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Global distribution patterns and geographic range of *Cymothoa* Fabricius, 1793 (Isopoda: Cymothoidae) associated with host fish

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Abstract: Over recent years, fish parasites of the genus *Cymothoa* Fabricius, 1793, have received increased attention due to both their ecological and their economic importance to aquaculture and fishery. As the studies about *Cymothoa* have increased this improve our understanding on the host specificity and distribution of these parasites. The aim of this paper was to review the current global geographic distribution, distribution patterns and parasite-host interactions patterns of *Cymothoa* spp. associated with fish from marine and brackish water bodies around the world. A total of 144 samples were analyzed, from which 23 species of *Cymothoa* were found parasitizing 84 teleost fish species of 35 families and 20 orders. Most of these parasites were found in the mouth of the host fish, including in wild fish. The highest occurrence of parasites was found in host species belonging to the families Carangidae and Lutjanidae. Host specificity was an important factor in the geographic distribution of *Cymothoa* species as also environmental temperature. *Cymothoa indica*, *Cymothoa exigua* and *Cymothoa excisa* were the species with lowest specificity for host family and widest geographic distribution.

Key words: Buccal cavity, fish, infestation, parasites, prevalence.

INTRODUCTION

Crustaceans are one of the major groups of the phylum Arthropoda and a significant proportion of them exhibit parasitic life, infecting fish species. In this phylum, the order Isopoda is an exceptionally speciose group, with more than 10,000 species, which mostly but not exclusively live in aquatic habitats (Zou et al. 2018). Isopods of the family Cymothoidae Leach, 1818, parasitize marine, brackish water and freshwater fish (Kumar et al. 2015). *Cymothoa* Fabricius, 1793, are members of Cymothoidae that usually infest wild marine fish species, in diverse ecosystems around the world. This genus includes 46 valid species (WoRMS 2023). *Cymothoa* is morphologically the most challenging genus within the family Cymothoidae, due to inadequate species descriptions, species without type material, intraspecific variability and differences in how its species attach to host fish (Martin et al. 2016).

Cymothoa are ectoparasites that cause deleterious effects in host fish, given that some of them induce atrophy of the host's tongue (Ravi & Rajkumar 2007, Parker & Booth 2013, Aneesh et al. 2015, Sukumaran et al. 2019). These ectoparasites infest teleost fish inhabiting diverse ecosystems and play an important role in their biology. They affect their hosts' behavior, growth and distribution through decreasing their growth and feeding efficiency, which subsequently affects the health condition and survival of the host fish (Ravi & Rajkumar 2007, Parker & Booth 2013, Bonilla-Gómez et al. 2014, Vigneshwaran et al. 2019, Sukumaran et al. 2019).

Cymothoa spp. have different attachment sites in their host fish (Rajkumar et al. 2005, Ravi & Rajkumar 2007, Parker & Booth 2013, Kumar et al. 2017, Alves et al. 2019). Skin lesions, hemorrhage, thickening of gill arch and filaments, reduction of gill surface area and diminished swimming capacity are among the effects exerted by these parasites (Rajkumar et al. 2005, Ravi & Rajkumar 2007, Vigneshwaran et al. 2019). These effects sometimes lead to the death of the host fish. Some species of *Cymothoa* can induce atrophy of the host's tongue (Brusca & Gulligan 1983, Williams Jr & Bunkley-Williams 1994). Furthermore, in addition to the direct effects of the parasite infestations, secondary infections by bacteria and fungi may arise at lesion sites (Rameshkumar et al. 2013a). These infestations can affect fish species that are commercially important within aquaculture and fisheries, thus leading to economic and foreign exchange losses (Sukumaran et al. 2019).

Cymothoa species display a vast spectrum of strategies for when and how they infest a host fish. They generally search for a host during either its juvenile or its mature adult stage (Cook & Munguia 2013). Some *Cymothoa* species exhibit high host-specificity while others can infest numerous species of host fish. Host species represent an inherently patchy and dynamic resource for these parasites (Parker & Booth 2013, Cook & Munguia 2013). In most species of *Cymothoa*, a single parasite infects the host fish (Cook & Munguia 2015), while the other species exhibit different patterns. In addition, these isopods can present strategies for locating their host fish. It has been reported that some species locate host fish through visual and chemical clues, and that individuals display a host-locating strategy that maximizes the encounter rate while reducing energy expenditure (Cook & Munguia 2013, 2015).

The life cycle of *Cymothoa* spp. is poorly known, but some information has been obtained. It has been reported that some species show a change of sex, from male to female (protandrous hermaphrodite), in relation to infesting their hosts (Cook & Munguia 2013, 2015). Aneesh et al. (2015) found three stages (marsupial, free-living and infective) for *Cymothoa frontalis* Milne Edward, 1840. Studies on ovigerous females have indicated that these parasites use host fish to reproduce (Yamauchi & Hoshino 2021). In addition, in general, *Cymothoa* species can be divided into two groups according to the size and shape of the amphicephalic processes of pereonite 1. In some species, these processes are moderately or strongly developed; whereas in others they are poorly developed or undeveloped (Trilles & Bariche 2006).

The fauna of *Cymothoa* spp. can be considered to be reasonably diverse, but it is still poorly known. *Cymothoa* spp. have been reported to be distributed in a few regions around the world (Trilles et al. 2011, Luque et al. 2013, Hadfield et al. 2013, Joca et al. 2015, Olivas et al. 2016, Martin et al. 2016, Ortiz & Lalana 2018, Aguilar-Perera et al. 2018). Nonetheless, despite the importance of *Cymothoa* spp. in association with fish, this has been relatively poorly studied or not surveyed at all, in many parts of the world. Thus, there is a growing global interest in the ecological value of *Cymothoa* spp. Moreover, the diversity of this genus is only now beginning to be understood.

