

Article

Metazoan Parasite Communities of Two Sympatric Shortnose Chimeras (Holocephali: Chimaeridae) from Deep Waters Associated with the Humboldt Current System: Ancient Fishes Harbor Ancient Parasites

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Abstract

A total of 61 specimens of deep-sea chimaeras (*Hydrolagus melanophasma* = 41; *Chimaera* sp. = 20) were obtained during September 2017 as by-catch of the local fishery of the Patagonian toothfish (*Dissostichus eleginoides*, Pisces: Nototheniidae) along the northern Chilean coasts ($\approx 22^{\circ} 20' S$) at depths ranging from 950 to 1500 m using a deep-sea longline. Nine species of metazoan parasites were found in *H. melanophasma* and seven in *Chimaera* sp. Four species were shared between both host species. *Gyrocotyle* sp.1 (Cestodaria) and *Multicalyx elegans* (Aspidogastrea) showed the higher prevalence in *H. melanophasma* (68.3% and 65.38%, respectively), whereas *Plectognathotrema hydrolagi* (Digenea), *Gyrocotyle* sp.1 (Cestodaria), and *Chimaericola* sp. (Monogenea) showed higher prevalence in *Chimaera* sp. (90%, 55% and 55%, respectively). Beta diversity analysis reveals that the parasite communities of these two related and sympatric species are strongly differentiated. Our results suggest a strong relationship between the ancient Holocephali, which harbor ancient parasites belonging to Rugogasteridae and Multicalycidae (Aspidogastrea), and two Cestodaria species. *Chimaera* spp. are also parasitized by some highly specific monogeneans, such as *Chimaericola* spp. Our results demonstrate the differences in the parasite community structures—both of ecto- and endoparasites—of two related and sympatric hosts.

Keywords: deep-sea chimaeras; parasites; atacama trench; humboldt current; beta diversity



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1. Introduction

Without doubt, the deep sea—encompassing depths from 200 to 11,000 m—is the largest biotope on earth and remains largely unexplored [1]. Its biodiversity is still poorly understood, and the ecological relationships among the species inhabiting this environment remain almost unknown [2,3].

Despite the low values of primary production in the deep sea, important marine resources inhabit this environment, including the Patagonian toothfish *Dissostichus eleginoides* in the southern hemisphere [3]. Consequently, as coastal fisheries collapse, the deep-sea region may offer new resources [4]. It is therefore critical to possess not only clear and adequate knowledge of these potential new resources but also a sound understanding of the biodiversity of these ecosystems [5,6].

Parasites are an important component of any ecosystem, with the number of such species potentially being higher than that of the free-living species; for instance, the number of helminth species infecting vertebrates is at least 50% higher than the number of their hosts [7]. Parasites are also important because of the role they play in ecosystems, regulating the abundance or density of host populations, stabilizing food webs, and structuring host communities [8], as well as potentially providing critical information regarding ecology and phylogenetic information of the host species [9]. Data regarding the parasite fauna harbored by deep-sea fishes are available for less than 10% of the ichthyofauna that inhabit these ecosystems [6,10,11]. The economic and logistical difficulties in accessing hosts that inhabit these ecosystems are the main reasons explaining the scarcity of knowledge regarding the parasite fauna of deep-sea fishes. An alternative is to study host species from the by-catch of deep-sea commercial fisheries, providing additional opportunities for sampling [11].

Knowledge regarding the parasite community of Holocephali is particularly scarce. The class includes 55 species in six genera and three families [12]. Except for the three species of *Callorhynchus*, which are restricted to shallow waters in the southern hemisphere [13], and *Hydrolagus colliciei*, the remaining species are considered deep-sea fishes [14]. Quantitative data regarding metazoan parasites have been gathered for only four species: *Chimaera monstrosa* from Norway [15], *Callorhynchus capensis* from South Africa [13], *Hydrolagus affinis* from Greenland [16], and *Callorhynchus callorhynchus* from Perú and Central Chile [17,18]. Although at least 54 parasitic species have been specifically recorded for 18 species of *Chimaera*, at least 17 additional taxa have been reported at the generic or higher taxonomic level (see Table S1 in the Supplementary Materials).

