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# Global distribution patterns of *Caligus* Müller, 1785 (Copepoda: Caligidae) associated to teleost fishes, with physiological and histopathological data and description of treatment strategies

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**Abstract:** This review surveyed information on *Caligus* Müller, 1785 to identify global infestation patterns and geographic distribution in teleost fishes, as well as physiological and histopathological data and description of treatment strategies. A total 990 samples of *Caligus* spp. (N = 212 species) obtained of 233 scientific papers on farmed and wild teleost species from 99 families and 30 orders were used, and the highest number of occurrences was on Carangidae. *Caligus* spp. was predominantly found in marine environments, and only *Caligus lacustris* and *Caligus epidemicus* were found in teleost fish of freshwater environments. There was a high prevalence of *Caligus* spp. on hosts and infestation occurred predominantly in both the tegument and the gills. *Caligus* species are distributed across different countries and some particularities were identified and discussed. *Caligus elongatus* and *Caligus bonito bonito* had the broadest geographic distribution. Histomorphological and hematological disorders caused by infestation by *Caligus* spp. were reported and discussed, as well as chemotherapeutic products used for controlling and treating the infestations. Variation in the distribution and geographic patterns of *Caligus* spp. were little evident in many ecosystems and due to the limited data on the infestation of these sea lice on teleost populations in different regions.

**Key words:** *Caligus*, culture, crustacean, ectoparasites, infestation.

## INTRODUCTION

Caligidae Burmeister, 1835 are parasitic copepods that are distributed around the world. This family comprises 31 valid genera and more than 500 species (Öktener et al. 2016, Ho et al. 2016, Oliveira et al. 2020, Hemmingsen et al. 2020, Hamdi et al. 2021a), which predominantly utilize marine and brackish fish as their hosts. In marine and brackish water fish, members of the Caligidae family caused 61.0% of infestations (Hemmingsen et al. 2020). Members of this family occupy a privileged place in the world of parasitism because of their extraordinary adaptive capacity, and are predominantly external parasites, mainly of fishes (Oliveira et al. 2020).

The genus *Caligus* Müller, 1785 are sea lice primarily marine, but a few smaller taxa routinely inhabit brackish or fresh water. *Caligus* is most speciose genus of this family, and currently comprises 268 species (Hamdi et al. 2021a, WoRMS 2022). These are copepods, and cause caligidosis in a variety of farmed fish species (Arriagada et al. 2019), as well as infecting economically important wild fish. Morales-Serna et al. (2016) listed 58 species of *Caligus* infesting fish in the Neotropical region.

*Caligus* spp. are globally distributed ectoparasites, and have been considered harmful pathogens for marine fisheries, with major economic consequences in the marine aquaculture industry (Hamre et al. 2011, Araya et al. 2012). Infestations by *Caligus* spp. can cause the mortality in wild fish populations (Chatterji et al. 1982, Hayward et al. 2008, 2009, Abdelkalek et al. 2021) and also result in economic losses due to mortality, reduced growth rate and poor feed conversion ratio among farmed fish populations (Rojas et al. 2018, Arriagada et al. 2019), leading to the use of chemical products to control and treat infestations in the hosts (Bravo et al. 2010, Hamre et al. 2011, Agusti et al. 2016, Arriagada & Marín 2018, Arriagada et al. 2019, 2020).

*Caligus* spp. feed on the mucus and blood of their host fish and can cause damages to the tegument, increasing the risk of secondary infections, leading to a deterioration in the physical conditions of the host fish population (Bruno & Stone 1990, González et al. 2020). Consequently, it causes the loss of millions of US dollars per year to global aquaculture, making the control of these sea lice economically important and a priority for fish farms (Costello 2009, Araya et al. 2012, Dresdner et al. 2019). *Caligus* spp. can be vectors and act in the horizontal transmission of the infectious salmon anemia virus among fish (Oelckers et al. 2015, Elgendy et al. 2015, Brookson et al. 2020). Infestations by these ectoparasites can influence the fish recruitment and population growth through direct mortality and potentially through parasite-mediated sublethal effects on host behavior, growth, predation risk, and reproductive success (Brookson et al. 2020).

Some species of *Caligus* are generalist parasites, infecting multiple host fish species in the environment, although this issue still needs to be investigated further. These parasitic crustaceans can also be found in plankton from different aquatic ecosystems (Byrne et al. 2018, Kim et al. 2019, Ohtsuka & Boxshall 2019, Ohtsuka et al. 2020). The life cycle of *Caligus* species has recently been clarified. In general, it undergoes two free-swimming naupliar stages, one infective copepodid stage, four sessile chalimi stages and a reproductive adult stage. However, *Caligus epidemicus* Hewitt, 1971 have 10 stages of development: two nauplii, one copepodid, six chalimus, and one young adult (Lin et al. 1996). In addition, these phases can vary seasonally (Byrne et al. 2018, Khoa et al. 2019a). Females of these sea lice can produce a varied number of eggs in each egg string pair, depending on species. Once the eggs hatch, a free-swimming larval phase commences that is shared among sea lice and generally consists of two naupliar stages, followed by one infective copepodid stage. The development of sea lice through the various life stages is temperature and salinity-dependent for copepodids, if they are to be capable of successful host infestation (González & Carvajal 2003, Byrne et al. 2018). However, since much information on *Caligus* spp. is dispersed and requires further discussion, the aim of this review was to gather information from published research that focuses on the association between *Caligus* species and teleost fish the around world. Focus was also given to potential harm to fish physiological and histopathological data, and description of treatment strategies.

## MATERIALS AND METHODS

A review on the *Caligus* species in teleost fish was performed by searching the SciELO, ISI, Scopus, Science Direct, Zoological Records, CAB Abstracts, Lilacs, Capes periodicals and Google Scholar databases. Data from 233 scientific papers were subsequently systematized and used. Terms used in searching were *Caligus* and fish, and all articles on the *Caligus* associated to fishes were used. A dataset of *Caligus* species parasitizing fish populations was compiled, using the taxonomic descriptions of species, and surveys on the occurrences of these parasites published between 1898 and 2021. These data comprise surveys on *Caligus* species parasitizing wild and farmed teleost fish distributed throughout the world.

The taxonomy for *Caligus* species was obtained from WoRMS (2022). The taxonomy for each host fish species was obtained from Froese & Pauly (2022), and the sampling unit was the number of individuals parasitized by a *Caligus* 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) mean prevalence and (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. In addition, physiological and histopathological data and a description of treatment strategies were also evaluated here (https://github.com/DrTavares/Supplementary-material).

Geographic distribution maps of *Caligus* species were made using information from the collection sites of the parasites contained in the compiled works. Two maps were made, one taking into account all the parasite species to show locations of occurrence, and one using only species that occur in five or more countries, in order to make the map more readable when superimposing information on it. Coordinates were plotted using Google Earth software and the generated database was exported to Quantum Gis (QGIS) to produce the maps.

### Data analysis

The ecological terms (prevalence, intensity and abundance) used were those recommended by Rohde et al. (1995) and Bush et al. (1997). The prevalence, abundance and intensity data of the parasites were tested for normal distribution and homoscedasticity of variances. As the parameters did not present normal distribution, the Kruskal-Wallis test was used (Zar 2010).

To determine the *Caligus*-host relationships at species level, a bipartite package (Dormann et al. 2008) was used to construct a bipartite network, in addition to calculating network-level indices (Dormann et al. 2009), such as the c-score, number of compartments and specificity index of the species (SSI) (Dormann 2011). The c-score index measures the co-occurrence rate of species in the network and is an indicator of the degree of specificity of the species that compose it, with values ranging from 0 (high co-occurrence) to 1 (low co-occurrence). Compartments are independent groups of ectoparasites and hosts within the network and are indicators of patterns of specificity. The SSI measures the level of species specificity of parasites, ranging from 0 (low specificity) to 1 (high specificity). Range is the number of fish species with which a species of ectoparasites interacts. Finally, the strength of species is the sum of the participation proportions of a species in all interactions within the network. The volume of connecting bars and lines represents the proportion of interactions performed by each species, and between species, respectively. These analyses were performed using the R software package (R Development Core Team 2017).

## RESULTS

Our search resulted in a total of 990 samples of *Caligus* spp., of which 186 were from farmed fishes and 804 were from wild fishes. In total, 212 species of *Caligus* were found parasitizing 368 teleost fish species, from 99 families and 30 orders. A total of 42 of these species were found in farmed fish and 171 in wild fish. The species richness of *Caligus* spp. and families from host fishes are shown in Table I, which shows higher numbers of occurrences on Carangidae (Figure 1).

