 15          | 14           | 4.1  | 0.53 | 4.5 ± 1.9     | 93.3              | 17.0 ± 17.0           | -0.222                   | -0.116                   |
| Zapotalito Feb 2017 | 36-40 cm          | 10          | 10           | 13.6 | 0.43 | 3.4 ± 1.3     | 100               | 10.7 ± 6.4            | 0.484*                   | 0.142                    |
| Dec 2017            | > 40 cm           | 38          | 38           | 6.46 | 0.50 | 3.5 ± 1.3     | 100               | 23.2 ± 21.7           | 0.116                    | 0.123                    |
| 36-40 cm            | > 40 cm           | 17          | 12           | 8.7  | 0.50 | 1.7 ± 0.6     | 70.6              | 5.1 ± 1.2             | -0.085                   | -0.115                   |
| Jan 2019            | > 40 cm           | 11          | 9            | 2.2  | 0.50 | 1.6 ± 0.7     | 81.8              | 2.2 ± 1.6             | 0.038                    | 0.139                    |
| Feb 2020            | > 40 cm           | 40          | 40           | 4.6  | 0.61 | 3.8 ± 1.6     | 100               | 17.5 ± 18.9           | -0.086                   | 0.019                    |
| 36-40 cm            | > 40 cm           | 11          | 11           | 4.3  | 0.50 | 5.9 ± 1.0     | 100               | 77.5 ± 48.4           | -0.389                   | -0.355                   |
| Lázaro Cárdenas     | Nov 2013          | 21          | 19           | 5.1  | 0.50 | 3.9 ± 1.3     | 90.5              | 19.6 ± 19.5           | -0.370                   | -0.376                   |
| Puerto Vicente      | Apr 2018          | < 35 cm     | 64           | 7    | 5.2  | 0.20          | 1                 | 1.0                     | 1.0                      | 1.0                      |

*CV* Coefficient of variation in fish length (%). *Diet* 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.

Similarity 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 monogenes, three didymozoids, five copepods and two isopods) numerically dominated the parasite communities, accounting for 82% of the total number of individual parasites recovered. Monogenes 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 (Mendlová 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 communities and infracomunities in *Scomberomorus sierra* (Jordan & Starks) from Mexican Pacific coast (Zapotalito, Oaxaca, Acapulco and Puerto Vallarta, Jalisco).

| Location    | MEI | Examined | SST °C | Date         | Length (cm) | C.V. % | No. of parasites | Component communities | No. of fish species | Mean of Brillouin Index | H Shannon-Wiener diversity index | BPI Berger-Parker Index | Diet | Species numbers | Diet | Species numbers | Diet | Species numbers | Diet | Species numbers | Diet | Species numbers | Diet | Species numbers |
|-------------|-----|----------|--------|--------------|-------------|--------|-----------------|------------------------|----------------------|-----------------------|----------------------------|---------------------|-------|----------------|-------|----------------|-------|----------------|-------|----------------|-------|----------------|-------|----------------|
| Acapulco    | -1.8| 76       | 26.2   | Mar 2011     | 44.4 ± 3.3  | 76.2   | 14              | 3.3 ± 0.0              | 25.0 ± 0.0           | 28.0 ± 1.9            | 12.1 ± 0.0               | 0.35 ± 0.0            | 3.4 | 6.29          | 3.1  | 1.15           | -1.8 | 1.35           | 1.0  | 1.08           | 3.3  | 4.4           | 3.3  | 4.4           |
|             |     |          |        | Mar 2012     | 47.2 ± 1.4  | 29.5   | 14              | 3.3 ± 0.0              | 25.0 ± 0.0           | 28.0 ± 1.9            | 12.1 ± 0.0               | 0.35 ± 0.0            | 3.4 | 6.29          | 3.1  | 1.15           | -1.8 | 1.35           | 1.0  | 1.08           | 3.3  | 4.4           | 3.3  | 4.4           |
| Zapotalito  | 1.6 | 76       | 26.2   | Jan 2018     | 44.4 ± 3.3  | 76.2   | 14              | 3.3 ± 0.0              | 25.0 ± 0.0           | 28.0 ± 1.9            | 12.1 ± 0.0               | 0.35 ± 0.0            | 3.4 | 6.29          | 3.1  | 1.15           | -1.8 | 1.35           | 1.0  | 1.08           | 3.3  | 4.4           | 3.3  | 4.4           |
|             |     |          |        | Dec 2017     | 47.2 ± 1.4  | 29.5   | 14              | 3.3 ± 0.0              | 25.0 ± 0.0           | 28.0 ± 1.9            | 12.1 ± 0.0               | 0.35 ± 0.0            | 3.4 | 6.29          | 3.1  | 1.15           | -1.8 | 1.35           | 1.0  | 1.08           | 3.3  | 4.4           | 3.3  | 4.4           |
|             |     |          |        | Apr 2018     | 47.2 ± 1.4  | 29.5   | 14              | 3.3 ± 0.0              | 25.0 ± 0.0           | 28.0 ± 1.9            | 12.1 ± 0.0               | 0.35 ± 0.0            | 3.4 | 6.29          | 3.1  | 1.15           | -1.8 | 1.35           | 1.0  | 1.08           | 3.3  | 4.4           | 3.3  | 4.4           |
|             |     |          |        | May 2019     | 47.2 ± 1.4  | 29.5   | 14              | 3.3 ± 0.0              | 25.0 ± 0.0           | 28.0 ± 1.9            | 12.1 ± 0.0               | 0.35 ± 0.0            | 3.4 | 6.29          | 3.1  | 1.15           | -1.8 | 1.35           | 1.0  | 1.08           | 3.3  | 4.4           | 3.3  | 4.4           |

**Table 3** Differences in the parasite communities and infracomunities in *Scomberomorus sierra* (Jordan & Starks) from Mexican Pacific coast (Zapotalito, Oaxaca, Acapulco and Puerto Vallarta, Jalisco). The table shows the location, date, number of fish examined, SST, MEI, length, CV, number of parasites, number of species, mean of Brillouin Index, Shannon-Wiener diversity index, Berger-Parker Index, diet, and species numbers for each sample. The data suggest that there is variation in the parasite communities and infracomunities between these locations, which may be influenced by factors such as temperature, salinity, and population density.

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). 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 *Didymociliindrus* sp. and *Prosorhynchoides cybii* were most prevalent in the Zapotalito 2020 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 these three parasitid species: * Mexicotrema 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 infracomunities 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     | R²      | % 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           |
| R²didy      | 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 | 31.50 | 55.10 |                 |
| Accumulative variance | 31.50 |         |         |         |                 |

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, R²didy = 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, climatic season and ENSO index) had a substantial effect on parasite infracommmunity 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 (Bárceñas 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, Aguierre-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 infracommmunity 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 infracommmunities 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 scrombid 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   |          |            |             |            |         |
| *Mexicoytle mexicana* | 0.136   | 0.538*     | 0.261       | 0.000      |
| *Prosoxynchoidecybii* | 0.029   | 0.114      | 0.527**     | 0.022      |
| *Didymocilindrus* sp. | 0.094   | 0.054      | 0.273*      | -0.001     |
| *Glomeritrema* sp. | -0.017  | 0.287*     | -0.040      | 0.000      |
| *Didymocystis* sp. | -0.063  | -0.077     | 0.457*      | -0.001     |
| *Caligus omissus* | 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 infracommmunity 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 infracommmunity 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 infracommmunity species composition can be attributed to variations in the prevalence and/or abundance of dominant taxa (Garcia 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 infracommmunities (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 infracommmunities 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), 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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