In this light, the aim of the present study was to investigate the global geographic range, distribution patterns and parasite-host interactions of *Cymothoa* spp. associated with host fish. Studies on the distribution patterns of *Cymothoa* species are increasingly recognized as the key to mapping and improving knowledge of the dynamics of these ectoparasites in different aquatic ecosystems. Such knowledge may lead to more precise mapping of the zoogeographic patterns of these parasites in host fish in endemic regions and geographic hotspots. Through this, the numbers of species can be estimated and the understanding of infestation patterns can be improved, in relation to host fish with wide geographic distribution, in addition to determining the global geographic range limits of *Cymothoa* spp.

MATERIALS AND METHODS

A review on *Cymothoa* species in teleost fish was performed by searching the SciELO, ISI, Scopus, Clarivate, Science Direct, Zoological Records, CAB Abstracts, Lilacs, Capes periodicals and Google Scholar databases. The keywords used in search were "*Cymothoa* and fish", and only papers in English and Spanish were used. Data from 86 scientific papers were subsequently systematized and used. A dataset of *Cymothoa* species parasitizing host fish populations throughout the world was compiled, using the taxonomic descriptions of these species and surveys on the occurrences of these parasites published between 1976 and 2022.

The taxonomy for each *Cymothoa* species was obtained from WoRMS (2023). The taxonomy for each fish species was obtained from Froese & Pauly (2023), and the sampling unit was the number of individuals parasitized by a *Cymothoa* species at a certain location and time. Some of the information used in samples included data on more than one host species. The data were organized in a data frame (extension ".txt") with a list of the following variables: (i) parasite species, (ii) infestation site, (iii) prevalence, (iv) mean intensity and (v) mean abundance; along with categorical factors such as: (i) host fish species, (ii) location of sample collection and (iii) family and order of host fish species.

A map of the annual average earth temperature was generated (using data from Wordclim: https://www.worldclim.org/data/index.html) in order to plot the global geographic distribution of *Cymothoa* species, from geographic coordinates compiled from the articles in the database used for this review. For articles that did not report geographic coordinates, we plotted the reference location provided in the article. The plotting of the coordinates was done using the Google Earth software, and the database thus generated was exported to Quantum GIS (QGIS) for map composition. Parasites only identified at the genus level (*Cymothoa* spp.) were not included in the map.

Data analysis

The ecological terms (prevalence, mean abundance and mean intensity) used were those recommended by Bush et al. (1997).

To determine the parasite-host and parasite-country relationships at species level, a "bipartite" R software package was used to construct a bipartite network and to calculate indices at network level. This included calculating the C-score, number of compartments, species range and strength and species specificity index (SSI) (Dormann et al. 2008, 2009, Dormann 2011). The C-score index measures the rate of co-occurrence of species in the network and is an indicator of the degree of specificity of the species that form it, with values ranging from 0 (high co-occurrence) to 1 (low co-occurrence). The compartments are independent groups of ectoparasites and hosts within the network and are indicators of specificity patterns. The degree is the number of host families with which a parasite species interacts. The species specificity index (SSI) measures the specificity level of the parasite species and can range from 0 (low specificity) to 1 (high specificity). To determine the specificity levels within SSI variation from 0 to 1, we considered that the values were high when > 0.66, moderate when < 0.66 and > 0.33 or low when < 0.33. Lastly, the species strength is the sum of the proportions of participation of a species in all the interactions of the network. The volume of the bars and connection lines represents the proportion of the interactions with the host families and countries performed by each parasite species and between species, respectively. The reach is the number of species of fish and countries with which a parasite species interacts. Parasites that were only identified at genus level (*Cymothoa* spp.) were not included. These analyses were performed using the R software package (R Development Core Team 2017).

RESULTS

Our search resulted in a total of 144 samples of *Cymothoa* spp., of which six were from farmed fish and 140 were from wild fish. In total, 23 species of *Cymothoa* were found parasitizing 84 teleost fish species from 35 families and 20 orders. The species richness of *Cymothoa* spp. and families of host fish from different orders are shown in Table I, which indicates that the highest numbers of occurrences were in the families Carangidae and Lutjanidae (Figure 1).

Cymothoa pulchrum Lanchester, 1902, particularly infested species of Tetraodontiformes; *Cymothoa oestrum* Linnaeus, 1758, and *Cymothoa eremita* Brunnich, 1783, infested species of Carangiformes; *Cymothoa excisa* Perty, 1833, and *Cymothoa exigua* Schioedte & Meinert, 1884, infested species of Lutjanidae; while *Cymothoa indica* Schioedte & Meinert, 1884, and *Cymothoa spinipalpa* Thatcher, Araújo, Lima & Chellapa, 2007, infested fish of diverse orders and families (Figure 1).

In the interaction network between parasite species and host fish families, we found that there were low rates of co-occurrence of ectoparasites (C-score = 0.799). This indicated that the majority of the species did not share the same host families and, thus, they presented specificity for host families (Figure 1). Overall, 71.43% of the parasite species presented high specificity for host families, while 23.81% showed moderate and 4.76% low specificity. The species with the highest numbers of host families registered were *C. indica* (10), *C. exigua* (9) and *C. excisa* (6) (Figure 1 and Table II).

In the interaction network correlating parasite species with countries, the rate of parasite co-occurrence was low at network level (C-score = 0.780). This indicated that the majority of *Cymothoa* species presented geographic distribution restricted to one country or continent (Figure 2). Overall, 80.95% of the parasite species had high specificity for their geographic region and 19.05% had moderate specificity, thus indicating that their geographic distribution was very restricted. The species with the largest numbers of countries registered were *C. exigua* (8), *C. excisa* (7) and *C. indica* (6) (Figure 2 and Table III).

The infestation sites for *Cymothoa* species were in external organs because these are usually ectoparasites; however, the parasites were predominantly found in the mouth cavity of the host fish, followed by the gills (Figure 3).

The prevalence (N = 62) of *Cymothoa* species varied from low to high, while the intensity (N = 24) and abundance (N = 14) were low (Figure 4).