**Table I.** Richness of *Caligus* species by taxonomic groups in 368 teleost species.

| Host order | Host family | Host species number | Parasite species richness |
|---|---|---|---|
| Acanthuriformes | Acanthuridae | 4 | 5 |
| | Chaetodontidae | 1 | 1 |
| | Drepaneidae | 1 | 1 |
| | Ephippidae | 2 | 4 |
| | Leiognathidae | 1 | 1 |
| | Lobotidae | 2 | 4 |
| | Pomacanthidae | 3 | 3 |
| | Scatophagidae | 2 | 4 |
| | Siganidae | 3 | 5 |
| Acropomatiformes | Lateolabracidae | 1 | 1 |
| Albuliformes | Albulidae | 1 | 1 |
| Atheriniformes | Atherinopsidae | 2 | 5 |
| | Atherinidae | 1 | 1 |
| Aulopiformes | Synodontidae | 2 | 2 |
| Beloniformes | Belonidae | 6 | 9 |
| | Hemiramphidae | 2 | 2 |
| Blenniiformes | Blenniidae | 3 | 2 |
| | Clinidae | 2 | 1 |
| | Tripterygiidae | 1 | 1 |
| Carangiformes | Carangidae | 35 | 35 |
| | Centropomidae | 4 | 5 |
| | Coryphaenidae | 3 | 7 |
| | Echeneidae | 1 | 1 |
| | Latidae | 2 | 9 |
| | Nematistiidae | 1 | 1 |
| | Polynemidae | 3 | 3 |
| | Sphyraenidae | 4 | 6 |
| Centrarchiformes | Girellidae | 1 | 2 |
| | Kyphosidae | 4 | 6 |
| | Scorpididae | 1 | 1 |
| | Terapontidae | 1 | 2 |
| Cichliformes | Cichlidae | 3 | 5 |
| Clupeiformes | Chirocentridae | 1 | 1 |
| | Clupeidae | 3 | 3 |
| | Engraulidae | 2 | 2 |
| Cypriniformes | Leuciscidae | 1 | 1 |
| | Cyprinidae | 1 | 1 |
| Dactylopteriformes | Dactylopteridae | 1 | 1 |
| Gadiformes | Gadidae | 8 | 4 |
| | Merlucciidae | 2 | 3 |
| Gobiesociformes | Gobiesocidae | 1 | 1 |
| Gobiiformes | Gobiidae | 4 | 1 |
| Gonorynchiformes | Chanidae | 1 | 1 |
| Labriformes | Pomacentridae | 8 | 6 |
| Lophiiformes | Lophiidae | 1 | 1 |
| Mugiliformes | Mugilidae | 14 | 20 |
| Mulliformes | Mullidae | 5 | 5 |
| Orectolobiformes | Hemiscylliidae | 1 | 1 |
| Perciformes | Cyclopteridae | 1 | 1 |
| | Eleginopidae | 1 | 5 |
| | Embiotocidae | 1 | 1 |
| | Gasterosteidae | 1 | 1 |
| | Gerreidae | 5 | 7 |

**Table I.** Continuation.

| | | | |
|---|---|---|---|
| | Haemulidae | 11 | 12 |
| | Hexagrammidae | 1 | 1 |
| | Labridae | 16 | 8 |
| | Lethrinidae | 3 | 2 |
| | Lutjanidae | 19 | 23 |
| | Malacanthidae | 1 | 3 |
| | Moronidae | 1 | 9 |
| | Nemipteridae | 6 | 3 |
| | Nototheniidae | 1 | 1 |
| | Odacidae | 2 | 1 |
| | Pinguipedidae | 2 | 2 |
| | Platycephalidae | 1 | 1 |
| | Pomacentridae | 2 | 1 |
| | Priacanthidae | 5 | 5 |
| | Scaridae | 4 | 9 |
| | Sciaenidae | 14 | 7 |
| | Scorpaenidae | 1 | 1 |
| | Sebastidae | 1 | 1 |
| | Serranidae | 19 | 15 |
| | Sillaginidae | 5 | 6 |
| | Sparidae | 29 | 37 |
| | Triglidae | 8 | 6 |
| Pleuronectiformes | Bothidae | 1 | 1 |
| | Paralichthyidae | 5 | 5 |
| | Pleuronectidae | 4 | 5 |
| | Soleidae | 5 | 4 |
| Salmoniformes | Salmonidae | 9 | 8 |
| Scombriformes | Arripidae | 3 | 4 |
| | Polynemidae | 1 | 1 |
| | Pomatomidae | 1 | 7 |
| | Scombridae | 28 | 25 |
| | Stromateidae | 1 | 1 |
| | Trichiuridae | 3 | 5 |
| Siluriformes | Ariidae | 10 | 8 |
| | Plotosidae | 1 | 1 |
| Syngnathiformes | Aulostomidae | 1 | 3 |
| | Fistulariidae | 1 | 1 |
| Tetraodontiformes | Balistidae | 4 | 5 |
| | Diodontidae | 1 | 1 |
| | Monacanthidae | 5 | 6 |
| | Ostraciidae | 2 | 3 |
| | Tetraodontidae | 7 | 8 |
| | Triacanthidae | 2 | 2 |
| Zeiformes | Zeidae | 1 | 1 |

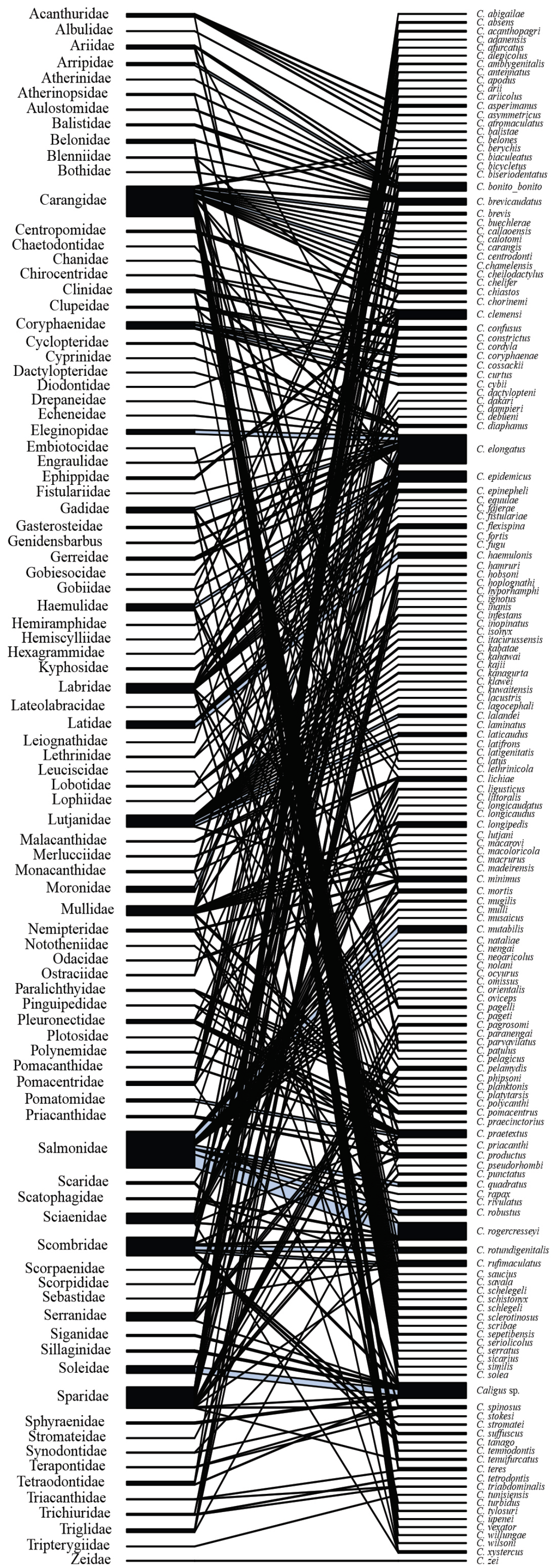


**Figure 1. Network of interactions between species of *Caligus* and families of host teleosts.**

In the network of interaction that relates parasites with host families, the co-occurrence rate of the ectoparasites was low at a network level (c-score = 0.88) (Figure 1), indicating that *Caligus* species do not share the same host families, and have a certain specificity for host families. In relation to the interaction between parasites and host families, at the parasite species level, most parasite species were recorded in only one host family in the network (Figure 1). *Caligus elongatus* Nordmann, 1832 was most widely distributed (Figure 1), registered in 19 host families and participating in 32.8% of the network interactions (range = 19.0, species strength = 10.6), followed by *C. epidemicus*, which featured in 31.3 % of the network interactions (range = 17, strength of species = 6.2). Carangidae was the most parasitized host family, featuring in 22.1% of network interactions (range = 38.0, family strength = 28.3), followed by the Labridae family, which was involved in 15.2% of the network interactions (range = 18.0, strength of species = 10.3). Most species exhibited high species specificity index values (SSI) in relation to host families. In contrast, the least specialist species were *C. elongatus* (SSI = 0.30), followed by *C. epidemicus* (SSI = 0.36).

