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Review

Metazoan Marine Parasites of Costa Rica: A Review

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Abstract: Many new marine parasite species are added every year. Still, in some places, mainly tropical regions, marine parasites have been little studied. An exhaustive review of the indexed publications where species of parasites are reported in the marine environments of Costa Rica was carried out. The history of research on marine parasites in this region is also reviewed. A total of 146 species of marine parasites have been reported in Costa Rica as parasites of 61 different species of hosts. Most of these parasites correspond to trematodes and cestodes, found mainly in the digestive tract of their vertebrate hosts. In Costa Rica, marine parasites have been studied mainly in sea turtles, elasmobranchs, fish, and dolphins. Most marine parasites have been reported based on morphological identifications of adult stages, and most of the work done so far consists of taxonomic identifications (species reports), with little contribution to the pathology and other aspects of the parasites–hosts interactions. The technical difficulties for research in marine parasitology, the lack of sampling in certain groups of hosts, and the lack of a consolidated research group in marine wildlife parasitology in Costa Rica are factors that have prevented a greater and faster advance in the knowledge of the biodiversity of marine parasites in this country.

Keywords: platyhelminthes; trematodes; cestodes; monogeneans; acanthocephalans; nematodes; annelids; copepods; isopods; barnacles; marine environments; diversity

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1. Introduction

The parasitic lifestyle is successful. An initial estimation of nearly 40% of known species to be parasitic was made by Rhode [1]. New data have made researchers change their minds about the diversity of parasite fauna. The awareness of the numbers of potential hosts, cryptic species, and the exponential growth in the discovery rate of new parasite species is increasingly revealing the actual numbers, which now are thought to be more than half of all organisms known [2–5]. In marine environments, many new parasitic species or new reports are added every year. Still, even so, marine parasites of certain diverse groups, like fish, have been under-sampled worldwide, especially in the tropics [3]. Sampling effort is known to be positively correlated to parasite species richness [5].

Several factors have been proposed as determinants of parasite richness. One of them, apart from sampling effort, is latitude. As latitude values become lower, overall species richness increases, and parasite species richness is also predicted to increase. Interestingly, that has been demonstrated only for microparasites (virus, bacteria, protozoans) from primates and rodents. It has been hypothesized that this could result from comparatively little sampling effort of the many other groups of hosts that are harder to sample [5]. Such a gradient in parasite species could tell us about the importance of factors such as temperature variation, humidity, rainfall, and biodiversity of potential hosts as determinants of parasite species richness [6]. The analysis of parasite richness becomes more complex as many parasites in aquatic systems have significant seasonal variations depending on the taxonomic group and the specific environment [7].

Hosts and their parasites communities have complex relationships; the characteristics of the hosts, parasites, and environment affect each other. For one species of host, the environment could be a powerful predictor of the diversity and abundance of parasites, whereas, in other situations, biological variables of hosts and parasites might be more important in determining how these communities are shaped [8]. Parasites also help shape community structure by reducing host fitness. They not only have a role in organizing a given community structure, but they also influence interspecific interactions and destabilize community dynamics when certain environmental conditions change considerably [9]. In a global climate change era, this is of major concern.

The information on marine parasites of the neotropical regions is dispersed. In Costa Rica, there have been some prolific moments of studies on marine parasites in the past, led by just a few enthusiastic researchers, mostly foreigners, who described several new species and contributed many new species reports for the region. Nevertheless, research on this topic has been scarce in the last decade. This review aims to provide a comprehensive overview of the research that has been done so far on the marine parasites of Costa Rica. We present a list of the metazoan marine parasites reported for Costa Rica and point out gaps in research of parasite groups, geographic regions, and hosts.

2. Results

2.1. Brief History of Marine Parasites Research in Costa Rica

More than 50 papers have been published with information on marine parasites of Costa Rica, 43 of them from the Pacific waters and eight from the Caribbean, starting in the 1930s, with peaks of publication in the 1990s, 2000s, and 2010s decades (Figure 1; Appendix A, Table A1). The first reports were based on collections by Harold W. Manter, done at Bahía Culebra on 24–25 February 1934, during the third Allan Hancock Expedition to the Galápagos Islands (and the neighboring Pacific) [10]. The first paper was on parasitic copepods of fish by Charles B. Wilson in 1937 [11], followed by the description of a new species of a monogenean by Frank G. Meserve [12], while Manter (1940) reported and described new species of digenetic trematodes of fishes [13]. Harley J. Van Cleave (1940) described a new species of acanthocephalan from the stomach of a fish [14]. Schmitt (1939) visited Isla del Coco during the US Presidential Cruise of 1938 and collected parasitic copepods from fish and a fleshy cirripedian [15].

The next set of publications was in the late 1950s and early 1960s by Rodrigo R. Brenes-Madrigal, of the Universidad de Costa Rica (UCR) and his Mexican colleagues of the Universidad Nacional Autónoma de México (UNAM). They published on helminth parasites of fish [16–18]. Only one paper was published in the 1970s on monogenean parasites of the skin of *Carcharhinus leucas* and elasmobranch trematodes in Barra del Colorado, north Caribbean [19]. Two papers were published in the 1980s, one that mentions parasitic copepods of scombrids (mackerel and tuna) [20], and another is a thesis on trematodes of marine fishes [21].

The 1990s was the most productive decade with 13 papers, most by research groups headed by Daniel R. Brooks and Fernando Marques, University of Toronto, and UNAM, on parasites of elasmobranchs and teleost fish. Six of these papers are on cestodes, and a total of 15 new species and two new genera were described, including all groups of helminth parasites [22–28]. Not only vertebrate parasites were found in this decade. Patricia Jiménez and Mario Vargas of UCR (1990) reported the presence of an isopod in a shrimp [29], while V.A. Zullo found an ectoparasitic barnacle on a lobster [30], and J.C. Markham found new ectoparasitic bopyrid isopods on porcellanid crabs [31]. Finally, Lamothe-Argumedo and collaborators listed 11 marine parasitic species from Costa Rica in the Mexican National Helminth Collection Catalogue [32].