Regarding distribution across continents, eight species of *Cymothoa* have been reported in Africa, eight species in Asia, four species in Oceania, two species in North America, two species in Central America and six species in

Table I. Number of *Cymothoa* species according to taxonomic groups in 84 fish species.

Host order	Host family	Host species number	Parasite species number
Acanthuriformes	Siganidae	1	1
	Scatophagidae	1	1
	Ephippidae	1	1
Aulopiformes	Aulopidae	1	1
Beloniformes	Belonidae	2	2
Carangiformes	Carangidae	13	9
Carangaria	Latidae	1	1
	Sphyraenidae	3	2
	Centropomidae	1	1
Cichliformes	Cichlidae	3	4
Cyprinodontiformes	Anablepidae	1	1
Elopiformes	Elopidae	1	1
Eupercaria	Scaridae	2	2
	Sciaenidae	8	3
	Sillaginidae	1	1
	Haemulidae	4	4
	Nemipteridae	1	1
	Lutjanidae	10	5
	Sparidae	4	4
	Gerreidae	3	2
Gobiiformes	Gobiidae	3	2
Holocentriformes	Holocentridae	1	1
Lampriformes	Veliferidae	1	1
Mugiliformes	Mugilidae	5	3
Mulliformes	Mullidae	1	1
Perciformes	Serranidae	2	2
Pleuronectiformes	Psettodidae	1	1
Scorpaeniformes	Scorpaenidae	1	1
Siluriformes	Ariidae	1	1
	Bagridae	1	1
Syngnathiformes	Fistulariidae	1	1
Tetraodontiformes	Tetraodontidae	1	1
	Diodontidae	5	1

South America. *Cymothoa excisa* has distribution in Africa (Algeria), South America (Brazil, Colombia and Venezuela) and North America (Mexico, USA and Panama). *Cymothoa exigua* has distribution in South America (Colombia and Peru), North America (Mexico, Costa Rica and Honduras) and Africa (Egypt, Nigeria, Sudan and Yemen). *Cymothoa indica* has distribution in Oceania (Australia), Africa (Egypt) and Asia (China, India, Lebanon and Yemen). Overall, *Cymothoa* species have wide geographic distribution but notable concentration in the equatorial zone, in regions with the highest temperatures (Figure 5).

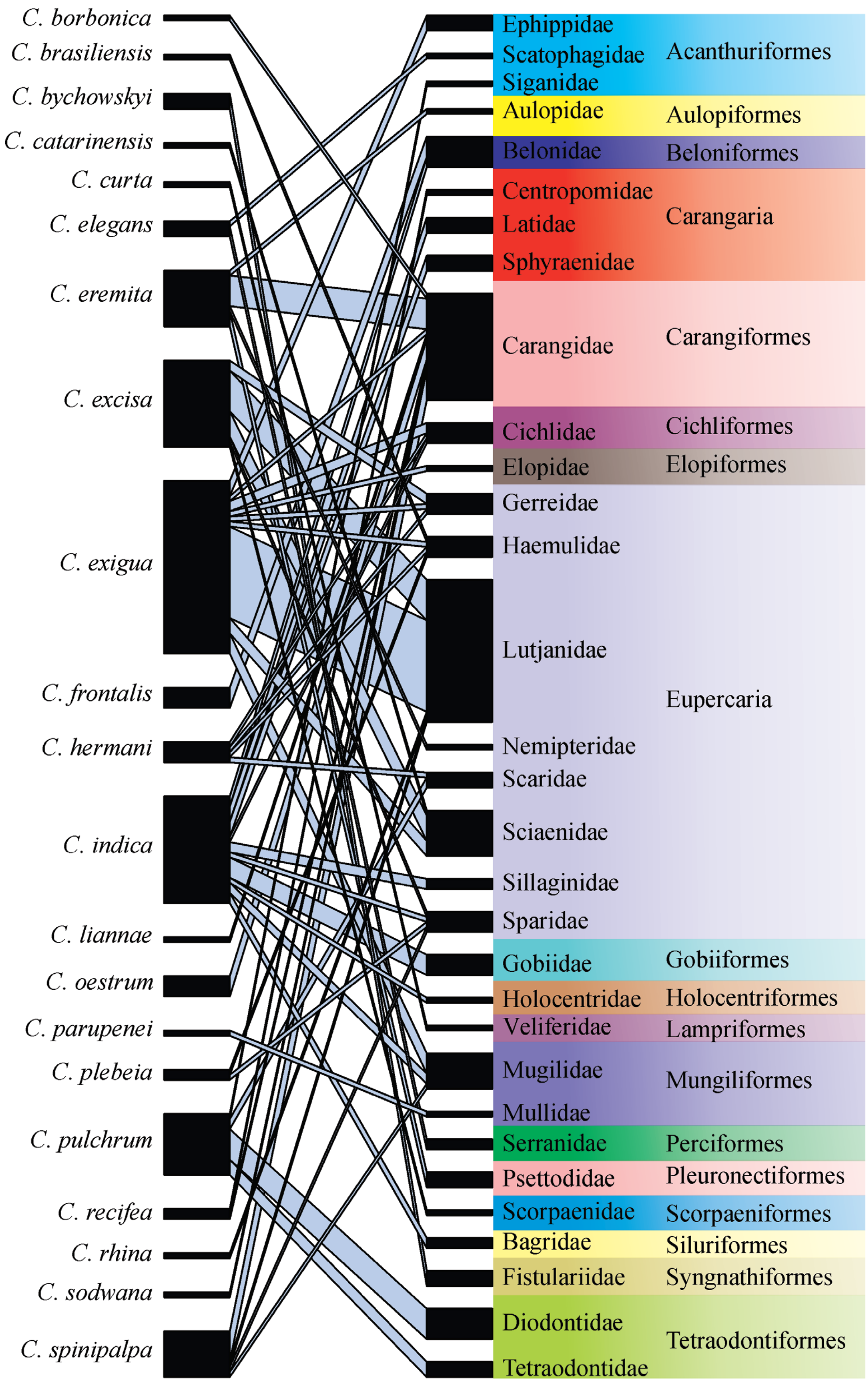

Figure 1. Network of interactions between species of *Cymothoa* and families of host fish.

