



ECOSYSTEMS

Structure of the metazoan parasite communities of haemulid fish (Actinopterygii: Perciformes) in the South Atlantic Ocean: a comparative approach

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Abstract: Haemulidae represents one of the most diverse, widespread and conspicuous families of Perciformes, in which most species are marine, some brackish and rarely from freshwater. From April 2009 to July 2012, 120 specimens of *Conodon nobilis*, 60 *Orthopristis rubra* and 50 *Anisotremus virginicus* were collected off the State of Rio de Janeiro, Brazil, and analyzed for metazoan parasites. A total of 16 parasite taxa were found on/in *A. virginicus*, 19 on/in *Co. nobilis* and 21 on/in *O. rubra*, in which ectoparasites were most common on *A. virginicus* and *Co. nobilis* and endoparasites in *O. rubra*. All parasites showed aggregate pattern of distribution (discrepancy index values higher than 0.70). Mean abundance, species richness and Brillouin index (diversity) differed among the host species, *i.e.*, *O. rubra* showed the highest values, followed by *A. virginicus* and *Co. nobilis* with intermediate and lowest values, respectively. At infracommunity level was possible to observe high similarity of parasite composition among the three host species. The digeneans *Leurodera decora* and *Monorchis latus*, and the acanthocephalan *Koronacantha* sp. represent new locality records off Brazil. Moreover, five, four and two taxa are reported, for the first time, parasitizing *Co. nobilis*, *A. virginicus* and *O. rubra*, respectively.

Key words: Brazil, ecology, Haemulidae, marine fish, neotropical region, parasite community.

INTRODUCTION

Haemulidae is one of the most diverse, widespread, and conspicuous families within the largest suborder of teleost fish Percoidei (Nelson et al. 2016). Haemulids or grunts are represented by about 134 species, occurring through the Pacific and Atlantic Oceans in the Nearctic and Neotropical Regions, as well as in the Indian Ocean, in which most are marine, some are brackish and a few from freshwater. These fish are benthic, with diet composed by broad spectrum of items, *i.e.*, crustaceans, mollusks, polychaete worms, echinoderms, annelids, and rarely small fishes (Rocha et al.

2008, Tavera et al. 2012, Pombo et al. 2014, Nelson et al. 2016, Froese & Pauly 2021).

The Brazilian coastal zone extends for more than 7,000 km, bathed by the Atlantic Ocean, supporting about 1230 species of fish (Froese & Pauly 2021). Within this diverse fish fauna, haemulids are represented by 25 species, allocated in eight genera, mainly found in coastal waters, over sand, rock or mud bottoms. Haemulids are considered very important among the reef fish in Brazil, since they occur in large shoals that have both ecological and commercial importance (Rocha et al. 2008, Carvalho et al. 2020, Cerqueira et al. 2021).

According to the checklist of Paschoal et al. (2015), the parasite fauna of haemulids may be well considered high diverse. In this sense, 231 species of parasites have been reported from haemulids in the Neotropical and Nearctic Regions, with predominance of trematodes (97 species), followed by monogeneans (39 species). In fact, several studies suggest species-rich parasite faunas within Haemulidae, which demand approaches regarding patterns and processes shaping these parasite community structures, in order to better understand the complex relationships among host, parasite and environment (Luque et al. 1996a, b, Centeno et al. 2002, Iannacone & Alvarino 2009, Chero et al. 2014, Bashirullah & Díaz 2015, Iannacone et al. 2015, López-Zacarías et al. 2021, Montoya-Mendoza et al. 2021).

The structure of parasite communities is reported to be related to host biological features, phylogenetically close species that share dietary habits and are sympatric, for example, may show similarities on their parasite's fauna, since the exchange of parasite species over the evolutionary time is favored (Poulin 2007, Luque et al. 2008, Alarcos & Timi 2012). Therefore, it is plausible that the Porkfish *Anisotremus virginicus* (Linnaeus, 1758), the Barred grunt *Conodon nobilis* (Linnaeus, 1758) and the Corocoro grunt *Orthopristis rubra* (Cuvier, 1830), haemulids which occur in sympatry off the State of Rio de Janeiro, show somewhat similar parasite community structures. However, such approach has never been done. Therefore, the present work evaluated and compared the parasite fauna of these three sympatric haemulid species, off Rio de Janeiro, Brazil, using quantitative and qualitative tools, in order to detect and discuss possible similarities among them.