While there was a predominance of samples collected in a marine environment (Figure 2), *Caligus lacustris* Steenstrup & Lütken, 1861 and *C. epidemicus* infest hosts from a freshwater environment. The prevalence (n = 309), intensity (n = 197) and abundance (n =186) data of *Caligus* species in the host fish analyzed are shown in Figure 3. A high prevalence of *Caligus* spp. was found in both farmed and wild fish and a higher intensity was found in farmed fish species. Infestation sites by *Caligus* spp. occurred predominantly in the tegument and gills of host

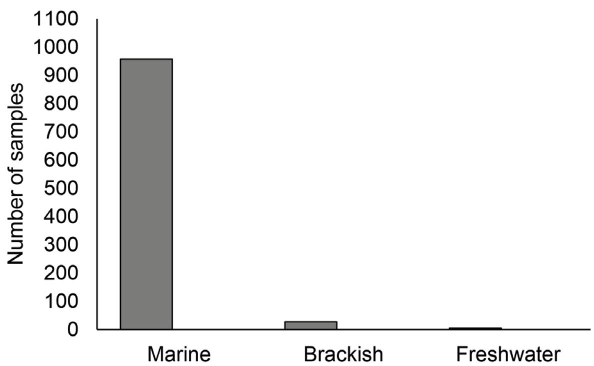


**Figure 2. Number of samples on host teleost according to environment of collection.**

fish, but other organs were also infested (Figure 4).

*Caligus centrodonti* (Baird, 185) infested only species of Labridae; *Caligus lalandei* Barnard, 1948 infested only species of Carangidae; *Caligus clemensi* Parker & Margolis, 1964 infested species of Gasterosteidae, Salmonidae, Clupeidae, Hexagrammidae and Gadidae; *Caligus absens* Ho, Lin & Chen, 2000 infested species of Priacanthidae, Latidae and Cichlidae; *Caligus asperimanus* Pearse, 1951 infested species of Lutjanidae, Haemulidae and Sparidae; *Caligus biaculeatus* Brian, 1914 infested species of Aulostomidae, Scaridae, Labridae, Acanthuridae and Malacanthidae; *Caligus bonito bonito* Wilson, 1905 infested species of Coryphaenidae, Scombridae, Arripidae, Mugilidae, Carangidae, Coryphaenidae, Pomatomidae and Lutjanidae; *Caligus chiastos* Lin & Ho, 2003 infested species of Scombridae, Lutjanidae, Sparidae, Sillaginidae, Pomacentridae, Tetraodontidae and Latidae; *Caligus coryphaenae* (Steenstrup & Lütken, 1861) infested species of Scombridae, Carangidae, Coryphaenidae and Pomatomidae; *Caligus diaphanous* Nordmann, 1832 infested species of Triglidae, Sparidae, Pleuronectidae and Lutjanidae; *C. elongatus* infested species of Mullidae, Salmonidae, Gadidae, Labridae, Moronidae, Carangidae, Pleuronectidae, Lophiidae, Cyclopteridae, Triglidae, Clupeidae, Mugilidae, Gobiidae, Monacanthidae, Belonidae, Sciaenidae and Soleidae; *C. epidemicus* infested species of Sparidae, Mugilidae, Pomacentridae, Gerreidae, Girellidae, Kyphosidae, Tetraodontidae, Lutjanidae, Synodontidae, Sillaginidae, Latidae, Cichlidae, Serranidae, Siganidae and Scatophagidae; *Caligus haemulonis* infested species of Ephippidae, Ariidae, Sparidae, Sciaenidae, Monacanthidae, Haemulidae and Ephippidae; *Caligus laticaudus* (Shiino, 1960) infested species of Carangidae, Kyphosidae, Chaetodontidae, Labridae, Sparidae, Haemulidae, Lutjanidae, Mugilidae and Polynemidae; *Caligus lichiae* Brian, 1906 infested species of Carangidae and Sphyraenidae; *Caligus longipedis* Bassett-Smith, 1898 infested species of Arripidae, Acanthuridae, Carangidae, Haemulidae, Ostraciidae, Pomacanthidae, Scaridae, Serranidae, Paralichthyidae, Gerreidae and Moronidae; *Caligus mortis* Kensley, 1970 infested species of Clinidae, Blenniidae, Gobiesocidae, Mugilidae and Sparidae; *Caligus mutabilis* Wilson, 1905 infested species of Carangidae, Scombridae, Ephippidae, Serranidae, Gerreidae, Haemulidae, Sciaenidae, Mugilidae, Centropomidae, Balistidae and Ephippidae; *Caligus pageti* Russell, 1925 infested species of Mugilidae and Moronidae; *Caligus pagrosomi* Yamaguti, 1939 infested species of Ariidae, Latidae, Lobotidae, Lutjanidae, Sciaenidae and Carangidae; *Caligus pelamydis* Krøyer, 1863 infested species of Scombridae, Carangidae, Lateolabracidae and Pomatomidae; *Caligus pomacentrus* Cressey, 1991 infested species of Pomacentridae, Haemulidae, Aulostomidae, Bothidae, Malacanthidae and Scaridae; *Caligus praetextus* Bere, 1936 infested species of Sciaenidae, Centropomidae, Diodontidae, Sparidae, Gerreidae, Echeneidae, Lutjanidae, Synodontidae, Tetraodontidae, Mugilidae, Ephippidae, Merlucciidae, Haemulidae,

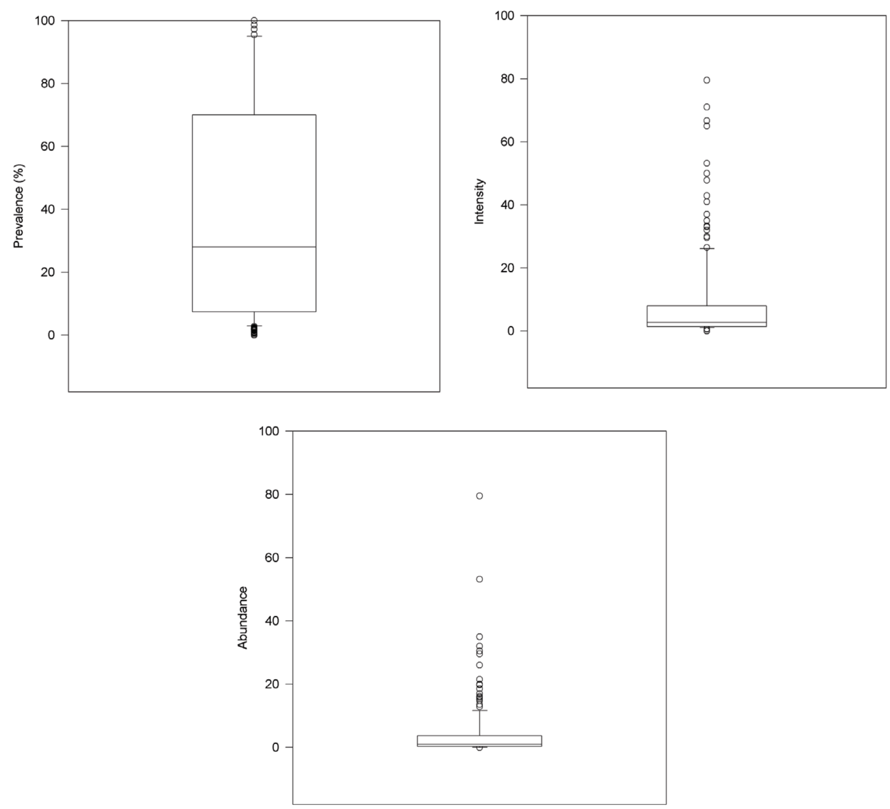


**Figure 3.** **Quantitative descriptors of infestation for *Caligus* species in samples of teleost species (Box plots represent medians, percentile ranges (25-75%), minimum-maximum and outlier values).**

Scombridae, Lutjanidae and Ariidae; *Caligus productus* Dana, 1852-1853 infested species of Coryphaenidae, Sparidae, Carangidae, Serranidae, Balistidae, Sphyraenidae, Scombridae, Lutjanidae and Centropomidae; *Caligus quadratus* Shiino, 1954 infested species of Coryphaenidae, Scombridae, Siganidae and Serranidae; *Caligus robustus* Bassett-Smith, 1898 infested species of Carangidae, Lutjanidae, Scombridae and Latidae; *Caligus rogercresseyi* Boxshall & Bravo, 2000 infested species of Salmonidae, Eleginopidae, Atherinopsidae and Paralichthyidae; *Caligus rotundigenitalis* Yü, 1933 infested species of Atherinidae, Leiognathidae, Mullidae, Scatophagidae, Terapontidae, Drepaneidae, Mugilidae, Latidae, Lutjanidae, Carangidae, Serranidae, Lobotidae and Cichlidae; *Caligus rufimaculatus* Wilson, 1905 infested species of Carangidae, Haemulidae, Pomatomidae, Lutjanidae, Mugilidae and Centropomidae; *Caligus schlegeli* Ho & Lin, 2003 infested species of Sparidae, Mugilidae, Scatophagidae, Terapontidae, Carangidae, Siganidae, Girellidae, Nemipteridae and Sillaginidae; *Caligus spinosus* Yamaguti, 1939 infested only species of Carangidae and Sphyraenidae; *Caligus suffuscus* Wilson, 1913 infested species of Acanthuridae, Labridae, Ostraciidae, Malacanthidae, Scaridae and Balistidae and *Caligus teres* Wilson, 1905 infested species of Salmonidae, Eleginopidae and Merlucciidae and *Caligus xystercus* Cressey, 1991 infested species of Haemulidae, Aulostomidae, Sparidae, Lutjanidae, Pomacanthidae and Priacanthidae. However, for the mostly of *Caligus* species the host records collected from a number of different localities clearly does not allow any conclusion on host specificity.