Table II. **Specificity indices for evaluating the relationships between Cymothoa species and fish families around the world.**

Cymothoa	Degree	Normalized degree	Species strength	Species specificity index (SSI)	Level of specificity	Proportional generality
C. borbonica	1	0.032	0.048	1.000	High	0.055
C. brasiliensis	1	0.032	0.250	1.000	High	0.055
C. bychowskyi	1	0.032	1.000	1.000	High	0.055
C. catarinensis	1	0.032	0.111	1.000	High	0.055
C. curta	1	0.032	1.000	1.000	High	0.055
C. elegans	2	0.065	2.000	0.735	High	0.104
C. eremita	4	0.129	3.286	0.607	Moderate	0.168
C. excisa	5	0.161	2.591	0.553	Moderate	0.201
C. exigua	9	0.290	4.595	0.542	Moderate	0.271
C. frontalis	1	0.032	0.667	1.000	High	0.055
C. hermani	4	0.129	1.083	0.474	Moderate	0.219
C. indica	10	0.323	7.119	0.301	Low	0.496
C. liannae	1	0.032	0.048	1.000	High	0.055
C. oestrum	1	0.032	0.190	1.000	High	0.055
C. parupenei	1	0.032	1.000	1.000	High	0.055
C. plebeia	2	0.065	0.500	0.695	High	0.110
C. pulchrum	4	0.129	3.667	0.570	Moderate	0.182
C. recifea	2	0.065	1.048	0.695	High	0.110
C. rhina	1	0.032	0.036	1.000	High	0.055
C. sodwana	1	0.032	0.048	1.000	High	0.055
C. spinipalpa	4	0.129	0.714	0.681	High	0.149

DISCUSSION

Distribution pattern of host-parasite interactions of *Cymothoa* species

Diseases caused by *Cymothoa* species are an important issue throughout the world, especially in areas where fishing is better developed and more frequent, because they can cause losses of fish stocks (Carvalho-Souza et al. 2009) and/or have detrimental effects on the quality of the fish caught. Weight loss reduces the volume of the catch without reducing the number of fish caught. Poor-quality fish are less acceptable to customers, thus resulting in economic losses and reduced fish landings (Rajkumar et al. 2005). Hence, *Cymothoa* spp. are potentially economically important parasites in relation to fishing and aquaculture. Among the valid *Cymothoa* species, we found that 23 of them were associated with host fish species around the world.

We detected the following patterns within *Cymothoa*-host interactions: (a) prevalence ranging from low to high (89.6-0.3%), with low abundance (0.001-1.3) and intensity (1.0-2.5); (b) association with other Ectoparasite infracommunities on the gills; (c) low occurrence in farmed fish; (d) occasional presentation of aggregated dispersion; and (e) the mouth was the commonest attachment site for parasites, followed by the gills. Thus, these parasitic isopods

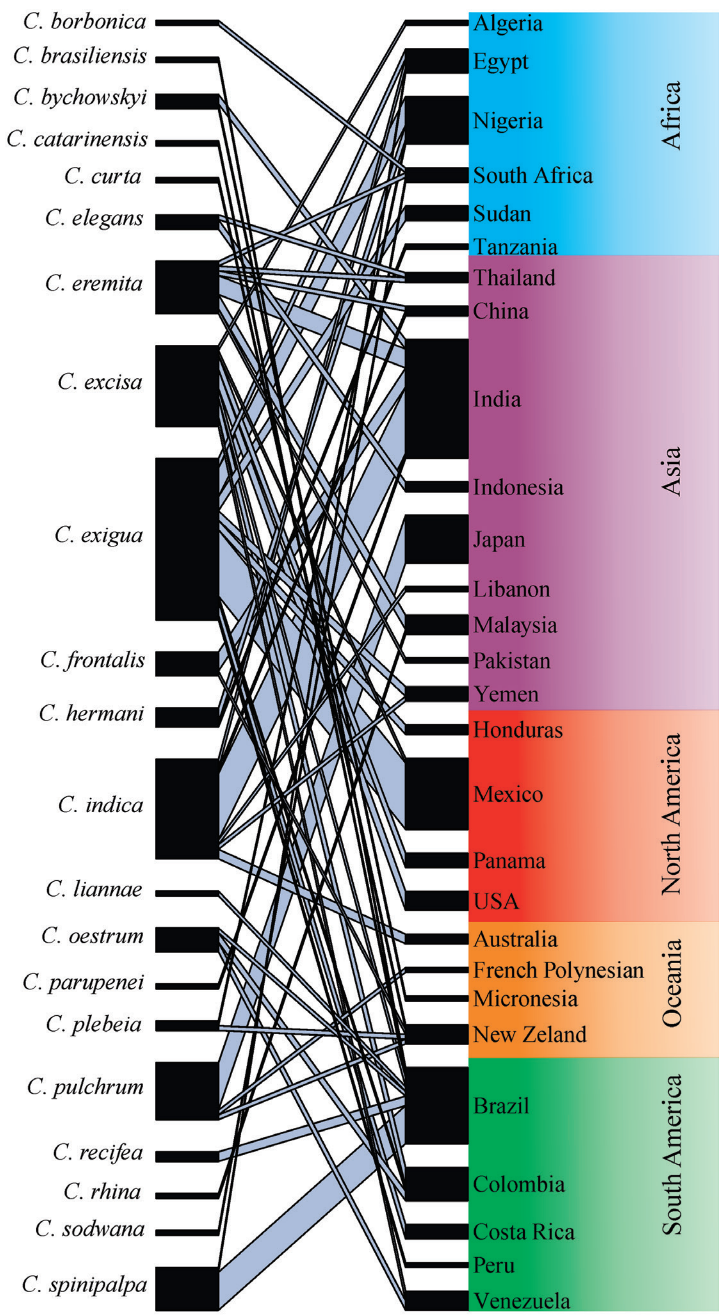

Figure 2. Network of interactions between species of *Cymothoa* and countries and continents.

have habitat specificity in the host fish. This present analysis on *Cymothoa*-host interactions provides important data for evaluating local adaptations of these parasites, which have relatively heterogeneous distribution in their hosts and infestation rates that vary among wild fish populations.