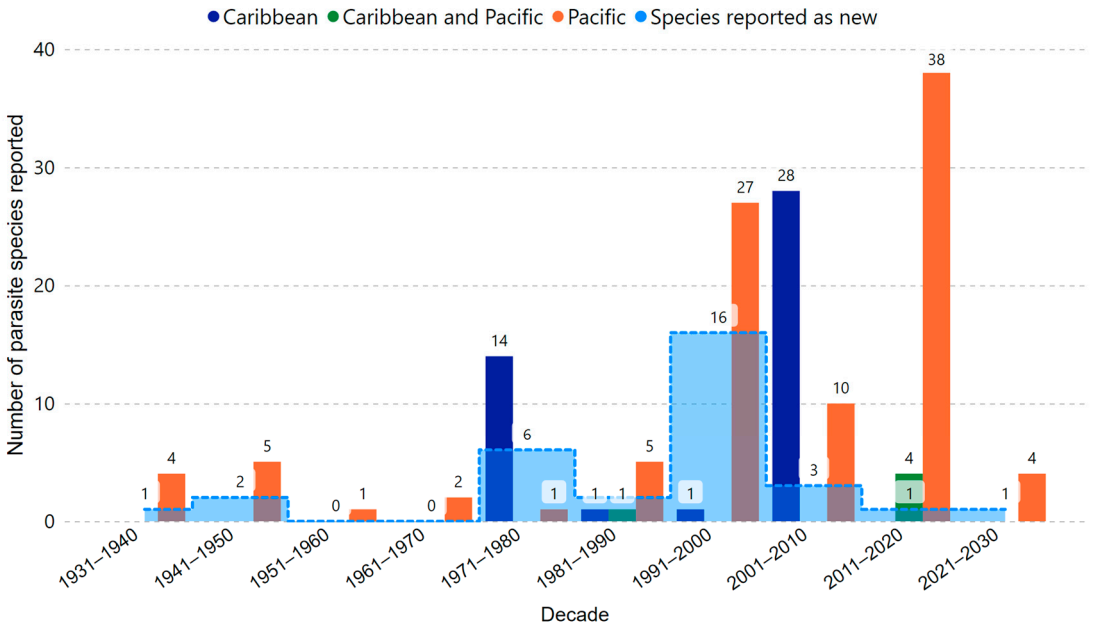

Figure 1. Number of new marine parasite reports for Costa Rica over the decades. The first parasite collection was done in the early 1930s, and the last one in November 2022. More species have been reported in any decade in the Pacific. For the Pacific, the most productive decade was 2011–2020 and 2001–2010 for the Caribbean. The orange line represents species reported as new; most species reported as new were reported in the 1991–1980 decade. The period between 2001 and 2020 has been highly productive. Four species of marine parasites, three new, have been published for Costa Rica in the first two years of 2021–2030.

The decade between 2001 and 2020 was very productive, with 81 new marine parasite reports in 21 publications, mainly from sea turtles and dolphins. Research groups headed by Dr. Mario Santoro reported the presence of 41 marine parasite species in sea turtles from Costa Rica. They published four papers on parasites of the green turtle *Chelonia mydas* from Tortuguero, in the Caribbean of Costa Rica, and synthesized this information in a book about the digenetic trematode community in nesting green turtles of this region. These contributions included the description of a new species of digenean parasite [33–37]. Majewska, Robinson, and Santoro, each in a different collaboration, contributed to studying parasites associated with nesting olive ridley turtles *Lepidochelys olivacea* in the north Pacific of Costa Rica [38–40] and parasites of the hawksbill turtle *Eretmochelys imbricata* were also studied by Santoro [41]. In the book on Costa Rica's marine biodiversity, Santoro and Mattiucci published a synthesis of the knowledge on marine turtle parasites of Cost Rica [42].

Other publications during these decades included one on an ectoparasitic copepod of a shark [43], another on fish-parasite isopods [44], and isopod parasites of crabs [45]. Rodriguez-Ortiz, in 2004 [46,47], compiled a checklist of helminth parasites of vertebrates in Costa Rica, including several marine vertebrate parasite species, while Cortés (2009) published a list of marine fish parasites [48]. In 2011 Oliveira and collaborators published on parasites of stranded cetaceans on the Pacific coast of Costa Rica [49]. In the late 2010s, there were two publications on fish parasites, one on monogenean parasites of marine fishes in the Gulf of Nicoya and one on acanthocephalan parasites of mullet fish that included material from Costa Rica [50,51].

The last publications regarding Costa Rica's marine parasites were published in 2021 and 2022. In one of these publications, the authors used molecular approaches to study the diversity of haploporid trematodes from mugilid fish in Central America and found two new species of these trematodes, including the new genus *Ekuarhuni* [52].

Finally, Angulo and Sibaja-Cordero made the most recent addition to the marine parasite fauna of Costa Rica by reporting the presence of an interesting parasitic cirripedian in the ninja lantern shark (*Etmopterus benchleyi*) [53]. By the end of 2022 and the beginning of February 2023, no more recent additions, or studies on the marine parasitic fauna of Costa Rica have been made.

2.2. Costa Rican Marine Parasite Diversity

A total of 146 species of marine parasites, belonging to 113 genera in five animal phyla, have been reported in Costa Rican marine and brackish water animals (Appendix A, Table A1). Thirty-two were reported as new species and described from material collected in Costa Rica. Three species were described as new genera, and 38 species were new reports for the eastern tropical Pacific when reported (Appendix A, Table A1). Of all these species, 47 (32%) are deposited as voucher specimens in any Costa Rican biological collection (Colección Helmintologica de Costa Rica or Museo de Zoología UCR), with more than two-thirds of the collected material deposited as voucher specimens in biological collections in other countries, mainly in the United States and México (Supplemental Figures S1 and S2).

More researchers have sampled sites in the Pacific in search of marine parasites than on the Caribbean coast (Appendix A, Figure 2). The number of species reported from each coast reflects this differential sampling effort, with more species reported in the Pacific of Costa Rica and significantly fewer marine parasite species reported for the Caribbean Sea (Figures 2 and S1). These efforts had rendered a total of 51 species reported for the Caribbean, 101 for the Pacific, and five species present on both coasts (Figure 2). Most species have been sampled from coastal and brackish waters.