Although diverse species of *Caligus* are distributed across continents and countries (Figures 5-6), some particularities were found. For example, there is a lack of studies on *Caligus*

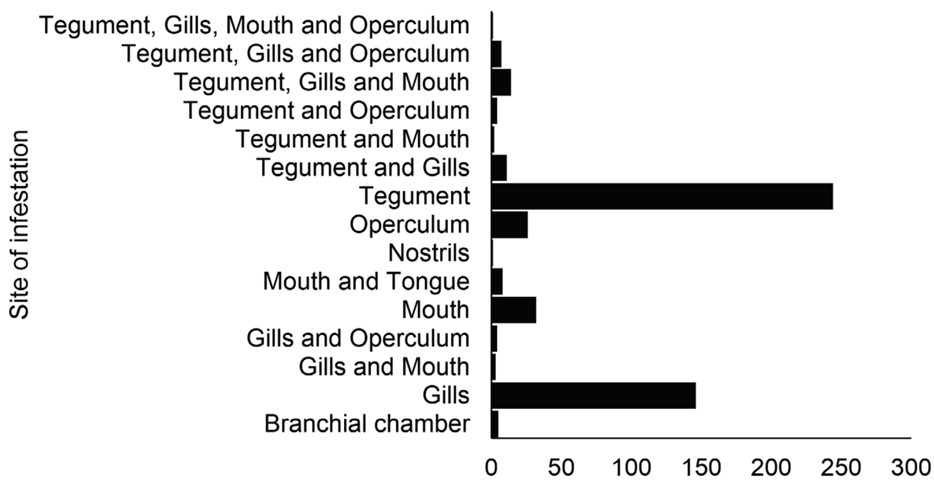


**Figure 4. Infestation sites by *Caligus* spp. in 508 samples for teleost species.**

spp. for the coast of Africa, with the exception of a few records for South Africa. These records were particularly scarce from the seas of tropical West Africa. In the interaction network that relates parasites to countries of occurrence, the co-occurrence rate of *Caligus* spp. was low at network level (c-score = 0.82), indicating the species are geographically restricted. Furthermore, most *Caligus* species have been recorded in one or two countries. *Caligus elongatus* had the widest geographic distribution (Figure 7), participating in 31.0% of the network interactions (range = 14.0, species strength = 6.74), followed by *C. bonito bonito*, which participated in 31.6% of network interactions (range = 11.0, strength of species = 1.0). Vietnam had the highest recorded occurrence of *Caligus* species, featuring in 32.71% of network interactions (range = 48.0, country strength = 31.1), followed by Greece, which featured in 28.3% of network interactions (range = 34.0, country strength = 14.4) (Figure 7).

Regarding to distribution by continents, for Europe are described 24 species of *Caligus*, for Africa 26 species, for Asia 81 species, for Oceania 49 species, for Central America 14 species, for South America 30 species and for North America 39 species (Figure 5-6). For the Asiatic continent are known the higher number of *Caligus* species, indicating therefore that these parasites are better studied.

The histopathological disorders caused by *Caligus* spp. infestation in the gills and skin of different fish species are shown in Table II. The hematological, biochemical, and immunological effects of *Caligus* spp. on different fish species are shown in Table III.

A variety of chemotherapeutic products has been used to effectively control and treat infestation by *Caligus* spp. (Table IV).

## DISCUSSION

### Global distribution pattern of host-parasite interaction

During the last decade, interest has increased in ecological studies of host-parasite interactions, which provide important information about the distribution of parasites in host fishes. Taxa of the ectoparasites *Caligus* spp. are widely distributed in oceans around the world, infesting both wild and farmed teleost fishes of commercial and biological importance. How the dynamics of *Caligus* species vary among wild fish species has not been fully established, and the same is true for the role of these species in the host-parasite system, as they can serve as a natural reservoir host population

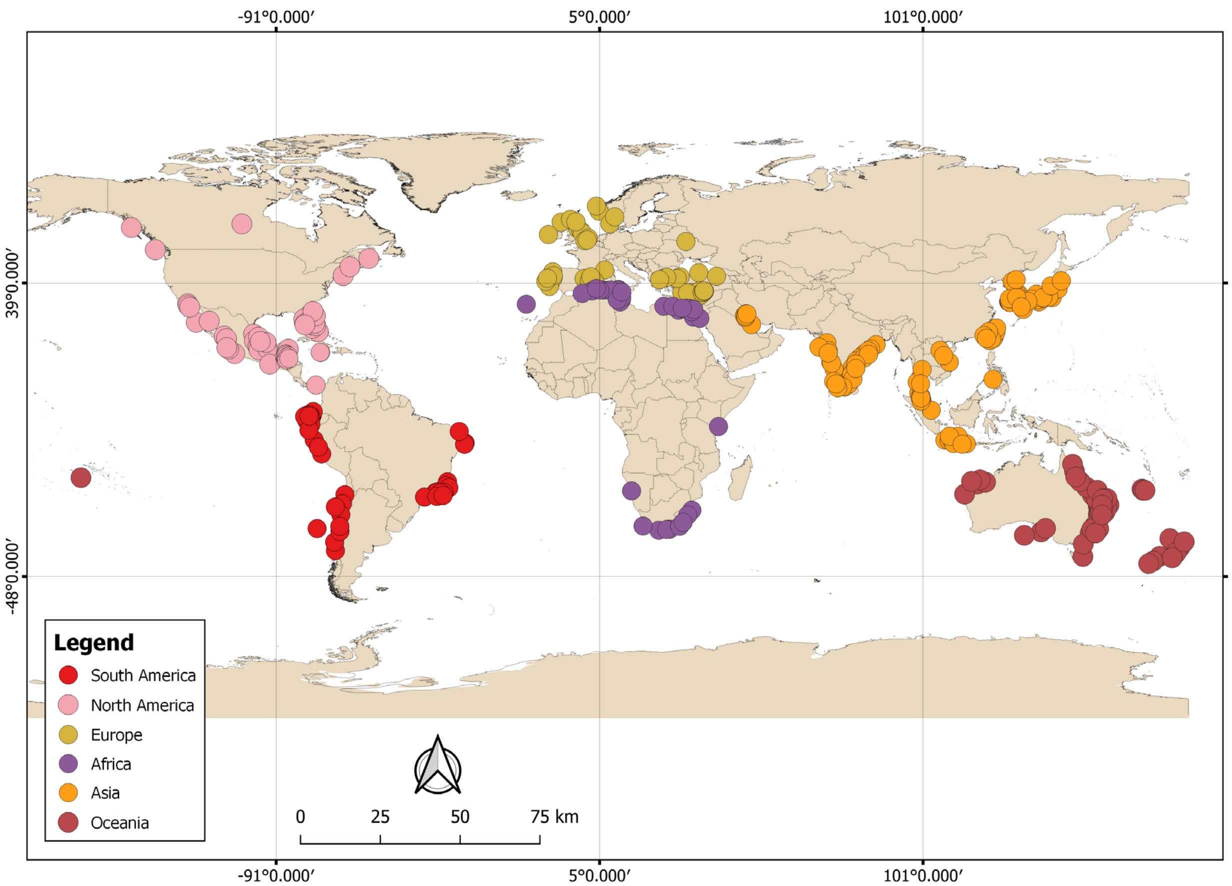


**Figure 5. Geographical distribution of *Caligus* species on the continents of terrestrial globe.**

for these copepods. It has been cited that the prevalence of *C. clemensi* on wild juvenile salmon correlated positively with the presence of the Atlantic salmon *Salmo salar* Linnaeus, 1758 in fish farms from British Columbia, Canada (Brookson et al. 2020). In addition, studies have indicated differences in the specialization of *C. clemensi* in *Oncorhynchus gorbuscha* Walbaum, 1792, *Oncorhynchus keta* Walbaum, 1792 and *Oncorhynchus nerka* Walbaum, 1792, which may arise via the initial infestation process, the survival of attached parasites, or parasite-induced host mortality (Brookson et al. 2020). In experimental trials, *C. elongatus* was transferred between wild *Pollachius virens* Linnaeus, 1758 and *S. salar* salmon farmed in net cages, and from salmon to salmon. Both moribund *S. salar* and *P. virens* appeared to attract more lice than healthy fishes (Bruno & Stone 1990).