MATERIALS AND METHODS

Collection and processing of fish

Fish were caught by local fishermen in the coast of the State of Rio de Janeiro (21-23°S, 42-45°W), Brazil. Hosts were mostly fresh, but some specimens were kept frozen at -20°C, until examination. Their taxonomic identification followed Menezes & Figueiredo (1980) and nomenclature and classification were updated according to Froese & Pauly (2021).

A total of 230 fish were analyzed as follows: 50 specimens of *A. virginicus* (total length 27.0 ± 5.1 [20-41] cm; weight 431.0 ± 295.8 [155-1,450] g; 33 females and 17 males) collected from February 2010 to July 2011; 120 specimens of *Co. nobilis* (total length 29.3 ± 5.5 [18.6-38.4] cm; weight 427.0 ± 222.7 [93.5-908.0] g; 66 females and 54 males) collected from April 2009 to July 2010; and 60 specimens of *O. rubra* (total length 28.0 ± 3.7 [21.0-35.5] cm; weight 333.0 ± 138.8 [140.0-600.0] g; 43 females and 17 males) collected from December 2011 to July 2012. All specimens were in adult stage.

Parasitological procedures

All organs, body and nasal cavities, mandibular canals, fin rays and body surface were examined for metazoan parasites. Parasite collection and processing followed Humes & Gooding (1964), Eiras et al. (2006) and Madinabeitia & Nagasawa (2012), and their taxonomic identification followed specific literature, pertinent to each taxon.

Statistical analysis of parasites

Prevalence, mean intensity and mean abundance were used as parasite population descriptors (at component population level), according to Bush et al. (1997). The following parasite community descriptors were also calculated (at infracommunity level), according to Bush

et al. (1997): number of parasite individuals (total abundance), species richness, diversity estimated by the Brillouin index, dominance estimated by Berger-Parker index and frequency of dominance (percentage of infracommunities in which either parasite species was numerically dominant) (Magurran 2004). The variance to mean ratio (dispersion index) and the discrepancy index (Poulin 1993), were calculated to evaluate the distribution of parasite species within host populations. Parasite species with prevalence lower than 10% were excluded from statistical analyzes, following the recommendations by Bush et al. (1997).

All quantitative data used for statistical comparisons were $\log(x+1)$ transformed and previously tested for normality and homoscedasticity, using Shapiro-Wilk and Bartlett tests respectively (Zar 2010). Therefore, analysis of variance (ANOVA), followed by the *post hoc* test of Tukey (when pertinent), were used to compare total abundance, parasite richness, Brillouin diversity and Berger-Parker dominance among the three host species (Magurran 2004, Zar 2010). The similarity among parasite infracommunities was estimated quantitatively, using the Bray-Curtis index (based on abundances transformed by $\log[x+1]$), and qualitatively using the Jaccard index (based on presence/absence) (Magurran 2004). Analyses of similarities (ANOSIM) were run, considering host species as factor, using the ranked Bray-Curtis and Jaccard similarity matrixes, with 10,000 permutations (Magurran 2004). The level of statistical significance was $p < 0.05$. Statistical analyzes were performed in Quantitative Parasitology 3.0 and R software

(Rósza et al. 2000, R Development Core Team 2020, RStudio Team 2020).