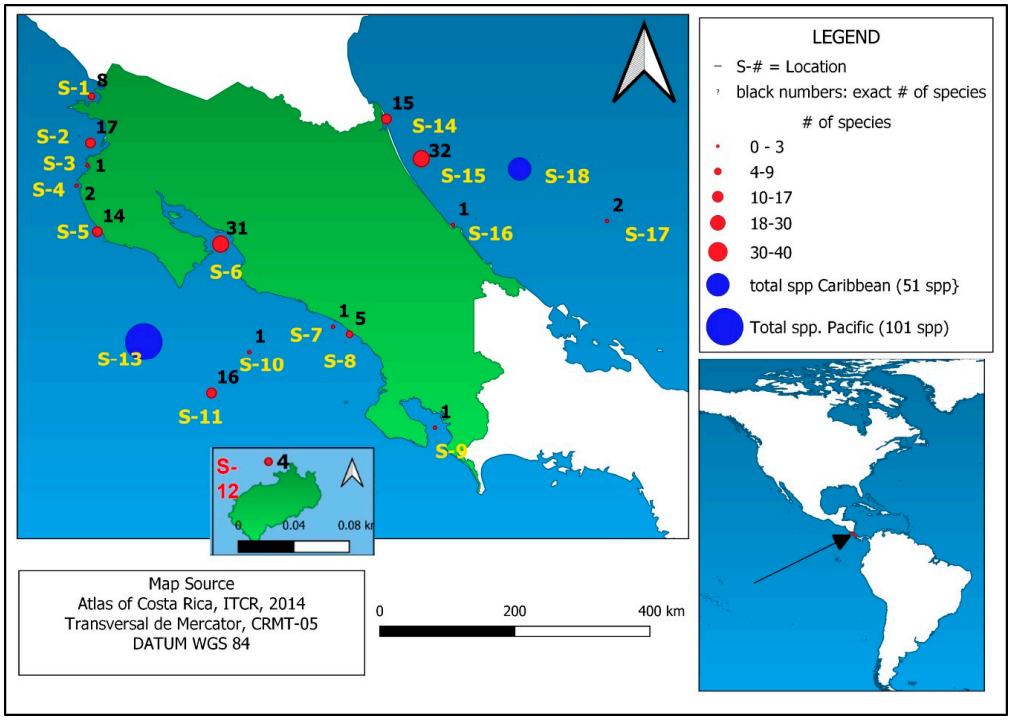

Figure 2. Map showing the main locations (S-1 to S-17) where marine parasites have been collected and identified in Costa Rica. The number of species per site (red dots, different sizes, exact number in black numbers) and the total number of species per coast (blue dots). Santa Elena Bay (S-1), Gulf of Papagayo (S-2), Prieta Bay (S-3), Tamarindo Bay (S-4), Ostional (S-5), Gulf of Nicoya (S-6), Mata Palo (S-7), Punta Dominical (S-8), Golfo Dulce (S-9), 60 km off Quepos (S-10), species with no exact location reported in the Pacific (S-11), Isla del Coco (S-12), Barra del Colorado (14), Tortuguero (S-15), Moín (S-16), Species with no exact location reported in the Caribbean (S-17). Total number of species reported in the Caribbean (S-18), total number of species reported in the Pacific (S-13).

Santoro and collaborators, during several years in the 2000–2015 period, and Watson and Thorson (1976) did most of the work that resulted in new reports for the Caribbean, while, in the Pacific, several authors (F. Marques, J.B Oliveira, M. Santoro, G. Ponce de León, and R. Majeuska) lead the description of new species of marine parasites for Costa Rica. Neodermata flatworms (Trematoda, Monogenea, and Cestoda) dominate the metazoan parasitic fauna known for Costa Rica, representing 71.9% of all the marine parasite species, all of which are parasites of vertebrates (Figure 3). Within Neodermata, 42.5% of the total reported species are trematodes, and most of them (55 out of 62) are classified in the order Plagiorchiida. Most trematodes reported were found in turtles (64.5%), and fish (29%), parasitic or epibiont crustaceans were found mainly in fish (32.2%), and cestodes have been found mainly in elasmobranchs (mostly in rays) (82.8%) (Figure 3).

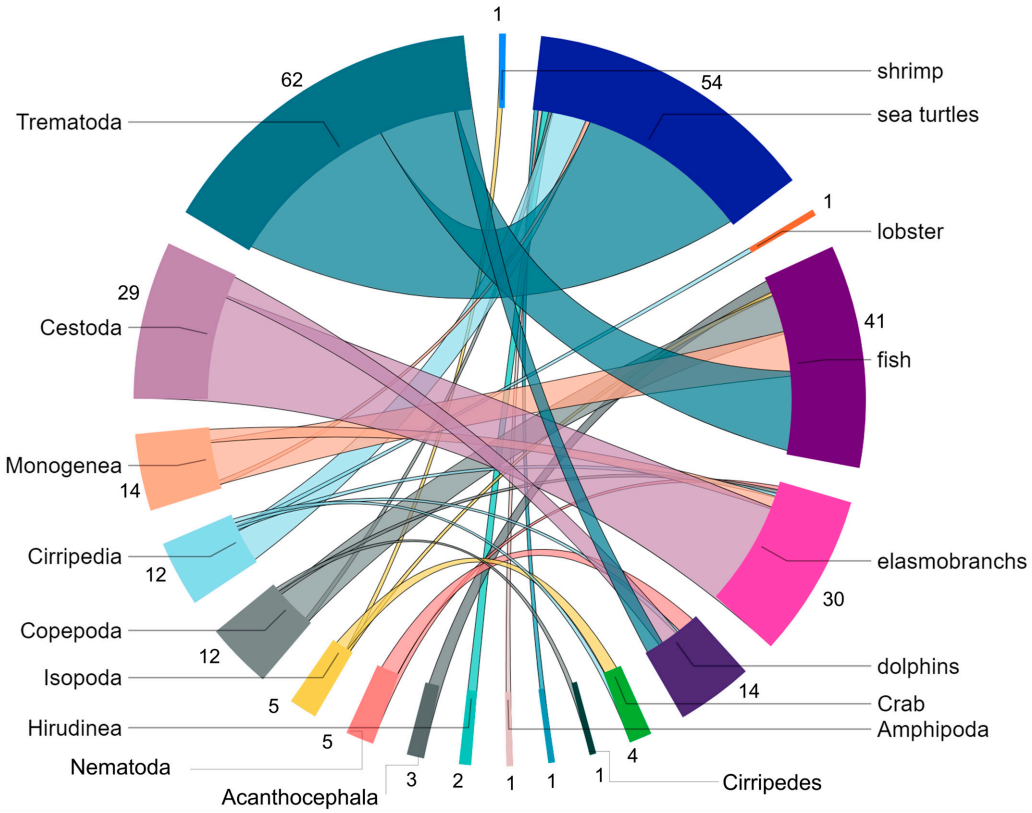

Figure 3. Number of marine parasite species reported for Costa Rica according to the taxonomic group (left side labels) in which they are classified and according to the type of marine host. The main groups of parasites are trematodes parasitizing sea turtles and fish, and cestodes parasitizing elasmobranchs.

Sixty-one different marine or brackish water species have been identified as hosts for this marine parasite diversity in Costa Rica. Sea turtle species (*L. olivacea*, *C. mydas*, and *Eretmochelys olivacea*) and fish species are the hosts for most of the marine parasites reported (Figure 4A). The rest of the species have been reported in elasmobranchs, dolphins, and a few species as parasites of some crustaceans, such as crabs, lobsters, or barnacles. Most parasites were obtained as adults from the digestive tract, while other common parasite collection sites were the gills of fish (Figure 4B).