In the present study, there was a predominance of infestation by *Caligus* spp. in 24.8% of the host families, comprising Carangidae (10.6%), Sparidae (7.6%) and Scombridae (6.6%) species. The Carangidae family consists of 30 genera and 147 species, while the Sparidae family consists of 38 genera and 158 species of teleost fishes, and the Scombridae family consists of 15 genera and 54 species (Froese & Pauly 2022). These results may therefore reflect a greater number of studies on *Caligus* spp. in these teleost fish taxa and may also reflect local priorities for parasitological research into these hosts. Despite studies on the presence of *Caligus* species in teleost fish, global distribution patterns in teleost fish in different

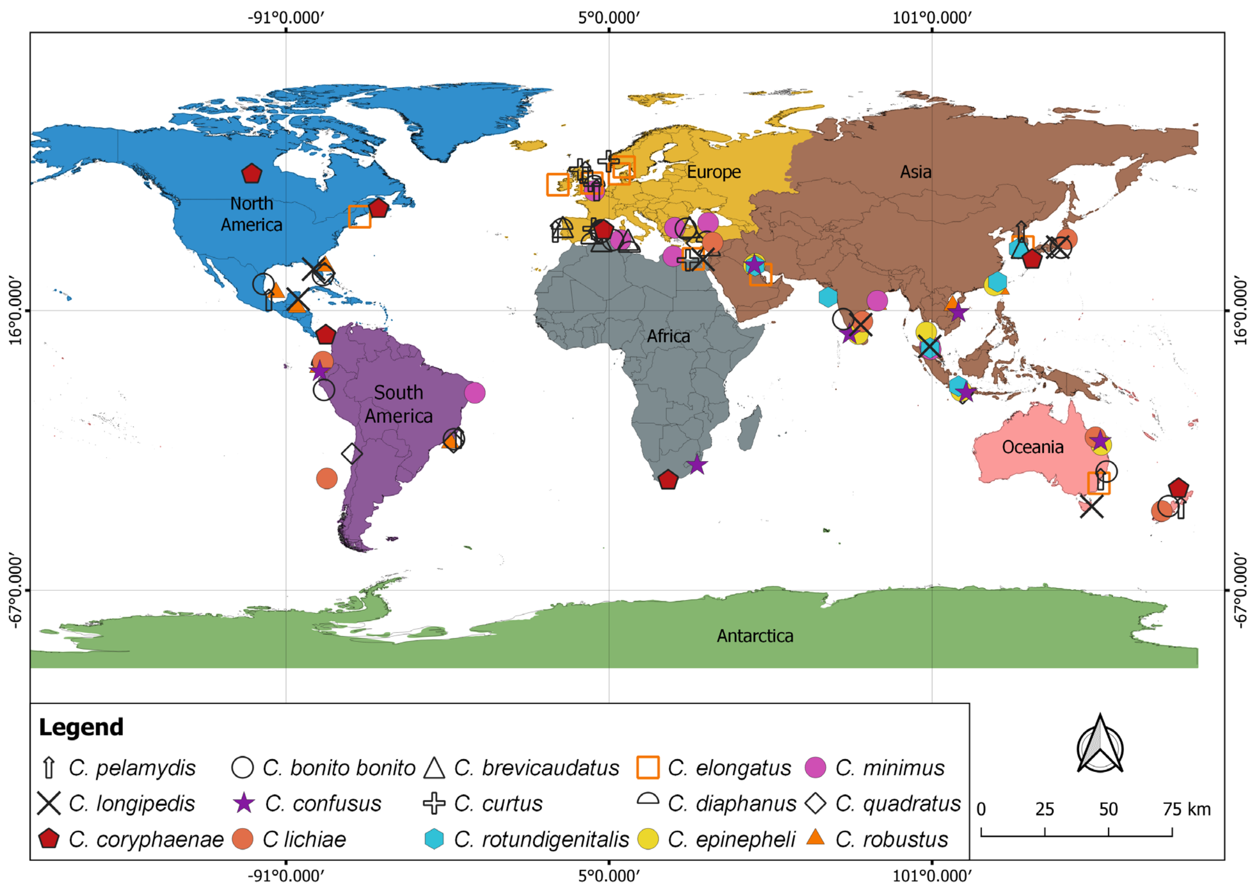


**Figure 6. Geographical distribution of *Caligus* species that occurred in five or more countries of terrestrial globe.**

aquatic ecosystems around the world have not thus far been studied.

Analysis of the *Caligus*-host interactions is an important way to evaluate the local adaptation of these ectoparasites with heterogeneous distribution in hosts, as infestation rates vary between host teleost populations. We detected the following global patterns within *Caligus*-host interactions: (a) a prevalence ranging from low to high, with abundance and intensity ranging from low to moderate; (b) association with other ectoparasites infracommunities, mainly *Lepeophtheirus salmonis* Krøyer, 1837; (c) typically aggregated distribution patterns; (d) occasionally positive correlations of prevalence and intensity with the body size of host fish at the infracommunity level; (e) 4.2% of parasite species are shared among farmed and wild teleost fish and (g) ectoparasites infect mostly the gills and tegument of hosts. Therefore, findings from the present study shows in the gills and tegument have been the sites most frequently infected by *Caligus* species when searching for the parasite-host systems, as they are selective in their choice of attachment site. We can therefore suggest that these parasites seem to have a certain microhabitat specificity in hosts.

Parasitism is a factor that may influence the fish recruitment and population growth via direct mortality and potentially through parasite mediated sublethal effects on host behavior, growth, predation risk, and reproductive success (Brookson et al. 2020). In teleost fish samples analyzed around the world, we found a moderate to high prevalence, low abundance

**Table II.** **Histopathological alteration caused by infestation of *Caligus* spp. in different teleost species.**

| Fish species | Parasite species | Organs | Tissue alterations | References |
|---|---|---|---|---|
| *Mugil cephalus* | *Caligus curtus* | Skin | Focal desquamation of the most superficial layer of the epidermis. Areas of vacuolar degeneration with multiple bulla formations were noticed in the skin of most examined cases. Ulcerated areas displayed edema which overdistended the scale pockets. The dermis showed congested blood vessels as well as infiltration, with numerous leukocytes, mainly lymphocytes and macrophages, together with melanomacrophage cells. Numerous melanin-carrying cells were seen in the tunica compacta. The underlying muscles showed sarcoplasmolysis, myophagia, and migration of sarcolemmal nuclei, especially in the ulcerated areas. | Easa & El-Wafa (1995) |
| *Mugil cephalus* | *Caligus curtus* | Skin | The skin of fish showed hyperplasia of club cells of the epidermis, congested and hemorrhagic dermis with excessive aggregation of round cells, melanomacrophage cell and edema of the dermis | El-Atta & El-Ekiaby (2012) |
| *Salmo salar* | *Caligus elongatus* | Skin | Chalimus larvae were anchored to the host scales by a frontal filament that penetrates through the epidermis and anchors into the basement membrane around the scale. Larval stages remain in one place feeding on the mucus and epidermal cells. The tissue surrounding the third- and fourth stage chalimus larvae showed no tissue changes due to the presence of the filament or any evidence of damage caused by the initial attachment by the second antennae of the copepodid. The feeding of the larvae resulted in excavation of a hole in the epidermis of fish, down to the basement membrane, with detachment of the epidermal layer from the basement membrane in the area surrounding the hole in the majority of samples examined. Necrotic cells line the hole formed by the larva, and some samples of chalimus IV larvae showed evidence of slight hyperplasia around the excavated area. | Mackinnon (1993) |
| *Dicentrarchus labrax* | *Caligus minimus* | Skin | Ulceration of the epidermis with marked inflammatory, mainly mononuclear cellular infiltration of the dermis as a result of the attachment and feeding activity of the parasites. The attachment was achieved by means of second pair of the antennae which were inserted into the host epidermal tissue. A marked reactive epidermal hyperplasia was observed at those areas as well as at the periphery of ulcerated lesions. Many epidermal cells around the damaged area showed signs of necrosis, the vacuolar degeneration of basal cells was prominent and epidermis was also characterized by diffuse areas of spongiosis. In many cases, increased fibroplasia and spongiosis was noticed within dermal collagenous connective tissue | Ragias et al. (2004) |
| *Oncorhynchus mykiss* | *Caligus rogercresseyi* | Skin | Analyses revealed differences between the epidermis of the control and infected fish. In particular, attachment sites were characterized by varying degrees of epithelium erosion and disorganization, no epidermal hyperplasia was observed. Lesions extended into the underlying dermis, showing hyperplasia, inflammation of the stratum compactum connective tissue, disorganization of collagen fiber arrangement, and an increased number of melanophores. Furthermore, an increased quantity of goblet cells was interspersed between epithelial cells. The ultra-structural analysis of the skin from infected fish also showed collagen fiber disruption and an evident increase in subdermal melanophores. | Rojas et al. (2018) |