How the parasitic mode of life of *Cymothoa* species has developed and how attachment site specificity in host populations is maintained are fundamental questions for fish parasitology. These parasites have become specialized to many different host species and show a certain degree of specificity of attachment, along with feeding specializations. A number

Table III. **Specificity indices for assessing the relationship between Cymothoa species and the countries of the world, with the aim of understanding biogeographic aspects of this group of ectoparasites in fish.**

Cymothoa	Degree	Normalized degree	Species strength	Species specificity index (SSI)	Level of specificity	Proportional generality
C. borbonica	1	0.032	0.333	1.000	High	0.057
C. brasiliensis	1	0.032	0.063	1.000	High	0.057
C. bychowskyi	2	0.032	1.080	0.734	High	0.108
C. catarinensis	1	0.032	0.063	1.000	High	0.057
C. curta	1	0.032	0.250	1.000	High	0.057
C. elegans	2	0.065	1.500	0.734	High	0.108
C. eremita	6	0.129	3.243	0.460	Moderate	0.281
C. excisa	7	0.161	4.263	0.382	Moderate	0.354
C. exigua	9	0.290	6.743	0.447	Moderate	0.348
C. frontalis	2	0.032	0.410	0.817	High	0.094
C. hermani	2	0.129	1.300	0.782	High	0.100
C. indica	6	0.323	3.793	0.671	High	0.181
C. liannae	1	0.032	0.063	1.000	High	0.057
C. oestrum	3	0.032	0.848	0.580	Moderate	0.164
C. parupenei	1	0.032	0.040	1.000	High	0.057
C. plebeia	2	0.065	0.350	0.694	High	0.114
C. pulchrum	3	0.129	2.250	0.835	High	0.101
C. recifea	1	0.065	0.125	1.000	High	0.057
C. rhina	1	0.032	0.250	1.000	High	0.057
C. sodwana	1	0.032	0.333	1.000	High	0.057
C. spinipalpa	2	0.129	0.700	0.892	High	0.081

of adaptations to obligate parasitic existence occur in cymothoid species, such as their body shape, which is influenced by the attachment site on the host fish. Most *Cymothoa* species are highly specific regarding their attachment sites in their host fish (Rajkumar et al. 2005, Ravi & Rajkumar 2007, Parker & Booth 2013, Hata et al. 2017, Ravichandran et al. 2019, Alves et al. 2019). We found that Cymothoa species primarily infest the mouth of their hosts, but also infest the gills and, occasionally, the skin. They may also burrow into the musculature of their host fish (Rajkumar et al. 2005, Ravi & Rajkumar 2007, Parker & Booth 2013, Alves et al. 2019, Ravichandran et al. 2019). Thus, isopods of the genus *Cymothoa* can exploit different attachment sites in their host fish and can consume different foods from them; however, some particularities occur and need be addressed.

Cymothoa borbonica Schioedte & Meinert 1884 almost always occurs in male-female pairs in the buccal cavity of *Trachinotus botla* Shaw, 1803 (Parker & Booth 2013), as also does *C. eremita* in *Parastromateus niger* Bloch, 1795. Females of *C. exigua* were found located in the mouth cavity of *Lutjanus peru* Nichols & Murphy, 1922, while males occurred mostly in the pharyngeal cavity of these hosts (Violante-González et

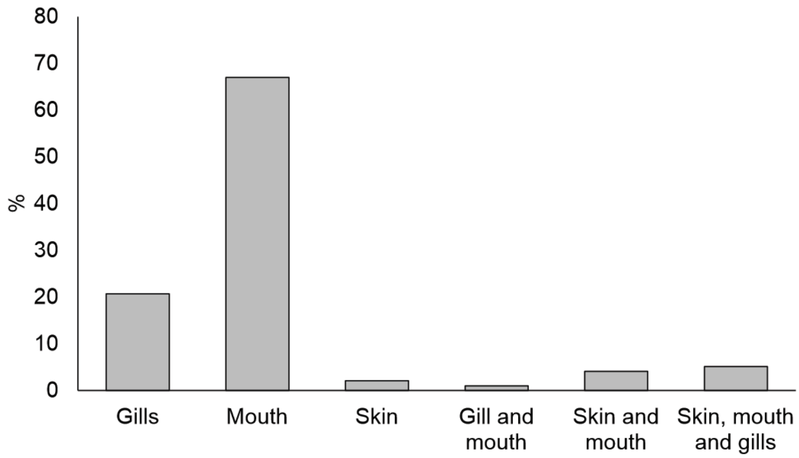

Figure 3. Infestation sites used by *Cymothoa* spp. in 97 teleost fish species.