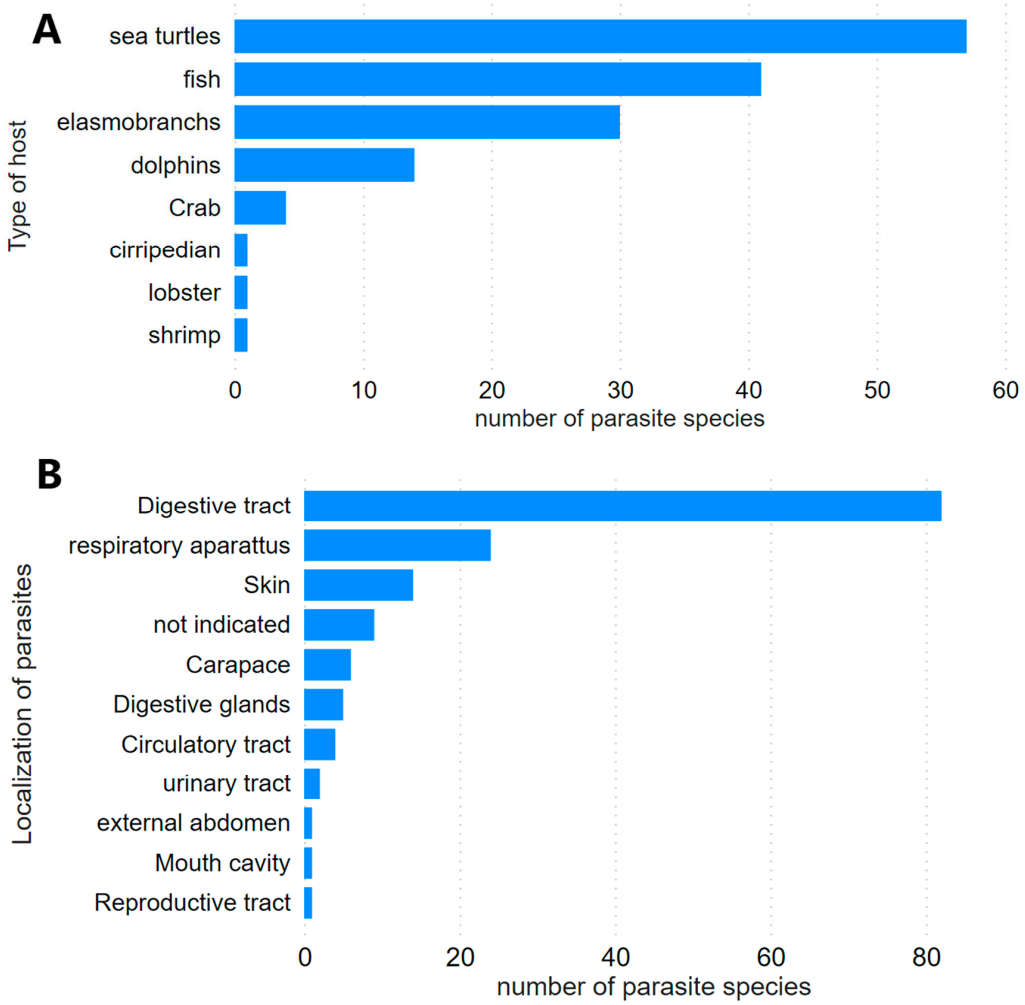

Figure 4. (**A**) Number of parasite species per type of host species. (**B**) number of parasite species per anatomical localization.

2.3. Platyhelminthes

Most marine parasites reported in Costa Rica are intestinal neodermatan platyhelminths, mostly trematodes and Cestodes.

2.3.1. Trematodes

Most of the reports on marine parasites of Costa Rica are trematodes (Figure 3). Digenean trematodes have been the most reported marine parasites in the Caribbean and the Pacific (Appendix A, Table A1). They have been found parasitizing bony fishes, sea turtles, and dolphins. Several families of the order Plagiorchiida are present as parasites of Costa Rica's marine vertebrates, and 7 out of these 62 reports were new species when reported (Supplementary Table S1). The digestive tract of hosts was the most frequent localization. Even when no marine trematode parasites have been reported in elasmobranchs (rays and sharks), 62 marine trematode species are informed for Costa Rica: 40 species in sea turtles, 18 species in fish, and 4 species in dolphins. These trematodes belong mainly to the order plagiorchiida and are classified into 21 different families. Families Pronocephalidae and Hemiuridae are the most diverse in sea turtles and fish, respectively, while the Brachycladidae family has been the only found up to now in dolphins from Costa Rica.

2.3.2. Trematdoes from Sea Turtles

The biodiversity and other aspects of trematode infections in turtles of Costa Rica are better known today thanks to the work of Mario Santoro and his collaborators. They

devoted much of their work over several years investigating these aspects, mainly in the north Caribbean and North Pacific [29–33,36–38]. Thanks to their work, they described one new species and six new reports of marine parasites of sea turtles of the Caribbean and the Eastern Tropical Pacific (ETP) as a part of the reports of 40 marine turtle parasites not previously known for Costa Rica (Appendix A, Table A1).

A total of 33 species of plagiorchiid and 7 diplostomid trematode parasites have been reported in Costa Rican sea turtles: 20 species in the family Pronocephalidae, 6 species in Spirorchiidae, 5 in the family Microscaphidiidae; and the rest are in the families Cladorchidae, Opecoelidae, Gorgoderidae, Pachypsolidae, and Plagiorchiidae (Figure 5). Such diversity has been recorded from only three out of the seven sea turtle species arriving on Costa Rican coasts: the green turtle *C. mydas* (mostly from Tortuguero National Park, in the north Caribbean), the olive ridley turtle Lepidochelys olivacea (mostly from Ostional beach, in the north Pacific), and *E. imbricata* (also from Ostional beach). *Pleurogonius tortugeroi* sp.n was described from material collected from the lower intestine of *C. mydas* from Tortuguero National Park in 2007 [30].