**Table II. Continuation.**

| | | | | |
|---|---|---|---|---|
| *Acanthopagrus australis* | *Caligus epidemicus* | Skin | Copepodids eroded the epidermis and usually attached their frontal filament to the basement membrane on the inter-ray region of fins, as well as the fin rays or scales. The most extensive tissue response was associated with the redundant frontal filament, and was characterized by infiltrating macrophages, multinucleated giant cells, and epidermal and fibroblast proliferation. | Roubal (1994) |
| *Dicentrarchu labrax* | *Caligus clemensi* | Gills | Partial or complete sloughing of their lamellar epithelium which results in denuded filaments. Sometimes hyperplastic secondary lamellar epithelium in the adjacent area which led to fusion of the filaments were encountered thickened filaments by numerous inflammatory cells and edema beside dilated capillaries were observed. Fragments from the parasite were detected between primary filaments with ulceration and distortion of the adjacent filaments. Sometimes, heavy parasitic infestation with atrophy, distortion and blunting of the gill filaments could be seen. The base of primary filaments was covered by sheath from hyperplastic lamellar epithelium. The gill arch contained congested blood vessels beside edema, hemorrhage and inflammatory cells infiltration mainly eosinophil, granular cells in their necrotic muscles. | Abdelkalek et al. (2021) |
| *Mugil cephalus* | *Caligus curtus* | Gills | Parasites induced severe congestion of brachial blood vessels, telangiectasia, and also sloughing of secondary lamellae and desquamation of secondary lamellar epithelium | El-Atta & El-Ekiaby (2012) |
| *Mugil cephalus* | *Caligus sp.* | Gills | Many branchial lesions showed severe inflammatory reactions to advanced degenerative and hyperplastic changes. The inflammatory changes were mainly observed in gill arch and congestion of lamellar blood vessels and adhesion of most gill filaments and lamellae | El-Deen et al. (2012) |
| *Dicentrarchus labrax* | *Caligus elongatus* | Gills | Variety of circulatory, degenerative and proliferative changes evident in tissues of infected fish. Severe congestion of lamellar blood vessels was common among pathological findings. Diffuse hyperplasia at the base of the secondary lamellae as well as lamellar fusion was frequently denoted. Increase in the activity of goblet cells was characteristic. In some other cases, gill arch demonstrated edema, hemorrhages together with some eosinophilic granular cell aggregations | Elgendy et al. (2015) |
| *Oncorhynchus mykiss* | *Caligus rogercresseyi* | Gills | The secondary lamellae showed evidence of hyperplasia, base and tip thickening, and complete or partial lamellar fusion. The gills presented ordered organization, with numerous parallel threadlike secondary lamellae arranged at nearly right angles to the primary lamellae. Moreover, at the primary lamellae of the infected fish, the connective tissue showed an increased quantity of MCs/EGCs, macrophages, and lymphocytes). Increase in mucus-secreting or goblet cells in the epithelium of secondary lamellae and the distal tip of the gill filaments | Rojas et al. (2018) |

and low to moderate intensity of *Caligus* species, in contrast to farmed fish, which had higher abundance and intensity. The prevalence, intensity and abundance of different species in the *Caligus* infracommunities sampled of the present study are clearly unequal. Therefore, we detected variation in the infestation rates of *Caligus* species in the host fishes, which may reflect the fluctuations in the environmental conditions and factors related to host fish (González et al. 2000, Gargan et al. 2016, Bravo et al. 2017, 2021, González-Gómez et al. 2020).

*Caligus* spp. ectoparasites are widely distributed in seas around the world and infest wild and farmed fish of commercial importance. Large aggregations of wild fish are attracted to fish farms, attracted by fish feed waste. Some of the wild fish species attracted in this way are natural hosts for *Caligus* spp. and could be an important source of infestation for farmed fish (Hemmingsen et al. 2020). Infestations and diseases caused by *Caligus* species have become a constant problem in farmed fish production, where high densities in fish farming, and within each farm, increase the frequency of contact between fish (Bravo 2003, Bravo et al. 2010). These infestations are a problem for the viability of the global salmon industry, and may be a major constraint to biological sustainability as well as the main factor limiting the future growth of fish aquaculture.

Many fish parasites are generalists, infecting multiple host species, which can lead to apparent competition (indirect competition via shared natural enemies), among fish host populations. Generalist parasites can persist even when the abundance of a focal host species is low, by infesting a reservoir host species, leading to spillover and spillback dynamics that are important for the management of farmed and wild fish populations (Brookson et al. 2020). *Caligus bonito bonito* and *C. coryphaenae* are cosmopolitan in distribution. These caligid species are not host specific and are thus found on a variety of host fish. Hogans & Trudeau (1989) cited that *C. elongatus* has infected more than 80 species of marine fish around the world. *Caligus rogercresseyi* has a low host specificity as they have been identified on several species of wild fish commonly present around salmon farms (Carvajal et al. 1998), and similar findings were observed in this study. Morales-Serna et al. (2013) reported that *Caligus serratus* Shiino 1965 has low host specificity, as it infects at least 13 fish species.

## Global geographic distribution of *Caligus* spp.

In fish assemblages, regional patterns of *Caligus* spp. may provide insights for the creation of global distribution maps. For fish from the Carangidae Rafinesque, 1815 family, which are globally distributed, 80 species of *Caligus* were listed by Özak et al. (2019). For scombrid hosts, Morales-Serna et al. (2017) listed 26 species of *Caligus*, while 33 species of *Caligus* have been listed for fish from the Mediterranean (Özak et al. 2012). Six species of *Caligus* were reported parasitizing tunas *Auxis* spp., *Euthynnus affinis* Cantor 1849, *Katsuwonus pelamis* Linnaeus 1758, and *Thunnus* spp. in Japan (Nagasawa et al. 2018). Recently, it was reported that fish from Turkey had been infested by 20 species of *Caligus* (Özak 2020), and these ectoparasites have been cited in marine fish from South Korea, China, Japan, Philippines and Taiwan (Ho et al. 2016). Hamdi et al. (2021a) listed 12 species of *Caligus* infecting 12 host fishes from the Tunisia coast, and thirteen species of *Caligus* were listed infecting 18 species of marine fish from Portugal (Hamdi et al. 2021b).

The establishment of global geographic distribution patterns of *Caligus* species is one of the main current goals of fish parasitology (Hamdi et al. 2021a, b). Hence, efforts to characterize these parasite species in host fishes may be crucial for monitoring and mitigating threats of disease in fishery and aquaculture. Despite the diversity of global fish fauna, there is little knowledge about the distribution of *Caligus* species across biomes distributed worldwide. Host specificity was not an important factor in the geographic distribution of *Caligus* spp. in seas around the world, since the distribution of these ectoparasites do not reflect that of the host fish species.

**Table III. Hematological, biochemical, and immunological effects of *Caligus* spp. for different teleost species.**

| Fish species | Parasite species | Alterations | References |
|---|---|---|---|
| *Salmo salar* | *Caligus rogercresseyi* | Increase in plasma glucose and decrease in osmolality in 1day post infestation, with decrease in glucose and increase in osmolality in 16day post infestation, and decrease in triglycerides levels | González et al. (2015) |
| | | | |
| *Salmo salar* | *Caligus rogercresseyi* | Decrease in plasma glucose, $pCO_2$ and hematocrit, and increase in hemoglobin and lymphocytes | González et al. (2016a) |
| | | | |
| *Salmo salar* | *Caligus rogercresseyi* | Increase in plasma cortisol levels, and decrease in plasma level of glucose and triglycerides | González et al. (2016b) |
| | | | |
| *Salmo salar* | *Caligus rogercresseyi* | Increase in plasma cortisol and glucose levels | González et al. (2020) |
| *Thunnus maccoyii* | *Caligus chiastos* | Increase in plasma cortisol and glucose levels | Hayward et al. (2010) |
| *Netuma bilineata* | *Calugus sp.* | Decrease in hematocrit, hemoglobin and total erythrocytes | Jori & Mohamad (2008) |
| *Eleginops maclovinus* | *Caligus rogercresseyi* | Decrease in hematocrit, total erythrocytes and monocytes, and increase in hemoglobin, MCV, MCHC, leukocytes and lymphocytes | Peña-Rehbein et al. (2013) |
| | | | |
| *Salmo salar* | *Caligus rogercresseyi* | Decrease in plasma glucose and plasma total α-amino acids levels | Vargas-Chacoff et al. (2016) |
| *Oncorhynchus kisutch* | *Caligus rogercresseyi* | Increase in plasma glucose, triglycerides and total protein levels, and decrease in plasma total α-amino acids levels | Vargas-Chacoff et al. (2016) |
| *Salmo salar* | *Caligus rogercresseyi* | Increase in plasm a lactate dehydrogenase levels | Vargas-Chacoff et al. (2017) |
| *Oncorhynchus kisutch* | *Caligus rogercresseyi* | Increase in plasm a lactate dehydrogenase levels | Vargas-Chacoff et al. (2017) |

In the present study, an important factor related to the geographic distribution of *Caligus* species in sea ecosystems around the world was observed. These ectoparasites are widely distributed in the seas of many countries, particularly *C. elongatus and C. bonito bonito*. However, Vietnam had a highest occurrence of *Caligus* species, which may be due to a greater sampling efforts. This high occurrence of *Caligus* spp. may also be due to the fact that parasite species richness is greater in the tropics than at higher latitudes, with species richness of ectoparasites increasing at a greater rate towards the equator than that of host species (Rohde 2005). Studies on *Caligus* spp. for the coast of tropical West Africa were scarce and this is a region where we would expect to find a rich fauna as in other tropical oceans.