RESULTS

Composition of the whole community of parasites

The total parasite community was composed by 41 different taxa, 21 of which endoparasites, belonging to Acanthocephala, Aspidogastrea, Cestoda, Digenea and Nematoda, including larval and adult forms, and 20 ectoparasites belonging to Copepoda, Monogenea and Isopoda, all adult forms (Table I). A total of 2896 parasite individuals were collected, with a mean abundance and prevalence of 12.5 ± 21.1 and 85.6%, respectively. Adult endoparasites accounted for 56.3% (1631/2896) of the total specimens collected, being the most abundant group, followed by ectoparasites and endohelminth larval forms with 1153 (39.8%) and 112 (3.9%) specimens collected respectively. The monogenean *Encotyllabe spari* Yamaguti, 1934, found in the pharyngeal plates of *O. rubra*, showed the highest values of prevalence, while the digenetic *Infundiburictus longovatus* (Hopkins, 1941), found parasitizing the stomach of *O. rubra*, showed the highest values of mean abundance (see Table I for details). The least prevalent and abundant species were the copepods *Caligus longipedis* Bassett-Smith, 1898 and *Ca. rufimaculatus* Wilson, 1905, both found infesting the opercular cavity of *Co. nobilis* (see Table I for details). All parasite species showed the typical aggregated pattern of distribution within their host populations (discrepancy index values were higher than 0.70, see Table II for details).

Table I. Site of infection (SI), prevalence (P%), mean intensity (MI), mean abundance (MA) and frequency of dominance (FD%) of metazoan parasites of *Anisotremus virginicus*, *Conodon nobilis* and *Orthopristis rubra* from the coastal zone of Rio de Janeiro, Brazil.