al. 2014). In an experimental study on *Caranx hippos* Linnaeus, 1766, exposed to *C. oestrum*, it was reported that all the fish became infested and that this isopod became attached to the top of the tongue of these hosts (Williams Jr & Bunkley-Williams 1994). Brusca & Gulligan (1983) hypothesized that *C. exigua* served as a mechanical replacement for the tongue of *Lutjanus guttatus* Steindachner, 1869, when infested by this parasite. Hence, *Cymothoa* spp. that attach in the buccal cavity of their host fish are commonly referred to as tongue-replacement or tongue-biter isopods, given that the large female of the species is almost always found attached to the host's tongue (Hadfield et al. 2011, Parker & Booth 2013). The ancestral attachment mode of these parasites is most likely to have been opercular cavity-dwelling. The ability to live in the buccal cavity and on the body surface of the host fish evolved subsequently (Hata et al. 2017). If the parasite is unable to cope with the mastication associated with consumption of hard prey, it may become detached from the hosts' basihyal. Whatever the reason, these parasites have evolved to exploit the period before this ontogenetic dietary shift. This host-parasite relationship has the characteristics of an adaptive co-evolutionary strategy that enables the host to maintain its feeding ability while it grows to sexual maturity and then reproduces (Parker & Booth 2013). Since isopods of the genus *Cymothoa* have specificity of attachment sites in their host fish, some species have mouth appendages that are strongly modified to enable their parasitic habit. Their exhibited preference for the environments of the buccal cavity and gills may be due to the facts that the operculum acts as a protection and the gills have higher oxygen levels and blood irrigation. This specificity seems be caused by the combination of two factors: uniformity of diet (blood or epithelium) and morphological adaptation to the particular kind of epithelium (Rameshkumar et al. 2013b, Jithin et al. 2016).

The distribution of *Cymothoa* spp. is usually closely related to the occurrence and ecology of their host fish. The vigor of *Cymothoa* species seems be strongly driven by their ability to infest potential hosts. Infestation is a key component of their parasitic lifestyle and survival. In wild fish populations, the possible parasitic effects of *Cymothoa* species are difficult to assess or quantify, and it remains to be explained why some fish species have higher species richness of these parasites than others, and how these parasite communities build upon these hosts. In the present study, the prevalence of *Cymothoa* spp. in host fish in diverse localities varied from

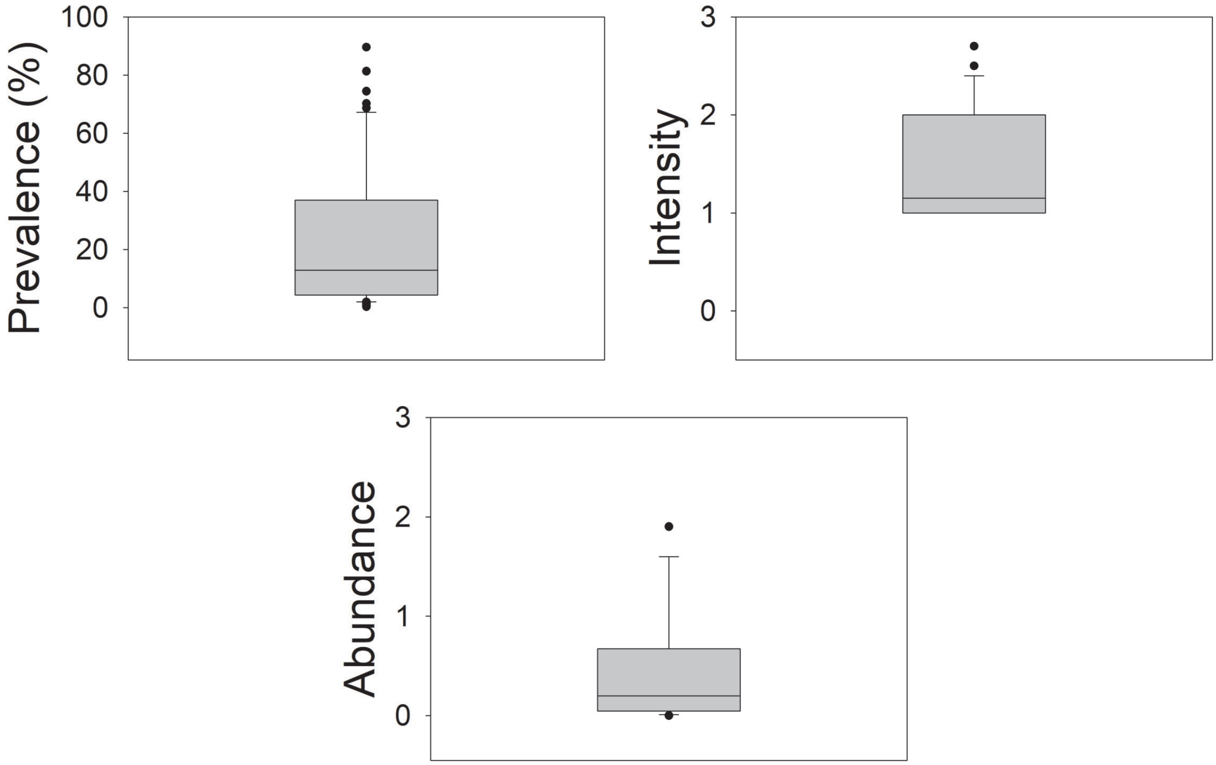

Figure 4. Quantitative descriptors of infestation for *Cymothoa* species in samples of teleost fish (Box plots represent medians, percentile ranges (25-75%), minimum-maximum and outlier values).

low to high, while the mean intensity and mean abundance were low, as expected, because these parasites usually occur in male-female pairs. This high level of prevalence suggests that fish may, under certain conditions, be appropriate hosts for *Cymothoa* species. The parasitic infestation rates in host fish depend on several factors such as the age, sex, size, behavior, breeding stage and life cycle of the host fish species (Kumar et al. 2017), as well as on environment factors, etc. *Cymothoa indica* was found to infest males of *Myripristis murdjan* Forsskål, 1775, much more than females of this host fish species (El-Shahawy & Desouky 2010). It has been suggested that the strong relationship between the growth of *P. niger* and *C. eremita* is synchronized, and that infestation by small parasites only occurs when the hosts are young (Vigneshwaran et al. 2019). The prevalence of *C. borbonica* in *T. botla* was found to be high and decreased with increasing host size (or age), likely due to the death of the parasites and not the death of infested fish as a consequence of parasite infestation. *Cymothoa* spp. typically have a short life cycle (Parker & Booth 2013). Nevertheless, the abovementioned factors remain poorly studied or even completely unknown for most *Cymothoa* species.