## Histomorphological and hematological alterations caused by *Caligus* spp.

Histopathology is an excellent tool for evaluating the effects of parasites on host fish tissues (Easa & El-Wafa 1995, Rojas et al. 2018).

**Table IV.** **Management strategies with chemotherapeutic products to control and treatment of infestation by *Caligus* spp. in different teleost species.**

| Parasite species | Products | Concentrations | Results | References |
|---|---|---|---|---|
| *Caligus rogercresseyi* | Cypermethrin | 15 µg/L | High efficacy | Agusti et al. (2016) |
| *Caligus rogercresseyi* | Cypermethrin | 0.4 mg/L | High efficacy | González-Gómez et al. (2019) |
| *Caligus rogercresseyi* | Cypermethrin | 15 ppb | Inefficacy | Marín et al. (2015) |
| *Caligus elongatus* | Cypermethrin | 5 µg/L | High efficacy | Treasurer & Wadsworth (2004) |
| *Caligus rogercresseyi* | Deltamethrin | 3 µg/L | High efficacy | Agusti et al. (2016) |
| *Caligus rogercresseyi* | Deltamethrin | 0.003 mg/L | Moderate efficacy | Bravo et al. (2013) |
| *Caligus rogercresseyi* | Deltamethrin | 2 µg/L | High efficacy | Bravo et al. (2014b) |
| *Caligus rogercresseyi* | Deltamethrin | 0.08 mg/L | High efficacy | González-Gómez et al. (2019) |
| *Caligus_rotundigenitalis* | Deltamethrin | 12.5 mg/L | High efficacy | Solanki et al. (2016) |
| *Caligus rogercresseyi* | Azamethiphos | 100 µg/L | High efficacy | Agusti et al. (2016) |
| *Caligus rogercresseyi* | Azamethiphos | 0.9 mg/L | High efficacy | González-Gómez et al. (2019) |
| *Caligus rogercresseyi* | Azamethiphos | 100 mg/m$^3$ | High efficacy | Jimenez et al. (2018) |
| *Caligus elongatus* | Azamethiphos | 0.2 mg/L | High efficacy | Roth et al. (1996) |
| *Caligus elongatus* | Ivermectin | 0.2 mg/kg | High efficacy | Palmer et al. (1987) |
| *Caligus teres* | Neguvon | 0.25 mg/L | High efficacy | Reyes & Bravo (1983) |
| *Caligus rogercresseyi* | Emamectin benzoate | 50 µg/kg | High efficacy | Agusti et al. (2016) |
| *Caligus rogercresseyi* | Emamectin benzoate | 50-100 µg/kg | Inefficacy | Bravo et al. (2012) |
| *Caligus rogercresseyi* | Emamectin benzoate | 70 µg/kg | Inefficacy | Bravo et al. (2013) |
| *Caligus curtus* | Emamectin benzoate | 50 µg/kg | High efficacy | Hamre et al. (2011) |
| *Caligus clemensi* | Emamectin benzoate | - | High efficacy | Byrne et al. (2018) |
| *Caligus elongatus* | Emamectin benzoate | 50 µg/kg | High efficacy | Stone et al. (2000) |
| *Caligus rogercresseyi* | Hydrogen peroxide | 1.5 g/L | Inefficacy | Bravo et al. (2010) |
| *Caligus rogercresseyi* | Hydrogen peroxide | 2.0 g/L | High efficacy | Chávez-Mardones et al. (2017) |
| *Caligus rogercresseyi* | Hydrogen peroxide | 825 mg/L | High efficacy | Marín et al. (2018) |
| *Caligus elongatus* | Hydrogen peroxide | 15.0-20.0 mg/L | High efficacy | El- Deen et al. (2013) |
| *Caligus rogercresseyi* | Hydrogen peroxide | 1200 mg/L | High efficacy | Valenzuela-Muñoz et al. (2020) |
| *Caligus rogercresseyi* | Freshwater | - | Inefficacy | Bravo et al. (2015b) |
| *Caligus curtus* | Freshwater | - | High efficacy | El-Atta & El-Ekiaby (2012) |
| *Caligus sp.* | Freshwater | - | High efficacy | El-Deen et al. (2012) |
| *Caligus elongatus* | Freshwater | - | High efficacy | El-Deen et al. (2013) |
| *Caligus elongatus* | Freshwater | - | High efficacy | Landsberg et al. (1991) |
| *Caligus orientalis* | Freshwater | - | Inefficacy | Urawa & Kato (1991) |
| *Caligus curtus* | Malathion | 0.02 mg/L | High efficacy | Easa & El-Wafa (1995) |
| *Caligus elongatus* | Malathion | 0.15-0.20 mg/L | High efficacy | El-Deen et al. (2013) |
| *Caligus sp.* | Trichlorfon | 20.0-30.0 mg/L | High efficacy | El-Deen et al. (2012) |
| *Caligus elongatus* | Trichlorfon | 20.0-30.0 mg/L | High efficacy | El-Deen et al. (2013) |
| *Caligus elongatus* | Trichlorfon | 0.25 mg/L | Inefficacy | Landsberg et al. (1991) |
| *Caligus elongatus* | Formalin | 250 mg/L | Inefficacy | Landsberg et al. (1991) |
| *Caligus platytarsis* | Formalin | 0.02% | High efficacy | Chatterji et al. (1982) |
| *Caligus elongatus* | Potassium permanganate | 5.0-10.0 mg/L | High efficacy | El-Deen et al. (2013) |
| *Caligus sp.* | Potassium permanganate | 5.0-10.0 mg/L | High efficacy | El-Deen et al. (2012) |
| *Caligus elongatus* | Copper | 150 mg/L | Inefficacy | Landsberg et al. (1991) |

Fish gills and skin have therefore been used as biomarkers in the evaluation of the health of fish infested by *Caligus* species in both laboratory and field studies. Fish gills and skin have multiple functions and thus respond to *Caligus* spp. infestations (Table II). These sea lice are ectoparasitic copepods that feed on the mucus, epidermal tissue and blood of hosts (Bruno & Stone 1990, González et al. 2020), with sublethal effects, such as stress, appetite loss, and immune system depression, as well as lethal effects in heavily infected fish (Rojas et al. 2018). The attachment of *Caligus* and their movements over the host surface contribute little or nothing to the damage from their activities, with their feeding mainly, or even solely, responsible for the damage caused. The lesions caused may be localized or extensive, depending on the size of the fish and the number of parasites. Infestations can result in a broad range of clinical signs (Hemmingsen et al. 2020).

Clinic signals such as lesions, erosions, ulcerations, and dark discoloration, especially at the tegument of *Mugil cephalus* Linnaeus, 1758 infested by *C. curtus* have been reported (Easa & El-Wafa 1995). *Mugil cephalus* infested by *C. curtus* rubbed themselves on solid substrates and presented excessive mucus. Opaque skin, frayed fins, hemorrhagic spots scattered on every part of the body especially the perianal, caudal and pectoral regions were observed. In severe cases, mechanical damage of the skin, erosion, ulceration, gasping for air and accumulation around the water inlet were observed (El-Atta & El-Ekiaby 2012). *Dicentrarchus labrax* Linnaeus, 1758 infested by *C. minimus* presented distress, surface swimming, excessive mucus production, sluggish movement, emaciation and rubbing of the body against hard objects. Opercula exhibited bulging from the gulping of atmospheric air (surface breathing). The gills of host fish had a marbling (mosaic) appearance (areas of congestion and paleness), while excessive mucous secretion and paleness was seen in the gills of some fishes. The gills exhibited areas of thickened mucus, petechial hemorrhages, protruding gill tips with grayish coloration and necrosis (Eissa et al. 2016). The clinical signs in *M. cephalus* infested by *Caligus* sp. were a loss of appetite, debilitation, with extensive mucous, rubbing against the plastic silk coating of the ponds, nervous behavior and respiratory manifestations. In addition, extensive focal brown spots on the skin and fins, and redness around the mouth were observed (El-Deen et al. 2012). Therefore, the clinic signals caused by *Caligus* spp. depend on the parasite and host species, and on the degree of infestation.

Blood parameters have been considered an important way to measure the health status of fish populations. In fish, physiological changes caused by sea lice are effective indicators welfare; however, in practice routine monitoring on fish farms is difficult to implement (González et al. 2020). Hematological and biochemical variables have been used for clinical diagnoses related to the physiology of fish and to determine the effects of stressors such as *Caligus* spp. infestations (Table III).