For the Southeastern Pacific Ocean (SEPO hereafter), eight species of Holocephali are known [12]; however, quantitative data regarding metazoan parasites have been obtained only for the shallow-water *C. callorhynchus*. Two species of shortnose chimaeras are commonly caught as by-catch in the deep-sea fishery (>1000 m) of the Patagonian tooth fish *D. eleginoides* in Northern Chile: the Eastern Pacific Black Ghostshark *Hydrolagus melanophasma*—with a wide geographic range along the Eastern Pacific Ocean, from Baja California, Mexico, to Valdivia, Chile [12]—and *Chimaera* sp.

Our goal is to report, for the first time, the compositions of the metazoan parasite communities of two deep-sea Holocephali from the SEPO, as well as to quantitatively describe the characteristics of these communities and evaluate the similarity/differences (in terms of alpha and beta diversities) between them.

2. Materials and Methods

A total of 61 deep-sea chimaera specimens (*H. melanophasma* = 41; *Chimaera* sp. = 20) were obtained as by-catch of the local fishery of the Patagonian toothfish (*D. eleginoides*) along the Northern Chilean coast (22°20' S, 70°37' W), using a deep-sea longline at depths ranging from 950 to 1500 m (Figure 1), during September 2017. Chimaeras were captured, stored in individual bags, and immediately frozen (−18 °C) on board, then transported to the laboratory for parasitological analyses.

After thawing, the chimaeras were measured (total length to the nearest 1.0 cm), dissected, and examined for metazoan ectoparasites and endoparasites. All specimens were examined first for ectoparasites, including the skin, gills, and mouth cavity and then for endoparasites. All viscera, including heart and blood vessels (arterial cone and branchial artery), were examined. To count endoparasites, each visceral organ was dissected separately and washed under running water. All material retained on a 0.3 mm mesh was examined under a LEICA M 125 stereoscope with an incorporated LEICA MC120 HD camera (Heerbrugg, Switzerland). Parasites were sorted by species for each host individual, fixed in AFA (alcohol/formalin/acetic acid), and preserved in 70% alcohol. Nematoda were

cleaned with Amann's lactophenol. Monogenea, Digenea, and Cestoda were stained (acetic carmine), cleaned with clove oil (Sigma-Aldrich, St. Louis, MO, USA), and mounted in Eukitt medium (O. Kindler Freiburg GmbH, Germany) [19]. Copepoda and Isopoda were stored in ethanol (70%) and dissected for taxonomic purposes. Parasites were identified to the lowest taxonomic level possible. Prevalence and mean intensity of infection were calculated [20].