Parasite species	SI	<i>Orthopristis rubra</i> (N= 60)				<i>Conodon nobilis</i> (N= 120)				<i>Anisotremus virginicus</i> (N= 50)			
		P(%)	MI±SD	MA±SD	FD(%)	P(%)	MI±SD	MA±SD	FD(%)	P(%)	MI±SD	MA±SD	FD(%)
DIGENEA													
<i>Aponurus laguncula</i>	Intestine	--	--	--	--	22	2±1.3	0.4±1	18.7	--	--	--	--
<i>Aponurus pyriformis</i>	Stomach	18	2.2±1.1	0.41±1	1.7	--	--	--	--	--	--	--	--
<i>Diphtherostomum brusinae</i>	Intestine	16	6.1±10	1±4.8	1.7	--	--	--	--	--	--	--	--
<i>Diplomonorchis leiostomi</i>	Intestine	11	10±8.8	1.2±4.5	5.3	--	--	--	--	--	--	--	--
<i>Genolopa ampullacea</i>	Intestine	11	4.4±2.9	0.52±1.7	--	4	2.2±0.7	0.09±0.4	3.1	12	1	0.1±0.3	--
<i>Infundiburictus longovatus</i>	Stomach	50	26±31.3	13.3±25.8	35.7	--	--	--	--	--	--	--	--
<i>Leurodera decora</i>	Stomach	--	--	--	--	--	--	--	--	28	3.7±2.5	1±2.1	11.3
<i>Monorchis latus</i>	Intestine	--	--	--	--	--	--	--	--	20	16.5±31.5	3.3±15.5	9
<i>Opecoeloides</i> sp.	Intestine	10	1.8±1	0.1±0.6	1.7	--	--	--	--	6	1.6±0.9	0.1±0.4	--
<i>Parahemiurus merus</i>	Intestine	--	--	--	--	10	2±1.4	0.2±0.8	7.3	--	--	--	--
<i>Prosorhynchus osakii</i>	Intestine	11	2.1±1.3	0.2±0.8	1.7	--	--	--	--	--	--	--	--
<i>Torticaecum</i> sp. (Immature)	Body cavity	13	3.6±1.7	0.48±1.5	1.7	19	1.9±1.5	0.3±1	12.5	--	--	--	--
ASPIDOGASTREA													
<i>Lobatostoma ringens</i>	Intestine	--	--	--	--	1.7	4±0.5	0.07±2	1	--	--	--	--
MONOGENEA													
<i>Choricotyle brasiliensis</i>	Gills	26	1.5±0.7	0.4±0.7	3.5	--	--	--	--	--	--	--	--
<i>Choricotyle cynoscioni</i>	Gills	3	1	0.03	--	--	--	--	--	--	--	--	--
<i>Choricotyle orthopristis</i>	Gills	15	2.1±1.5	0.3±0.9	1.7	--	--	--	--	--	--	--	--
<i>Choricotyle</i> sp.	Gills	--	--	--	--	--	--	--	--	12	1	0.1±0.3	--
<i>Encotyllabe spari</i>	Pharynx	78	4.9±5.1	3.8±5	25	5	1	0.05±0.2	2	30	3±2.1	0.9±1.8	16
<i>Mexicana anisotremum</i>	Gills	--	--	--	--	--	--	--	--	18	13±14.4	2.3±7.7	16
<i>Neobenedenia melleni</i>	Body surface	--	--	--	--	--	--	--	--	8	1.2±0.4	0.1±0.36	2.2
<i>Pseudotagia rubri</i>	Gills	66	3.9±2.8	0.4±2.9	14.2	--	--	--	--	--	--	--	--
CESTODA													
<i>Callitetrarhynchus</i> sp. (Plerocercoid)	Mesenterium	--	--	--	--	5	1.1±0.3	0.07±0.2	2	--	--	--	--
<i>Pterobothrium</i> sp. (Plerocercoid)	Mesenterium	--	--	--	--	3.3	1	0.03±0.1	2	--	--	--	--
NEMATODA													
<i>Cucullanus</i> sp.	Intestine	16	1.6±1.2	0.2±0.7	--	--	--	--	--	--	--	--	--
<i>Dichelyne tornquisti</i>	Intestine	35	4.8±5.7	1.7±4.1	3.5	2	10±1	0.17±1.2	2	--	--	--	--
<i>Dichelyne</i> sp.	Intestine	--	--	--	--	--	--	--	--	20	3±2.9	0.6±1.7	6.8
ACANTHOCEPHALA													
<i>Dollfusentis chandleri</i>	Intestine	18	1.4±0.6	0.2±0.6	--	--	--	--	--	20	3.4±2.4	0.6±1.7	6.8
<i>Koronacantha</i> sp.	Intestine	--	--	--	--	--	--	--	--	22	3±2.8	0.6±1.8	11.3
<i>Serrassentis</i> sp. (Cystacanth)	Intestine	26	2.6±1.4	0.7±1.3	1.7	10	1±0	0.1±0.2	5.2	2	1	0.02±0.1	--
COPEPODA													
<i>Acantholochus lamellatus</i>	Operculum	--	--	--	--	26	2±1.2	0.5±1.1	19.7	--	--	--	--
<i>Caligus haemulonis</i>	Operculum	41	3±2.2	1.2±2	12.5	32	1.8±1.2	0.6±1.1	24	--	--	--	--
<i>Caligus longipedis</i>	Operculum	--	--	--	--	0.8	1	0.01	1	4	1	0.04	--
<i>Caligus robustus</i>	Operculum	--	--	--	--	8	1.3±0.4	0.1±0.3	6.2	--	--	--	--
<i>Caligus rufimaculatus</i>	Operculum	--	--	--	--	1.7	1	0.02±0.1	1	--	--	--	--
<i>Caligus sepetibensis</i>	Operculum	3	1	0.03±0.1	--	--	--	--	--	--	--	--	--
<i>Caligus xystercus</i>	Operculum	--	--	--	--	1.7	1.5±0.5	0.03±0.2	1	10	1.2	0.12±0.1	2.2
<i>Hamaticolax</i> sp.	Gills	--	--	--	--	2.5	1.6±0.9	0.04±0.2	1	--	--	--	--
<i>Hatschekia nagasawai</i>	Operculum	--	--	--	--	--	--	--	--	50	6.3±5.5	3.1±5	25
<i>Lernanthropus rathbuni</i>	Gills	10	1.1±0.3	0.12±0.3	--	30	2±1.7	0.6±1.4	26	--	--	--	--
<i>Parashiinoa</i> sp.	Nasal cavities	3	1	0.03±0.1	--	--	--	--	--	--	--	--	--
ISOPODA													
<i>Gnathia</i> sp. (Larvae)	Operculum	--	--	--	--	6	4.1±3.3	0.2±1.3	5.2	10	2.8±2.6	0.2±1.1	2.2

Table II. Values of variance-to-mean abundance ratio (ID) and index of Discrepancy (D) of metazoan parasites of *Anisotremus virginicus*, *Conodon nobilis* and *Orthopristis rubra* from the coastal zone of Rio de Janeiro, Brazil.