Cymothoa excisa is a large parasite whose adult females reside in the buccal cavity of the host fish. Its juveniles are born male and, when released by the mother, exit the buccal cavity and remain free-swimming until a new host is found. If a manca finds a host, it will settle on the tongue if no other parasite is present. When another parasite is found in the host, then the manca will settle just behind the tongue, at the base of the gills (Cook & Munguia 2013).

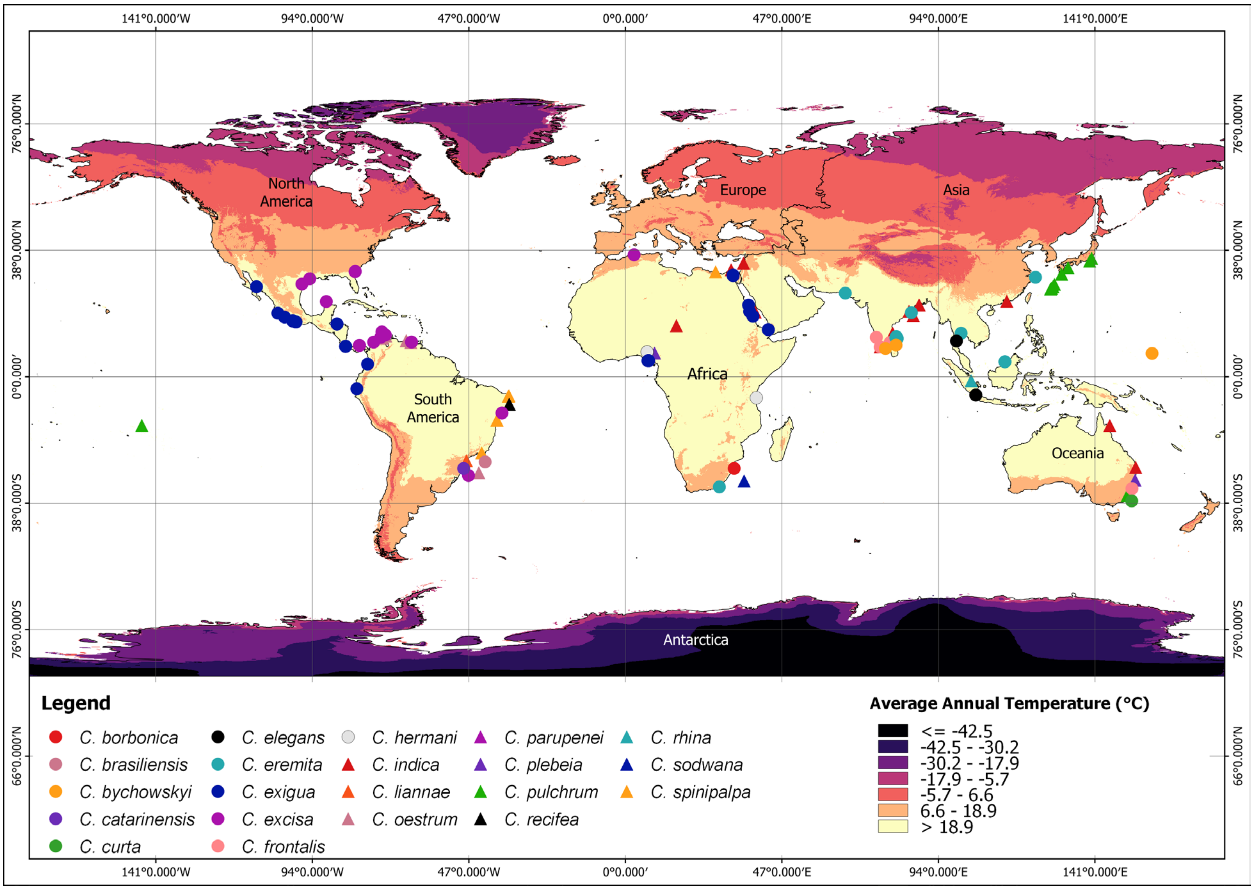

Figure 5. Geographical distribution of *Cymothoa* species on the continents of terrestrial globe.

Therefore, one constraint imposed by host body size on the evolution of these parasitic isopods is that there needs to be space available in the host for them to occupy.

Aquaculture systems provide a place in which several stages of hosts and large samples of both parasitized and unparasitized hosts are readily available. Studies on *Cymothoa* spp. within aquaculture are therefore important not only for this system for development of production, but also for gaining knowledge about the interactions between these parasites and their host fish. However, few studies have focused on such interactions between these parasites and farmed fish (Rajkumar et al. 2005). *Cymothoa indica* was reported infecting larvae of *Lates calcarifer* Bloch, 1790, under laboratory conditions, which had occurred through transfer to this host from wild zooplankton that was used as food (Rajkumar et al. 2005). In addition, Sukumaran et al. (2019) reported infestations of *C. indica* in *L. calcarifer* farmed in net cages. *Cymothoa elegans* Bovallius, 1885, was found infesting *Epinephelus fuscoguttatus* Forsskål, 1775, farmed in net cages (Rückert et al. 2010). Thus, *Cymothoa* spp. and their hosts in cultivation environments, their biological impacts on their hosts and the subsequent ecological consequences have been little addressed. The management practices and control of diseases caused by these parasitic isopods in farmed fish have also been little discussed.

Global geographic distribution of *Cymothoa* species

According to Martin et al. (2016), Schioedte & Meinert (1881-1884) carried out the first global review on the genus *Cymothoa*, with inclusion of 17 species. Even though these isopods were first mentioned in these earliest natural history references, there are many parts of the world where this genus is still incompletely known or even completely unknown. After almost 140 years of studies, the number of *Cymothoa* species has grown, as would be expected, such that currently there are 46 accepted species (WoRMS 2023).