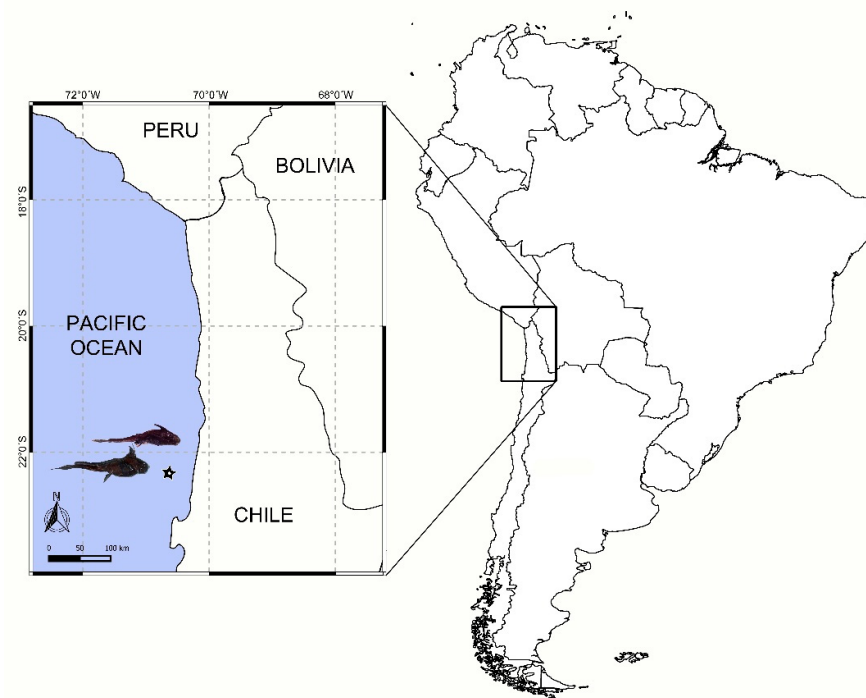


Figure 1. Approximate position (star) where samples were obtained.

Potential relationships between total length and richness (both raw data and $\log n + 1$) were explored (Pearson's correlation coefficient). Due to the small sample size, the relationship between host size and mean intensity of infection was estimated for those parasite species with prevalence higher than 20%, ensuring at least eight values (for a given species) for the intensity of infection for specimens of *H. melanophasma* and six values for specimens of *Chimaera* sp. Diversity indices (alpha and beta diversity) were compared between the two host species with non-parametric (richness, Wilcoxon–Mann–Whitney) and parametric (Shannon diversity, Pielou's J evenness, ANOVA) tests.

Shannon diversity was estimated using the following formula

$$H' = -\sum (p_i \ln p_i)$$

where H' = Shannon diversity index, and p_i = proportion of individuals of species i .

Pielou's J evenness was calculated as

$$J = H' / \ln S$$

where J = Pielou's evenness, and $\ln S$ = log of the number of species.

Differential analysis of alpha diversity was performed to evaluate the significance of differences in the richness, diversity, and evenness of metazoan parasites at infracommunity and community component levels [20]. The significance of differences in diversity at the community component level was graphically evaluated via principal coordinate analysis (PCoA) on a similitude matrix, using Primer 6.0 [21]. Multivariate discriminant

analysis (MDA) at the infracommunity level was used to test whether metazoan parasite communities could be suitable tools for discriminating between host species [22,23]. All statistical analyses were performed with the Minitab 17 statistical software.

3. Results

The total length of specimens of *H. melanophasma* ranged from 88 to 117 cm (mean = 104 cm; SD = 8.1), and the total length of *Chimaera* sp. ranged from 75 to 115 cm (mean = 84 cm; SD = 8.8).

A total of 228 parasites belonging to nine species were obtained from *H. melanophasma* (just two specimens were devoid of parasites), whereas 2085 parasites belonging to seven species were obtained from *Chimaera* sp.; notably, 100% of these hosts were parasitized (Table 1).

Table 1. Site of infection, prevalence (P), and mean intensity of infection (MI $\pm$ SD) of metazoan parasites found in two species of shortnose chimaeras from deep waters in Northern Chile.