Parasite species	<i>Anisotremus virginicus</i>		<i>Conodon nobilis</i>		<i>Orthopristis rubra</i>	
	ID	D	ID	D	ID	D
<i>Acantholochus lamellatus</i>	--	--	2.25	0.81	--	--
<i>Aponurus laguncula</i>	--	--	2.49	0.84	--	--
<i>Aponurus pyriformis</i>	--	--	--	--	2.47	0.85
<i>Caligus haemulonis</i>	--	--	2.35	0.78	3.48	0.73
<i>Choricotyle brasiliensis</i>	--	--	--	--	1.54	0.78
<i>Choricotyle orthopristis</i>	--	--	--	--	3.05	0.89
<i>Choricotyle</i> sp.	0.89	0.86	--	--	--	--
<i>Cucullanus</i> sp.	--	--	--	--	2.27	0.86
<i>Dichelyne tornquisti</i>	--	--	--	--	10.07	0.82
<i>Dichelyne</i> sp.	5.37	0.87	--	--	--	--
<i>Diptherostomum brusinae</i>	--	--	--	--	23.77	0.92
<i>Diplomonorchis leiostomi</i>	--	--	--	--	17.01	0.92
<i>Dollfusentis chandleri</i>	4.53	0.86	--	--	1.50	0.84
<i>Encotyllabe spari</i>	3.68	0.79	--	--	6.59	0.59
<i>Genolopa ampullacea</i>	0.89	0.86	--	--	6.08	0.90
<i>Hatschekia nagasawai</i>	8.26	0.71	--	--	--	--
<i>Infundiburictus longovatus</i>	--	--	--	--	50.91	0.77
<i>Koronacantha</i> sp.	5.10	0.85	--	--	--	--
<i>Lernanthropus rathbuni</i>	--	--	2.97	0.79	--	--
<i>Leurodera decora</i>	4.55	0.81	--	--	--	--
<i>Mexicana anisotremum</i>	25.72	0.89	--	--	--	--
<i>Monorchis latus</i>	82.33	0.92	--	--	--	--
<i>Prosorhynchus osakii</i>	--	--	--	--	2.79	0.90
<i>Pseudotagia rubri</i>	--	--	--	--	3.39	0.56
<i>Serrassentis</i> sp.	--	--	--	--	2.82	0.80
<i>Torticaecum</i> sp. (immature)	--	--	2.82	0.86	3.64	0.89

Structure of the parasite community of *Anisotremus virginicus*

Of the 50 *A. virginicus* analyzed, 44 (88%) were parasitized by at least one of the 16 metazoan parasite taxa found (see Table I). The copepod *Hatschekia nagasawai* Paschoal, Couto, Pereira & Luque, 2022 was the most prevalent and dominant species. On the other hand, the digenetic *Monorchis latus* Manter, 1942 was the most abundant, representing 24% of all parasite specimens collected (see Table I). Ectoparasites were slightly more abundant than adult endoparasites, representing 51.9% (355) and 48.0% (327), respectively, of the specimens

collected, and only 1 (0.1%) endohelminth larval form were found.

Structure of the parasite community of *Conodon nobilis*

Of the 120 *Co. nobilis* analyzed, 96 (80%) were parasitized by at least one of the 19 metazoan parasite taxa found (Table I). The copepod *Caligus haemulonis* Krøyer, 1863 was the most prevalent, and *Lernanthropus rathbuni* Wilson, 1922 was the most abundant and dominant species, representing 17% of all parasite specimens collected (see Table I). Ectoparasites represented 60.2% (277), adult endoparasites

24.6% (113) and endohelminth larval forms 15.2% (70) of the total specimens collected.