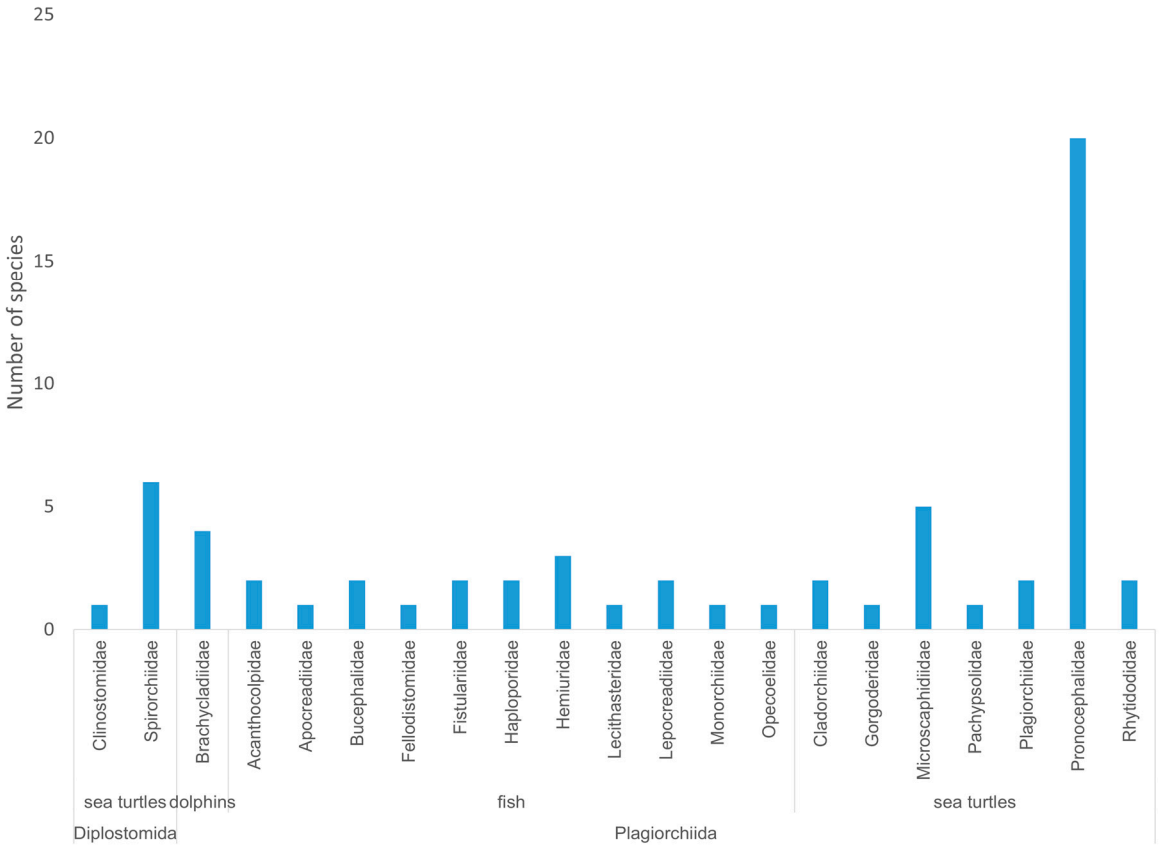

Figure 5. Diversity of families of marine trematodes reported for Costa Rica and type of host in which they were reported, data from 1937 to 2022. The Plagiorchiida order is the most diverse; only one other order has been reported, the order Diplostomida. Family Pronocephalidae (20 spp.) from sea turtles represents the majority of the species reported for Costa Rica.

Five more trematode species (four in Pronocephalidae and one in Spirorchiidae) found in *E. imbricata* were new reports for sea turtle parasites in the Eastern Pacific [37]. Up to now, research on sea turtle parasites has revealed that Pronocephalidae is a very common family of digenean sea turtle parasites in Costa Rica and that there is a significant overlap among digenean parasite species of sea turtles in the Pacific of Costa Rica and other places of the Pacific coast of the American continent [33–42,54–56]. Within the trematodes, only partial genetic sequences of some ribosomal genes have been published for *Homalometron lesliorum*, *Ekuarhuni papillatus*, and *Forticulcita isabelae* (Appendix A, Table A1).

Using histopathological analyses, Santoro and collaborators have additionally provided information on the pathological changes caused by the parasites on its hosts, mainly at Tortuguero (Caribbean Coast) and Gulf of Nicoya (Pacific Coast). They found lesions in the heart and great vessels caused by spirorchiids in nesting *C. mydas*, killed by jaguars *Panthera onca*, at Tortuguero National Park. Lesions were caused mainly by *Learedius learedi*, *Hapalotrema postorchis*, and *Monticellius indicum*. Eggs of these parasites were found affecting other tissues and organs like the digestive tract, spleen, gall bladder, urinary bladder, and other sites in the host [37].

Most studies on sea turtle parasites have been performed on relatively few stranded or nesting individuals. Santoro [42] pointed out that it is difficult to clarify how ontogenetic and ecological factors such as diet, foraging habits, habitat, or population density influence the helminth community of a given turtle species with a such scarcity of data. Many of the previously cited factors are also affected by global warming and habitat loss [5]. Still, there is no data on what is happening with parasites of sea turtles concerning those changes.

2.3.3. Monogeneans

Fourteen species of monogeneans in nine families have been reported for Costa Rica. Four of them were reported as new species (Appendix A, Table A1). Adult monogeneans are inhabitants of the gills of fish or cloacal membranes of aquatic turtles or amphibians. In marine environments of Costa Rica, they have been found in 12 different species of hosts, mainly carangid fish in the Gulf of Nicoya and the north Pacific coast [12,50], bull sharks in brackish environments of Barra del Colorado [18], and one species, *Jaliscia caballeroi*, was found parasitizing the skin of olive ridley turtles in the Pacific coast [46]. All monogenean marine parasites of Costa Rica have been found parasitizing their hosts' gills or skin (Appendix A, Table A1). The latest additions of monogenean species for Costa Rica were made by Aguilar-Aguilar and collaborators in 2018 [50]. Their reports increased the marine monogenean reports by adding three species to the list. The family Microcotylidae is represented by three species, one in the skin of the olive ridley turtle, *L. olivacea*, one in the red snapper fish *Lutjaus colorado*, and one in the bull shark *Carcharhinus leucas*. Hexabothriidae, Diclidophoridae, and Chauaneidae (each with two species reported) have been found in fish and elasmobranchs (Figure 6).