Parasite Species	Site of Infection	<i>Hydrolagus Melanophasma</i>	<i>Chimaera</i> sp.		
		P	MI $\pm$ SD	P (%)	MI $\pm$ SD
Monogenea					
<i>Calicotyle hydrolagi</i>	R/CI	14.6	2 $\pm$ 2		
<i>Chimaericola</i> sp.	G			55	2.1 $\pm$ 1.8
Copepoda					
<i>Lernaeopodina longibrachia</i>	Sk	31.7	1.5 $\pm$ 0.7		
Isopoda					
Praniza larvae	Sk	2.4	1 $\pm$ NA		
Aspidogastrea					
<i>Multicalyx elegans</i>	GB	65.8	4.2 $\pm$ 3.6	35	1.7 $\pm$ 1
<i>Rugogaster callorhynchid</i>	R/Rg	4.9	3.5 $\pm$ 3.5	15	2.0 $\pm$ 1.7
Digenea					
<i>Plectognathotrema hydrolagi</i>	Es/SV			90	101.5 $\pm$ 222.2
<i>Spinoplagioporus</i> cf. <i>minutus</i>	Es/SV			10	98 $\pm$ 123.0
Cestodaria					
<i>Gyrocotyle</i> sp. 1	SV	68.3	1.9 $\pm$ 1.6	55	1.6 $\pm$ 1.3
<i>Gyrocotyle</i> sp. 2	SV	17.1	1.3 $\pm$ 0.5	10	1.5 $\pm$ 0.7
<i>Trypanorhyncha</i> gen. sp.	SV/St	2.4	2 $\pm$ NA		
Nematoda					
<i>Anisakis</i> sp.	SV	4.9	6 $\pm$ 7.1		

Site of infection: R = rectum; CI = cloaca; G = gills; Sk = skin; GB = gall bladder; Rg = rectal glands; Es = esophagus; SV = spiral valve; St = stomach.

Richness was not correlated with total length for both *H. melanophasma* and *Chimaera* sp. ($p > 0.10$ for all correlations). In a similar way, the significance of the correlation coefficient (r) for the relationship between the intensity of infection for selected parasite species and host size was always >0.05 .

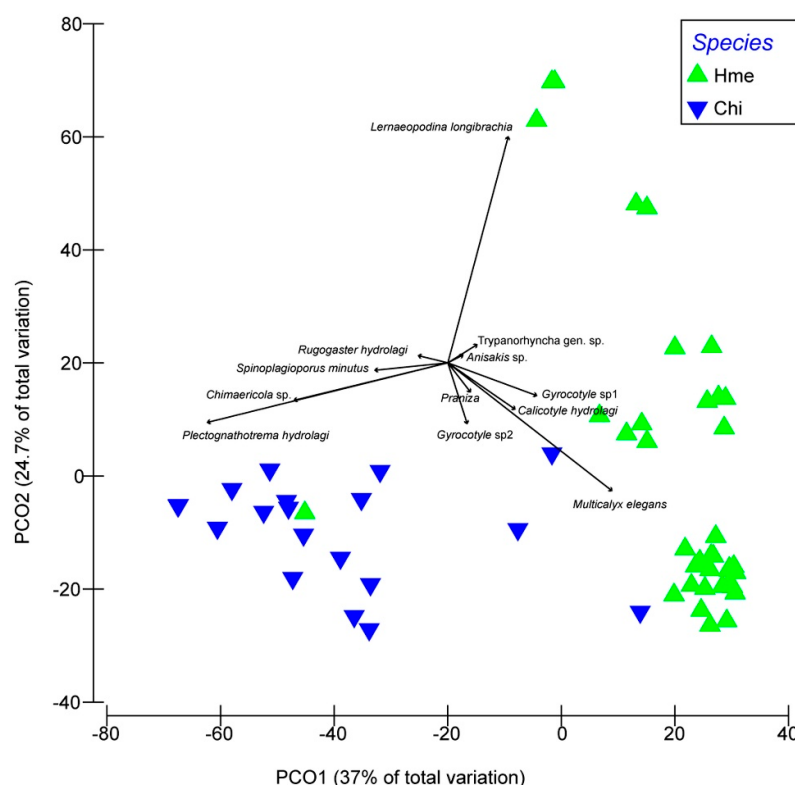
At the infracommunity level, mean richness did not differ significantly between host species ($W = 680$, $p = 0.082$), whereas diversity (H' Shannon Index) and evenness (J' index) differed significantly ($F_{17,26} = 9.08$ and 26.4 , respectively; $p < 0.001$ for both comparisons) (Table 2). At the community component level, diversity differed significantly (" t " test = 19.22 , estimated $gl = 231$, $p < 0.001$).