In *S. salar* infested by *C. rogercresseyi* no evidence of the upregulation of genes related to heme-biosynthesis was demonstrated, suggesting that parasitic feeding by parasites on fish skin does not cause microcytic anemia (Valenzuela-Muñoz & Gallardo-Escárate 2017). Results indicate that host tissue damage caused by *C. rogercresseyi* liberates molecules recognized by tlr22a2, thus activating the host immune response. In addition, the abundance of tlr13 in infested fish, the increased expression of this receptor in the skin, and the phylogenetic similarity of tlr22 and tlr13, suggest the possible role of tlr13 in the immune response to ectoparasites (Valenzuela-Muñoz et al. 2016). In

*S. salar* and *Oncorhynchus kisutch* Walbaum, 1792, infestation by *C. rogercresseyi* caused an increase in levels of lactate dehydrogenase in muscles, and a decrease in the liver (Vargas-Chacoff et al. 2017).

## Control and treatment strategies of *Caligus* species in teleosts

Aquaculture is the most consistently expanding industry in the world, and provides many products for human consumption, mainly fish species. However, diseases are a major constraint to fish aquaculture, affecting farmed fish systems, among which are those caused by *Caligus* spp. Thus, the management of diseases is a major challenge for the fish aquaculture industry, with current methods for controlling ectoparasites such as *Caligus* spp. mostly reactionary and reliant on chemical treatments. Antiparasitic control and treatment using chemotherapeutants are required for infested fish as they limit economic losses in fish farms. These antiparasitic interventions primarily rely on the treatment of infestation through baths or oral drug administration and usually focus on killing juvenile and adult parasites.

Studies suggests that the unit production costs of *S. salar* in Chile increased by an average of US$ 1.45/kg when treatments against *Caligus* spp. were included. However, such treatment costs are compensated by higher harvesting levels, with unit production costs unchanging in comparison with the situation without treatment (Dresdner et al. 2019). The treatment of feed with emamectin benzoate reduced infestation by *C. rogercresseyi* when applied for more than 14 days, but repeated use over time reduces sensitivity to the treatment (Bravo et al. 2014a). A study in *S. salar* demonstrated genetic variation in resistance to *C. rogercresseyi*, indicating that its selection at the sessile stage allows a reduction in the parasite load at the adult stage by modulating the reproductive cycle of the parasites (Lhorente et al. 2012).

The use of chemotherapeutants treatments to remove *Caligus* spp. is potentially harmful to these crustaceans, but there is strong evidence that the extensive use of these treatments results in the development of resistance. A study of salmonids reported a significant reduction in azamethiphos efficacy against *C. rogercresseyi* (Arriagada et al. 2020). The evaluation of cypermethrin, deltamethrin or deltamethrin was associated with lower juvenile, mobile adult, and gravid female *C. rogercresseyi* levels after treatment, when compared with an untreated pen. However, the three chemotherapeutants appeared to be less effective at reducing the number of juvenile sea lice compared to the mobile stages of farmed fish (Arriagada et al. 2014), in contrast to this parasite in native teleosts (González-Gómez et al. 2019). In *S. salar* and *Oncorhynchus mykiss* Walbaum, 1792 farms in the south of Chile, the immobilizing 50% effective concentration ($EC_{50}$) of *C. rogercresseyi* varied from 0.06 to 0.2 mg/L (Bravo et al. 2008). The $EC_{50}$ values of deltamethrin for *C. rogercresseyi* ranged from 0.14 to 0.24 g/L (Helgesen et al. 2014), while the $EC_{50}$ of hydrogen peroxide was 709.8 mg/L for 100% immobilization of *C. rogercresseyi* (Marín et al. 2018). Differences in the 50% immobilizing concentration ($EC_{50}$) of *C. rogercresseyi* of azamethiphos, deltamethrin and emamectin benzoate for females and males have been reported, as females have higher values (Agusti et al. 2016). However, Agusti-Ridaura et al. (2018) reported the gene of enzyme acetylcholinesterase was probably involved in resistance to azamethiphos organophosphate. *Caligus elongatus* from a fish farm in Norway had lower immobilization rates at the highest hydrogen peroxide concentration than wild fish, which might be due to a loss of sensitivity, in contrast to azamethiphos, deltamethrin and emamectin benzoate, which showed resistance (Agusti-Ridaura et al. 2018). Prolonging treatment-time with azamethiphos in *C. rogercresseyi* appears to contribute to treatment success, reducing the number of treatments required throughout a production cycle, and reducing the risk of *S. salar* developing resistance to this drug (Jimenez et al. 2018). Studies by Valenzuela-Muñoz et al. (2014) have identified a relationship between Cr-Pgp expression and the detoxifying gene Cr-P540, suggesting the role of Cr-Pgp in pyrethroid metabolism for exposure to *C. rogercresseyi*.

An apparent loss in the sensitivity of *C. rogercresseyi* to emamectin benzoate due to the exclusive use of this chemotherapeutic to control this sea lice for long periods was reported by Bravo et al. (2008). Oral treatment with emamectin benzoate reduced *C rogercresseyi* juveniles but did not reduce the abundance of gravid females in *S. salar* (Mancilla-Schulz et al. 2019). However, studies in *O. mykiss* suggest that treatment against *C. rogercresseyi* using emamectin benzoate is regulated by the transcriptional expression of proteins involved in the metabolism, distribution and elimination of endobiotics and xenobiotics, such as hormones and drugs, and could even affect the pharmacokinetics of emamectin benzoate in the same treatment (Cárcamo et al. 2011). The extensive use of chemotherapeutics in the aquaculture industry has negatively impacted the sensitivity of *Caligus* species to delousing effects with these chemotherapeutants.

Studies have indicated that the abundance of adult *C. rogercresseyi* on fish farms that synchronized treatments with neighbors within 5 km was lower than the abundance on non-synchronized fish farms, 4 to 11 weeks after the procedure. These findings suggest the treatment synchronization effect was distance dependent and greater when neighboring farms up to 5 km away took part in the procedure (Arriagada & Marín 2018). Troncoso et al. (2011) demonstrated that feeding of *S. salar* with polyunsaturated aldehydes 2-trans, 4-trans decadenial (A3) has a potentially antiparasitic effect against *C. rogercresseyi*.

Adding 1.5 g/L of hydrogen peroxide to *S. salar* baths had an effectiveness of 100% against male *C. rogercresseyi* and 98.3% in females, compared with an effectiveness of only 55.6% against chalimus, which recovered from the treatment and were available to infest new hosts (Bravo et al. 2010). Meanwhile, 24 h baths with 0.000.4 and 0.002 mg/L of azamethiphos, 0.0002 and 0.001 mg/L of deltamethrin, 0.1 mg/L and 0.5 mg/L of emamectin benzoate, and 42 mg/L and 336 mg/L of hydrogen peroxide, negatively affected the fecundity rate of *C. rogercresseyi* (Bravo et al. 2015a).

Although effective, chemotherapeutants all involve environmental risks, can affect fish health and can negatively affect the public image of aquaculture. They also carry the risk of reduced sensitivity and resistance to chemical treatments on the part of the parasites. Efforts have therefore been made to replace them with more environmentally friendly methods. Oil of *Azadirachta indica* A. Juss used against *Caligus* spp. exhibited a median lethal concentration ($LC_{50\text{-}96h}$) of 2.0 mg/L, and *in vivo* assays indicated that 10.0 mg/L resulted in 100% antiparasitic efficacy within 96 h of exposure (Khoa et al. 2019b). Some fish species are not particularly selective in their food choices and will readily ingest both adult and larval *Caligus* spp. Alternatively, biological methods using cleaner fish, such as lumpfish *Cyclopterus lumpus* Linnaeus 1758 have been used for grazing on *Caligus* spp., reducing the parasitic infestations (Imsland et al. 2020).

Although varieties of chemotherapeutants are used to control the abundance of *Caligus* spp. on fish, some have not demonstrated the desired effectiveness. Despite the difficulties indicated above, however, the effective control and treatment of these sea lice may be achieved with the integrated management of a combination of measures.

## CONCLUSIONS

The identification of the global distribution patterns of *Caligus* species improved our knowledge on the dynamics of these ectoparasites in different ecosystems around the world. This knowledge can lead to a more precise mapping of the zoogeographical patterns of these parasites in host teleost from endemic regions and geographic hotspots, allowing the parasite species to be estimated and improving the understanding of infestation patterns in host fish with a wide geographic distribution, in addition to determining the global geographical range limits of *Caligus* spp. Biogeographical patterns of *Caligus* spp. diversity may also be useful for determining how host–parasite interactions can influence speciation. The results of the present study provide several relevant insights into the distribution patterns of these parasites in host fish and across the major oceans of the world, and it represents the most extensive survey of species of *Caligus* in host teleost in such waters. Nevertheless, the variation in the distribution and geographic patterns of *Caligus* spp. were little evident in many ecosystems and due to the limited data on the infestation of these sea lice on teleost populations in seas in different regions. Since regions with significant deficits in sampling to describe the occurrence of *Caligus* species in host teleost were identified, the understanding of the distribution of these parasite species requires greater sampling in all countries, especially in regions where none was carried out.

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## Author contributions

Marcos Tavares-Dias: Conception, elaboration and redaction. Marcos Sidney Brito: Confection of Maps and statistical analyses.