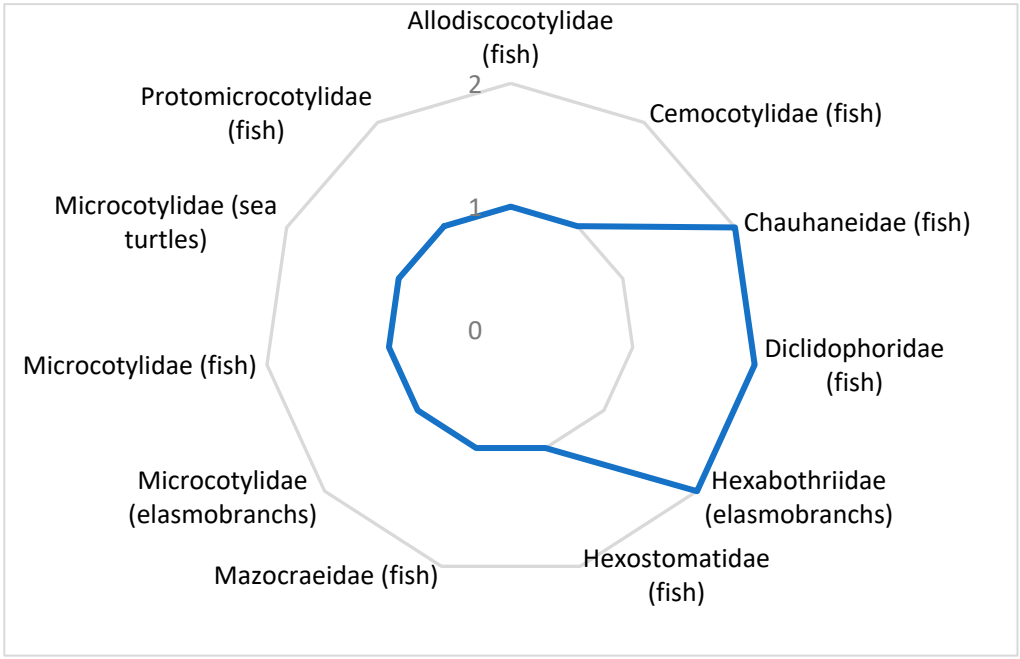

Figure 6. Diversity of Monogenea families reported for Costa Rica and type of host they were reported, data from 1937 to 2022. The circular axis represents the number of species.

2.3.4. Cestodes

A total of 29 species of cestode parasites of marine Costa Rican fauna have been reported since 1976 [19]. Tetraphyllideans (15 spp.) accounted for 51.7% of the cestode species found up to now, followed by Phyllobothriideans (5 spp.). The Tetraphyllidean family Onchobothriidae is the one with more species reported, all in elasmobranchs, mainly rays (Figure 7). Cestode parasites in marine environments of Costa Rica have been found parasitizing mainly rays of the Dasyatidae, Myliobatidae, Urotrygonidae, Narcinidae, and Pristidae; the bull shark *Charcharhinus leucas* and dolphins (three spp. in the tetrabothriidae family found in several *Stenella* species) (Appendix A, Table A1). All of them but two were found in the digestive tract (intestine, spiral valve, rectum) one species, *Phyllobothrium delphini*, was extracted from a subcutaneous blubber in the dolphin *Stenella coeruleoalba*, and one species, *Monorygma grimaldii*, was found in the intestine, testis, and uterine ligaments (Appendix A, Table A1).

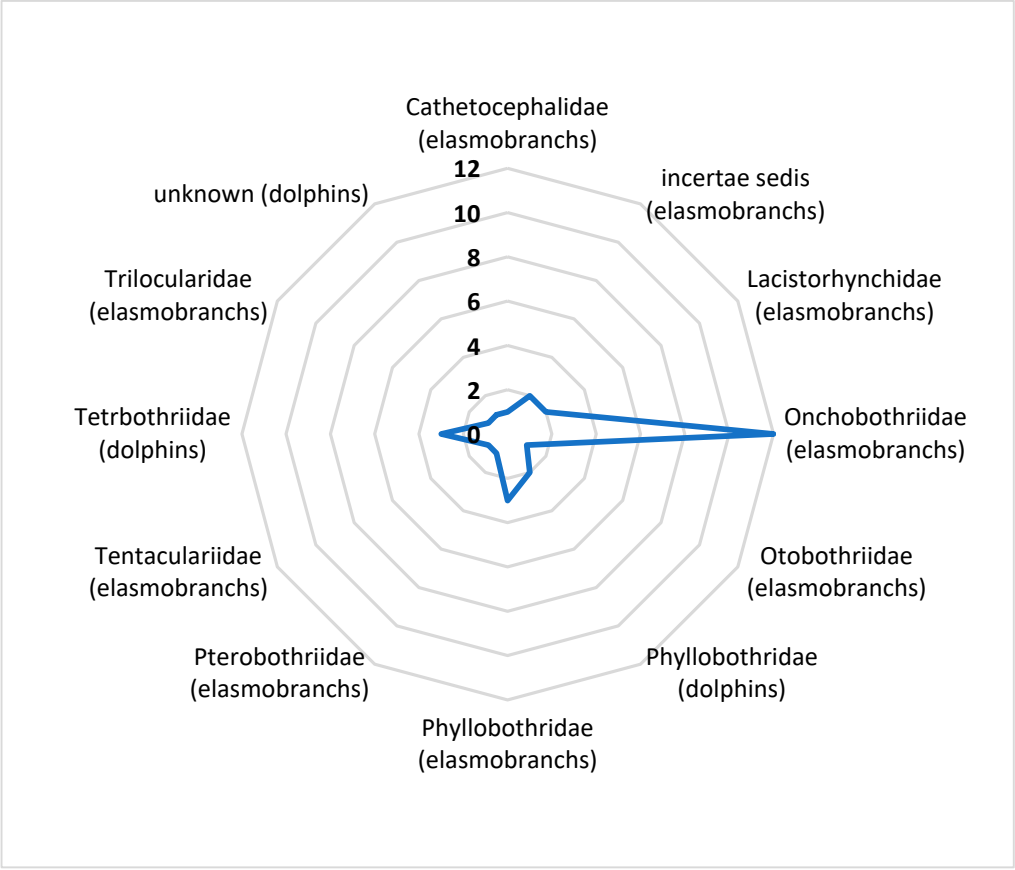

Figure 7. Diversity of marine parasitic cestodes families reported for Costa Rica and type of host they were reported, data from 1937 to 2021. The circular axis represents the number of species.

No cestode parasites have been reported in Costa Rican sea turtles or fish. The most diverse cestode genus of marine cestodes in Costa Rica is *Acanthobothrium* (Onchobothriidae), with eight species described in the 1990s in three papers published by the group headed by Marques; in these papers, they reported new species being those eight *Acanthobotrhium* species, plus one *Acanthobothrioides* species (*A. pacificus*, also in the Onchobothriidae family) while sampling different species of rays [22–25]. Cestoda is the parasite group where more new marine helminth parasites have been discovered and described as new species, with 15 species reported as new, including one new genus, *Escherbothrium*, represented by the species *E. molinae* found in a ray, *Urotrygon chilensis*, described by Berman and Brooks [57] (Appendix A, Table A1). DNA sequences from the r28S gene of *Escherbothrium* sp. were identified from a sample in *Urotrygon aspidura*, but morphological details were not anno-

tated by the author [58], within cestode marine parasites of Costa Rica; this is the only genetic sequences available. The latest additions to the list of marine cestode parasites were made by Oliveira and collaborators in dolphins in 2011 [49]. Besides the study by Oliveira, all other additions to the list of marine cestode parasitic fauna were made before 1998.