Establishment of global geographic distribution patterns for *Cymothoa* species was one of the main goals of this study. Despite the diversity of fish fauna worldwide, there is little knowledge about the geographic distribution of *Cymothoa* spp. The occurrence of six *Cymothoa* species in fish in the southwestern Indian Ocean was reported by Hadfield et al. (2013). Trilles et al. (2011) listed *Cymothoa asymmetrica* Pillai, 1954, *Cymothoa cinerea* Bal & Joshi 1959, *Cymothoa eremita* Brünnich, 1783, and *C. indica* infesting fish in India. Among fish species along the coast of Brazil, Luque et al. (2013) listed nine species of *Cymothoa*. Infestation by *C. excisa* (Joca et al. 2015) and *C. exigua* (Olivas et al., 2016) in fish in the Americas was reported by Joca et al. (2015) and Olivas et al. (2016), and *C. excisa*, *C. exigua* and *C. oestrum* were reported from fish in Cuba (Ortiz & Lalana 2018). Aguilar-Perera et al. (2018) reported that *C. excisa* infested 16 species of fish in the Caribbean Sea. In addition, we also found that *C. excisa* infested another 12 species of host fish, while *C. exigua* occurred in 18 fish species. Thus, both of these parasite species present low specificity for hosts.

Parasite specificity was seen to be an important factor in the geographic distribution of *Cymothoa* spp., since this distribution reflected the geographic region for most of these species. At the scale of geographic region, parasite diversity was shown to be strongly linked to the number of potential host species, which in turn was associated with the size of the region, such that larger geographic regions supported greater numbers of both host and parasite species (Paterson et al. 2021). Moreover, the validity of some species has been considered questionable, considering that details of their morphology remain poorly known. Hence, in order to better understand the distribution patterns of *Cymothoa* spp. according to biogeographic realm, these distribution patterns need to be clearly visible on maps displaying locality records of highest diversity (Figure 5). However, for most *Cymothoa* species, the host records collected from a number of different localities clearly do not allow any conclusion to be reached regarding host specificity.

It is difficult to discuss host specificity when only a few host fish records are available. Such situations might indicate a lack of sampling rather than the real host specificity. However, host specificity is the product of co-existence between both the parasite and the host lineage (Rameshkumar et al. 2013c). Hence, *Cymothoa* species with broad specificity are characterized by distribution over potentially wider ranges than those of species of narrow specificity, consequent to the diversity of factors involved.

Through the various studies on *Cymothoa* spp. over the past two decades, species identity concepts within this taxon and knowledge of the distribution patterns of these species have changed. Our study showed that *C. exigua*, *C. excisa* and C. *indica* have the largest geographic distribution, while most other *Cymothoa* species were seen to occur in exclusive geographic ranges. Recently, Al-Kandari et al. (2022) questioned the study carried out previously by Bowman & Tareen (1983), who reported the occurrence of *C.*

eremita in Kuwait, given that the type locality for this species is India. Nevertheless, we found that in addition to infesting fish in India, *C. eremita* has been also reported infesting fish species in South Africa, China, Malaysia, Thailand and Pakistan, thus indicating that this species has wide geographic distribution in Africa and Asia.

Interestingly, geographic distribution of *Cymothoa* was higher in fish populations in the equatorial zone, which was related to mean annual temperatures. We speculate that in this parasite-host system the relationship between latitudes and parasites is most likely due to variation in *Cymothoa* life history over their geographic range. In parasite-host system of cricetid rodents, helminth species followed a traditional latitudinal diversity gradient (LDG), with increasing species richness of parasites with decreasing latitude. Nematode richness appeared to drive this pattern, as cestodes and trematodes exhibited a reverse LDG and no latitudinal pattern, respectively. Overall helminth richness and nematode richness were higher in areas with higher mean annual temperatures. Cestodes richness was higher in areas of lower mean annual temperatures, annual precipitation and annual precipitation ranges and higher annual temperature ranges, while trematode richness showed no relationship with climate variables when phylogenetic comparative methods were used (Preisser 2019).

CONCLUSIONS

Globally, a large proportion of what is currently known about *Cymothoa* spp. in association with host fish is based on sampling and screening of commercial fish species. Therefore, to truly understand the diversity and host preference of *Cymothoa* species, further research should not only focus on under-sampled regions but also include smaller size classes of these fish, along with non-commercial host species. In the future, it will also be necessary to report the exact localities from which *Cymothoa* species are collected. For the global fauna of *Cymothoa* spp. in fish to become adequately known, sampling of sufficient localities in all countries on all continents is still required. There continues to be a lack of data, given that only a few studies have been conducted in some few zoogeographic regions, while others have not been investigated at all.

The capacity to identify parasite taxa is especially important for resolving questions regarding biological diversity around world. However, the opportunities to formally train in parasite taxonomy are diminishing in many regions.

Furthermore, identification of *Cymothoa* isopods is complicated, given the changes in morphology that occur during their development. Although knowledge of the hosts of *Cymothoa* has increased significantly over the past two decades, there are still some records that need validation, specifically those that involved misidentification of these isopods.

Considerable variation in the effects of *Cymothoa* species on their host fish can be observed. However, the pathogenicity of these parasites and the pressure exerted by their bodies, which affects the host's tissue and physiology, has been poorly studied or remains completely unknown. *Cymothoa* infestation in the buccal cavity can impair the host's growth and decrease its feeding efficiency, which subsequently affects the host's state of health and survival.

Since little information is available regarding these parasite-host interactions and the distribution of these parasites in their host fish, further studies should be carried out to improve knowledge of *Cymothoa* spp. To better understand the biodiversity, distribution and hosts of *Cymothoa* spp., more information on the ecology, behavior and life cycle of these enigmatic parasites is needed. Specifically, information on how these parasites detect their hosts, become attached to them and feed on them is required. In general, these cymothoid parasites are found to be protandrous hermaphrodites or males at the time of pre-sampling; however, they may become dislodged during the process of catching or handling the hosts.

Lastly, the aim of the present study was to summarize the currently known information on the genus *Cymothoa* for the purposes of future research, with updates and comments on some of the trends observed among these isopods, while noting points of caution to consider when working on these ectoparasites.

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