The results of principal coordinate analysis (PCoA) on the similarity matrix showed that the two species could be well identified according to the intensity of infection (Figure 2); the same conclusion was reached according to the multivariate discriminant analysis, with 100% of *H. melanophasma* specimens and 85% of *Chimaera* sp. specimens classified correctly (Table 3). Specifically, the *Chimaera* sp. were closely associated with two species of digenea (*S. minutus* and *P. hydrology*) and the monogenea *Chimaericola* sp., whereas *H. melanophasma* was associated with the copepod *L. longibrachia* as well as the Aspidogastrea *M. elegans*.

Table 2. Diversity indices at infracommunity and community component levels for metazoan parasites in two shortnose chimaeras from Northern Chile.

Infracommunity	<i>Chimaera</i> sp.	<i>Hydrolagus melanophasma</i>	Test	P
Mean Richness ($\pm$ SD)	2.7 (1.1)	2.1 (1.0)	W = 680	0.082 *
Mean Diversity ($\pm$ SD) (H')	0.22 (0.15)	0.34 (0.11)	F = 9.08	0.004
Mean Evenness ($\pm$ SD) (J')	0.9 (0.28)	0.84 (0.17)	F = 26.4	<0.001
Component Community				
Shannon Diversity Index	0.21	2.31	" t' " = 19.2	<0.001

* Adjusted for ties.

**Figure 2.** Principal component analysis based on metazoan parasite infracommunities from two species of shortnose chimaeras from Northern Chile. Hme: *Hydrolagus melanophasma*; Chi: *Chimaera* sp.**Table 3.** Classification matrix (cases in row categories classified into columns) for two host species based on metazoan parasite communities.

	<i>Chimaera</i> sp.	<i>H. melanophasma</i>	% Correct Classification
<i>Chimaera</i> sp.	17	3	85
<i>Hydrolagus melanophasma</i> *	0	39	100
Total	17	43	94.9

* Two specimens were devoid of metazoan parasites.

4. Discussion

Hosts were caught using the same fishing gear (deep-sea longline), on the same date and at the same locality. Accordingly, the differences in the number of hosts obtained suggest differences in their relative abundance—as similarly described for two deep-sea shark species also caught as by-catch of the Patagonian tooth fish in Northern Chile [22].

This is the first report regarding parasite communities of two sympatric deep-sea chimaera species—*H. melanophasma* and *Chimaera* sp.—associated with the deep waters of the Atacama Trench.

Chimaeras (Holocephali) are a small and enigmatic subclass of ancient Chondrichthyes, which hypothetically diverged from a common ancestor with the elasmobranch about 413 Ma [24]. To date, 55 Holocephalan species are recognized, while metazoan parasites (under a taxonomic approach) have only been reported for 18 species (see Supplementary Materials, Table S1 and Figure S1). Quantitative analyses of metazoan parasite communities (sample size > 30) have been performed for just three species: the shallow-water *Callorhynchus callorhynchus* from Chile and Perú [17,18], *Callorhynchus capensis* from South Africa [13], and the deep-water *Chimaera monstrosa* from Norway [15].

Holocephalans are the only host group for the unique and non-segmented *Gyrocotyle* spp. (Gyrocotylidae: Cestodaria), which represent a sister group of the true tapeworms (Eucestoda) [25] and, like their host, are considered to be “living fossils” of a vanished past [26]. Holocephalans are also unique hosts for some ectoparasites—such as members of Chimaericolidae (Monogenea: Polyophistocotylea) [24], which includes five species in two genera, and members of the genus *Callorhynchocotyle* (Monogenea: Hexabothriidae), which includes five species [27]. The four species of the primitive copepod *Vanbenedenia* (Lernaeopodidae) are parasites of Chimaeras [28]. *Multicalyx*—a genus of the family Multicalycidae (Aspidogastrea)—are parasites of Holocephali and Elasmobranchii [29], while the two species of *Rugogaster* (Rugogasteridae: Aspidogastrea) are also specific parasites of Chimaeridae [30].