Structure of the parasite community of *Orthopristis rubra*

Of the 60 *O. rubra* analyzed, 56 (93%) were parasitized by at least one of the 21 metazoan parasite taxa found (see Table I). The monogenean *E. spari* was the most prevalent, and the digenean *I. longovatus* was the most abundant and dominant, representing 45% of all parasite specimens collected (see Table I). Adult endoparasites represented 68% (1191), ectoparasites 29.7% (521) and endohelminth larval forms 2.3% (41) of the total specimens collected.

Comparison among component communities of haemulid fish

Values of the descriptors for parasite communities, according to each host species, are detailed in Table III. Significant differences were observed comparing the total parasite abundance, species richness and diversity among host species, in which *O. rubra* showed the highest values, followed by those of *A. virginicus* and *Co. nobilis*; the parasite dominance was statistically similar among host (Table III).

The ANOSIM indicated that, for both quantitative (Bray-Curtis) and qualitative (Jaccard) similarities, infracommunities of parasites were closer according within a fish species (Global R > 0.30; *p* < 0.001). Moreover, ANOSIM indicated that parasite infracommunities of *Co. nobilis* and *O. rubra* were closer to each other than that of *A. virginicus*, and that of *A. virginicus* was most similar to that of *Co. nobilis* than that of *O. rubra* (Table IV).

DISCUSSION

The digenetics *Leurodera decora* Linton, 1910 and *M. latus* and the acanthocephalan *Koronacantha* sp. found in the present study represent new locality records off the State of Rio de Janeiro, Brazil. Moreover, the following represent new host records: *Opecoeloides* sp. (Digenea), *Koronacantha* sp. (Acanthocephala), *Dichelyne* sp. (Nematoda) and *E. spari* (Monogenea) parasitizing *A. virginicus*; *Aponurus laguncula* Looss, 1907, *Genolopa ampullaceal* Linton, 1910 and *Parahemiurus merus* (Linton, 1910) (Digenea) and *Dichelyne tornquisti* Paschoal, Vieira, Cezar & Luque, 2014 parasitizing *Co. nobilis*; and *Torticaecum* sp. (Digenea) and *Parashiinoa*

Table III. Descriptors of parasite communities of *Anisotremus virginicus*, *Conodon nobilis* and *Orthopristis rubra* from the coastal zone of Rio de Janeiro, Brazil, represented as mean followed ± 1 standard deviation (range). Superscript letters indicate statistical differences (ANOVA, *p* < 0.05) among values within the same line.

Characteristics	<i>Anisotremus virginicus</i>	<i>Conodon nobilis</i>	<i>Orthopristis rubra</i>	F
Total parasite species	16	19	21	--
Ectoparasites	8	10	9	--
Endoparasites (adult)	7	5	10	--
Endoparasites (larval)	1	4	2	--
Total number of parasites	683	460	1753	--
Total abundance	13.66 ± 20.12 (0–125) ^a	3.83 ± 3.90 (0–18) ^b	29.21 ± 30.07 (0–166) ^c	38.4*
Species richness	2.68 ± 1.39 (0–5) ^a	1.91 ± 1.44 (0–6) ^b	4.91 ± 2.52 (0–11) ^c	55.7*
Brillouin index	0.49 ± 0.30 (0–1.06) ^a	0.34 ± 0.34 (0–1.09) ^b	0.88 ± 0.44 (0–1.60) ^c	43.3*
Berger-Parker index	0.48 ± 0.27 (0–0.89) ^a	0.53 ± 0.34 (0–1.00) ^a	0.50 ± 0.24 (0–1.00) ^a	0.63

sp. (Copepoda) parasitizing *O. rubra*. These new records reinforce that the parasitological knowledge pertaining to haemulid fish from South Atlantic, still needs to be improved.