2.4. Nematodes

Five species of nematode worms in four families have been reported as parasites of marine animals in Costa Rica, all of them in the Pacific [49]. Four of them were found to be endoparasites of dolphins (stranded), and one species in the spiral valve of a dasyatid ray (*Himantura pacifica*), which resulted in being a new species [59] (Appendix A, Table A1). *Anisakis* sp., the most prevalent, was found in the digestive tract of dolphins, causing gastritis [49], while *Halocercus lagenorhynchi* was collected from the lungs and air passage of dolphins causing granulomatous pneumonia [49], and individuals of *Crassicauda anthonyi* were collected from the kidneys of *Ziphius cavirostris* with partial destruction of these organs [49]. All those nematode parasites were new geographic records for the Pacific coast of Central America and increased the reported occurrence of the parasites in new hosts [49]. Even though sea turtle parasites have been thoroughly investigated in Costa Rica, no parasitic nematodes from sea turtles have been reported in Costa Rica. Furthermore, nematodes are the most diverse group of parasitic helminths; however, to date, very few species have been identified as parasites of Costa Rican marine fauna.

2.5. Acanthocephalans

Only three species in two families of acanthocephalan marine parasites have been reported for Costa Rica, all from the Pacific coast, each in the digestive tract of a different teleost fish species (Appendix A, Table A1). No acanthocephalan species in marine animals have been reported in the Caribbean. *Koronacantha pectinaria* (originally described as *Tegorhynchus pectinarius*) was described by Van Cleave in 1940 based on material obtained from an uncertain host in Bahía Culebra, Pacific coast of Costa Rica, with no other publications on this species since then [60]. Further investigations on parasites of marine fishes from Charmela Bay, México [61] found several specimens later identified as *T. pectinarius*. To make a comparison with the original material, researchers realized that the original material from Van Cleave was lost, so they collected more material in the type locality in Bahía Culebra. These specimens were redescribed based on 16 male and 32 female specimens from Costa Rica and México found in the fish *Microlepidotus brevipinnis* (Perciformes: Haemulidae) and assigned this parasite to the species *Koronacantha pectinaria*. The site of infection for all these specimens was the intestine and caecum. This one was the first report of males of this parasite, and until 2015, it was also the only report of an acanthocephalan parasitizing Costa Rica's marine fauna [60]. In 2015 Pinacho-Pinacho and collaborators found the species *Neoechinorhynchus mamesi* parasitizing the intestines of sleeper fish (*Dormitator maculatus*, *Dormitator latifrons*), and in 2020, Rosas-Valdés reported *Floridosentis pacifica* in the intestines of a mullet *Mugil curema*, collected during their research about the genetic variation of the genus *Floridosentis* in mullets from the Americas [51,62]. To our knowledge, studies on *K. pectinaria* other than taxonomic are lacking; the species has been used to explore molecular phylogeny within the Neodermata group [62], and genetic sequences (LSU, ITS, and cox 1) from *Floridosentis* specimens from this study are the only genetic sequences of any costarican marine acanthocephalan known up to now [51].

2.6. Hirudinean Annelids

Santoro and collaborators described lesions on the skin of sea turtle *C. mydas* from Tortuguero, Caribbean coast of Costa Rica, produced by leeches, *Ozobranchus branchiatus* [63]. They found traumatic purulent and ulcerative dermatitis lesions in more than 50% (n = 47) of turtles sampled associated with *O. branchiatus* and eggs of this leech on the surface of the carapace of 39 of those turtles. That information is relevant as *O. branchiatus* is one of the candidates to be a mechanical vector of fibropapilloma-associated turtle herpesvirus

in sea turtles [63,64]. Majewska and collaborators, in 2015, found a high prevalence of *O. branchiatus* in *L. olivacea* sea turtles from Ostional, Guanacaste, and found a much less prevalent presence of another *Ozobranchus* species, *O. margoi* also in the olive ridley turtle from Ostional [40].

2.7. Parasitic Crustaceans

Thirty-one species of marine crustaceans living as ectoparasites or as epibionts have been recorded for Costa Rica. Most of them are copepods (12 spp.) and cirripedes (12 spp.), and seven other species are isopods, amphipods, or decapods. Figure 8 illustrates the diversity of crustacean marine parasites at the family level in each type of host (Figure 8). Only two parasitic crustacean species have been recorded from the Caribbean, one cirripede and one copepod; the rest are reports from the Pacific (Appendix A, Table A1).