Gyrocotylidae is considered a group of distinct species that are mostly host-specific to Holocephali and cannot be distinguished by morphology [25]. Our data suggest the presence of two morphotypes of *Gyrocotyle*, which were found in both host species.

While the differences in richness between the host species were not significant, there were clear differences in their parasite species composition. The main differences include the presence of two species of digenea in *Chimaera* sp., one of which—*Plectognatotrema hydrolagi* (Zoogonidae), with prevalence of 90% and mean intensity of infection of 101.5—has been described from the shallow-water *Hydrolagus colliei* obtained off the coast of Oregon (USA) [30]. No quantitative studies regarding metazoan parasites of holocephalans have reported this species. Quantitative data for *Spinoplagioporus minutus* (Acanthocolpidae) parasitizing *C. monstrosa* were provided with the original description of the species [31], with a prevalence of 100% and an abundance ranging from 1 to 283 specimens in the host *C. monstrosa* from the Barent Sea. The species has also been registered from *Chimaera phantasma* [6]. The second intermediate hosts for members of Acanthocolpidae and Zoogonidae are bivalves [32,33]. The presence of both species of digenea—which are trophically transmitted—suggests that *Chimaera* sp. predate on invertebrates (bivalves) that are not a component of the diet of *H. melanophasma*, thus avoiding predatory competition for diet between these sympatric species. Unfortunately, data regarding the diets of deep-sea chimaeras are almost absent.

Recently, it has been suggested that the main force shaping the parasite community structure in teleost marine fish is age, for which total length can serve as a surrogate [34]. Our results showed an opposite picture: without exception, all relationships between richness, intensity of infection, and host size were non-significant. The expected positive relationship between richness and size (age) can be explained by the accumulation of long-lived encysted larval parasitic stages with age and/or an increased consumption rate of prey in longer-lived fish; however, this can only occur if colonization is higher than mortality [34]. According to the composition of the parasite community for both host species in this study, it is evident that larval stages are scarce; in particular, 6.1% of the total number of parasites in *H. melanophasma* were larval stages of *Anisakis* sp. (Nematoda) and *Trypanorhyncha* gen. sp. (Eucestoda), whereas *Chimaera* sp. harbored only adult parasites. Larval cestodes have been considered as “incidental parasites” in Chimaerids [15]. The

absence of larval stages of metazoan parasites strongly suggests a higher trophic level (at least for *Chimaera* sp.), as reported for *C. monstrosa* [35].

Our results strongly suggest a strong component of the evolutionary history of the host on the characteristic of the parasite fauna of the ancient Holocephali, including not only ancient parasites belonging to Rugogasteridae and Multicalycidae (Aspidogastrea) but also the unsegmented member of Gyrocotylidae. Holocephali are also parasitized by highly specific monogeneans, such as *Chimaericola* spp., *Callorhynchicola*, and *Callorhynchocotyle*, which are all parasites of Chimaeridae, while the last genus is also a parasite of Callorhynchidae. In a similar way, while other species are parasites of Holocephali, members of some genera (i.e., *Plectognathotrema*) are also parasites of teleosts. *Vanbenedenia* species are also specific parasites of Holocephali, whereas the observed larval forms (*Anisakis* sp. Trypanorhyncha gen. sp.) and caligids copepods (*Caligus* spp.) are non-specific and can also be found as parasites of teleosts. In summary, there exist ancient parasite species that are specific to some ancient Holocephalans, as indicated by the results of the multivariate analysis in this study.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d17090601/s1>. Table S1. Recorded metazoan parasites from Chimaeriformes. Figure S1. Pictures of parasites found in *Chimaera* sp. and *Hydrolagus melanophasma* (not identified at the species level).

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Data Availability Statement: Data available on request.

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