The component community of *O. rubra* showed the highest parasite species richness, followed by that of *Co. nobilis* and then that of *A. virginicus*. Regarding the present parasite species, it was possible to note that the parasite community of *O. rubra* showed a dominance by digeneans, similar to the findings by Luque et al. (1996a, b), Centeno et al. (2002), Bashirullah & Díaz (2015), López-Zacarías et al. (2021) and Montoya-Mendoza et al. (2021), reinforcing the information presented by Paschoal et al. (2015) in parasites of haemulid fish from the Neotropics. Regarding the diet basically composed of invertebrates and the trophic level it occupies, endoparasite taxa are very frequent in these hosts, with digenetic ones being the main dominant group. Some of the previous research conducted with fish in the coast of Rio de Janeiro also reveals high numbers of endoparasite specimens, *i.e.*, digeneans (Takemoto et al. 1996, Knoff et al. 1997, Silva et al. 2000, Alves et al. 2004, Tavares & Luque 2004a, Moreira et al. 2015, Chaves & Paschoal 2021), adult nematodes (Alves et al. 2002) or nematode larvae (Sabas & Luque 2003, Alves & Luque 2006). This could be associated with the feeding habits involving the intermediate hosts, their position in the marine trophic web and the distribution pattern of the hosts. However, some types of marine disturbances, such as periods of upwelling and resurgence

due to climatic variations can considerably affect the population dynamics of trophically transmitted endoparasites (Marcogliese 2002, Luque et al. 2004, Espínola-Novelo et al. 2020). The component communities of parasites in the present study were predominately composed by adult stages rather than larval forms. It indicates that *A. virginicus*, *Co. nobilis* and *O. rubra* probably are within higher trophic levels of their local food web (Pombo et al. 2014, Santos et al. 2021), but are preyed upon by larger fish acting as important intermediate/paratenic hosts of some helminth endoparasites, for example, *Serrassentis* cystacanths that were especially found in *O. rubra* (see Table I).

Unlike the pattern observed in *O. rubra*, the parasite communities of *A. virginicus* and *Co. nobilis* showed dominance by ectoparasites. According to previous parasitological studies of fish from Rio de Janeiro, this is not common but may occur and, probably, be favored by the aggregated behavior of this host, which also shows high population densities (Cezar & Luque 1999, Tavares et al. 2001, Tavares & Luque 2004b, Alves & Luque 2006). Concerning the parasite community of *Co. nobilis*, some copepods found in the present study have already been reported in the same area but parasitizing non-haemulid fish (Luque & Tavares 2007). In this sense and since copepods have direct transmission, these parasites may shift hosts by migrating from a fish to another depending upon environmental conditions (Cressey et al. 1983, Boxshall & Halsey 2004), which contributes to the enrichment of

Table IV. Results of the Analysis of Similarities (ANOSIM) with 10,000 permutations, for qualitative (Jaccard) and quantitative (Bray-Curtis) similarities, estimated at infracommunity level and considering fish species as factor. Level of significance is $p < 0.05$.

Pairwise comparison	Jaccard similarity		Bray-Curtis similarity	
	R statistic	p	R statistic	p
<i>A. virginicus</i> vs. <i>C. nobilis</i>	0.317	< 0.001	0.319	< 0.001
<i>C. nobilis</i> vs. <i>O. rubra</i>	0.247	< 0.001	0.250	< 0.001
<i>O. rubra</i> vs. <i>A. virginicus</i>	0.510	< 0.001	0.500	< 0.001

copepods in the population of *Co. nobilis* and indicates that some species have low host specificity. However, a different pattern can be found in *A. virginicus*, where some ectoparasite species, e.g., *Mexicana anisotremum* Cezar, Paschoal & Luque, 2012 and *H. nagasawai*, are found exclusively infesting this haemulid fish and may suggest a narrow degree of host specificity.

It seems that the parasite assemblages of haemulids off Rio de Janeiro tend to show higher richness, dominance, diversity and overall abundance when compared with those of haemulids from other parts of South America, for example, in the Atlantic coast of Venezuela and Pacific coast of Peru (see Centeno et al. 2002, Iannacone & Alvarino 2009). On the other hand, Montoya-Mendoza et al. (2021) reported a highly rich parasite community of *A. virginicus* from Veracruz, Mexican Atlantic coast. It should be mentioned that, despite the differences, the parasite communities reported by Centeno et al. (2002), Iannacone & Alvarino (2009), Montoya-Mendoza et al. (2021) and that of the present study, share some similarities regarding species composition. These differences may be related to the fact that different geographic regions have different biotic and abiotic factors that affects parasite communities (Lafferty 1997, Luque et al. 2004, Luque & Poulin 2007), which is known as part of an ecological component (Janovy Jr et al. 1992). The similarities observed on these parasite faunas may be related to a phylogenetic component, such as suggested by Janovy Jr et al. (1992).

The aggregated distribution is considered typical of parasitic organisms, in which most hosts may harbor few or no parasites while a small portion is heavily parasitized (Crofton 1971). Heterogeneous exposure to parasites and or susceptibility to parasite infections are believed to be the most important factors resulting in

aggregation (Poulin 2013). In the present study, the aggregated distribution was predominant among the metazoan parasites, like what has been observed for other haemulid hosts from Neotropical marine waters (Luque et al. 1996a, Centeno et al. 2002, Iannacone & Alvarino 2009). However, such pattern although common, is not absolute. For example, the infrapopulations of the copepod *Colobomatus belizensis* Cressey & Schotte, 1983 infesting *Haemulon atlanticum* Carvalho, Marceniuk, Oliveira & Wosiacki, 2020 (as *Haemulon steindachneri*) was reported to be highly uniform within its host population, due to the limited space available for host infestation (Luque et al. 1996a), reinforcing again that particularities of host features may also influence structures of parasite communities.

Several studies, conducted in the Atlantic Ocean (including the Brazilian coast), show that mixed schools or spatial overlapping by haemulid species have advantages for the fish, i.e., more efficient foraging and protection against predators (Quinn & Ogden 1984, Braga et al. 2009, Pereira et al. 2011, Paijmans et al. 2019). In the Southeastern Brazilian coast, the three haemulid species studied here are sympatric and share various dietary components, mostly crustaceans and small fish (Menezes & Figueiredo 1980, Pombo et al. 2014, Santos et al. 2021). In a general, the high similarity among parasite communities of sympatric and or phylogenetically close fish overlapping over time is expected (Tavares & Luque 2008). However, despite the high similarity expected and observed, the differentiation of the present parasite infracommunities according to host species was possible, as indicated by ANOSIM test. In this sense, there was a continuum where the parasite communities of *A. virginicus* and *Co. nobilis* were closer to each other than that of *O. rubra*, and those of *A. virginicus* and *O. rubra* were the most dissimilar. According to

Luque et al. (1996b), the degree of susceptibility to certain infections and/or infestations of *O. rubra* (as *Orthopristis ruber*), is different from those of other haemulid hosts. This different susceptibility may be related to specific characteristics of *O. rubra* such as its vagility, anatomy, physiology and feeding selectiveness of dietary items that act as intermediate hosts (Kennedy et al. 1986, Luque et al. 2004).

The parasite communities in the three haemulids were characterized by low to moderate diversity, with many taxa occurring in one host species and few occurring in more than one. These patterns indicate non-interactive parasite communities in nature, which is common among most fish hosts from marine environment, according to the conception by Holmes (1990). In fact, along decades of study some factors were highlighted as determinants of parasite community structure in marine teleosts, rather than species interaction (Timi & Poulin 2003, Luque & Poulin 2007, Tavares & Luque 2008, Timi et al. 2010a, b, Santoro et al. 2020). Among these factors, in the present study we believe that diet composition (for endoparasites) and the formation of mixed schools with spatial overlapping (for ectoparasites) showed by these haemulid fish, appear to be important for shaping their parasite community structures. Of the 25 species of haemulids currently reported along the Brazilian coast (Froese & Pauly 2021), only four, i.e., *A. virginicus*, *Co. nobilis*, *H. atlanticus* and *O. rubra* had their parasite communities studied, indicating that a gap of knowledge to be filled. Therefore, future studies using similar approaches as the present one, should be conducted involving more and different haemulid species, in order to fill this important gap.

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