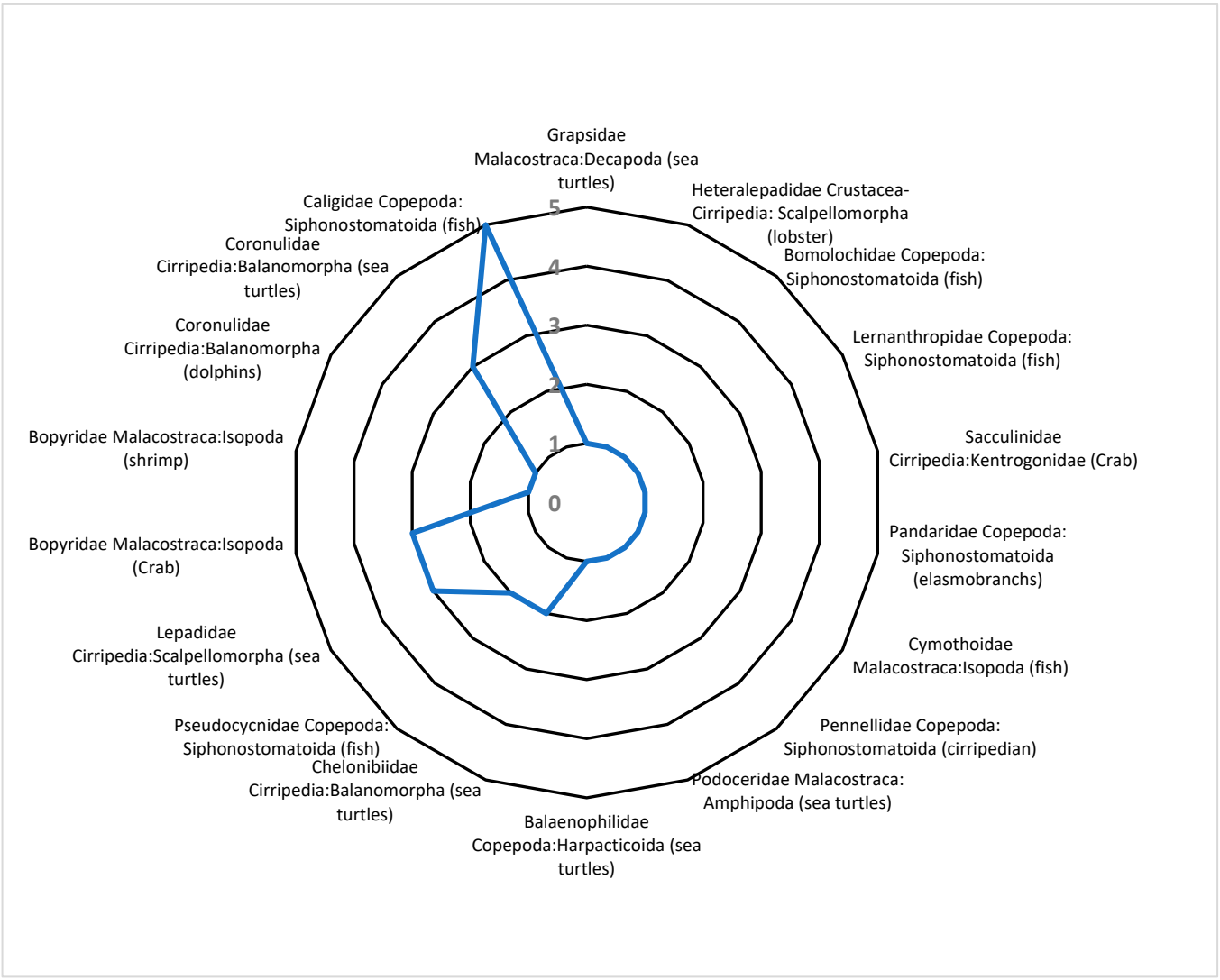

Figure 8. Diversity of marine parasitic crustacean families reported for Costa Rica and type of host where they were reported, data from 1937 to 2021. The circular axes represent the number of species. Caligid copepods are better represented in fish, while bopyrid isopods are in porcellanid crabs.

2.7.1. Parasitic Malacostracan Crustaceans

Five species of isopods have been found as parasites of marine animals in Costa Rica. Most of them (four) are in the family Bopyridae and are parasites of palaemonid and porcellanid crabs. One more species, *Cymothoa exigua* (Cymothoidae), has been found in

snapper fish (several species of Lutjanus). The material of *Aporobopyrus trilobatus* collected from Costa Rica was found in a new host for this parasite species, the crab *Petrolisthes ortmanni* [45]. In the same paper, Markham reports the presence of a new species in the genus *Aporobopyrus*, *A. bourdonis,* in *Petrolisthes edwardsi*, also collected in Costa Rica. Cymothoid isopods are parasites represented in Costa Rica by the species *Cymothoa exigua*, which is distributed from the Gulf of California to southern Ecuador and Islas Galápagos. This species was first collected from Golfo de Nicoya, between Isla Jesucita and Islas Negritos, between 1979 and 1981 as a parasite of *Pomadasys maculatus*; this fish does not occur in the ETP), so the identification of the host is uncertain. Later in 1990, three new host species for this parasite were reported in Costa Rica (*Lutjanus colorado*, *L. jordani*, and *L. peru*). Two of these hosts, *L. colorado* and *L. jordani*, from Costa Rica, were also new host reports for *C. exigua* in the eastern tropical Pacific [44]. Only one species of parasitic amphipod has been reported for Costa Rica, *Podocerus chelonophilus* in sea turtles, *L. olivacea*, from the Pacific [48]. Finally, one unidentified grapsid crab in the genus Planes was found on the carapace of *L. olivacea*; this is the only report of a decapod as a marine epibiont of sea turtles in Costa Rica [39].

2.7.2. Copepodes

Twelve species of marine parasitic copepods, most of them in the family Caligidae, have been reported to be present in Costa Rica (Figure 8, Appendix A, Table A1). These species were found mainly on the gills and fins of Scombrid and Carangid fishes [11,15,20,65], although one species was found on the pectoral fins of bluefin sharks [43], and one harpacticoid balenophilid copepod, *Balaenophilus manatorum* was found in the olive ridley turtle, *L. olivacea* [39]. One additional new species of Caligid, *Lepeophtheirus alvaroi,* was found in a plankton sample in Isla del Coco and was found unattached to its host [65]. Three of the copepod species reported for Costa Rica were newly described species. One of the copepod species, *Pennella instructa* (Pennelidae), was found parasitizing the barnacle *Conchoderma virgatum* [15].

2.7.3. Cirripedians

Twelve species of ectoparasitic cirripedes have been reported for Costa Rica, most of them in the families Lepadidae and Coronulidae, mainly as ectoparasites of the olive ridley turtle *L. olivacea*. Also in sea turtles, two chelonibiid cirripedes were reported, *Stepnaholepas muricata* (on *C. mydas* and *E. imbricata*), and *Chelonibia testudinaria* (on *L. olivacea*) [40,66]. Two species of cirripedes were reported as ectoparasites of other crustaceans; one of them was a new species of sacculinid *Ptychascus barnwelli*, which was found under the abdomen of Ocypodid crabs (genus *Minuca*) in the Caribbean of Costa Rica [67]. The description of this new species was based on the ultrastructural study of the cyprid larval stage. The other is *Paralepas quadrata* which was found on the lobster *Panulirus penicillatus* [30]. Another Coronulid species, *Xenobalanus globicipitis*, was found over the caudal fluke of the dolphin *Stenella attenuata* in the Pacific of Costa Rica (Appendix A, Table A1) [49]. All but one of these reports were made after 2010; before this year, only the new species *Ptychaschus barnwelli* had been described for Costa Rica.

3. Discussion

To our knowledge, this is the first comprehensive list (all taxonomic groups recorded) of metazoan marine parasite species published for a country. In general, these types of reviews focus on listing the parasites of some group of hosts, in the case of the Americas, mainly marine fish parasites of North and South America [68,69]. Most reports are species lists made by a singular group of researchers that studied in a relatively short time a particular group of hosts (e.g., fish, elasmobranchs, dolphins, sea turtles). This list, therefore, provides information that will serve as a baseline for future research on the diversity of parasites in the marine environments of Costa Rica.

Few authors who have studied marine parasites in Costa Rica have been working in this country for a prolonged period and published more than one paper reporting marine

parasite species for Costa Rica, as seen in Figure 1. Although marine parasitology in Costa Rica started in the decade of 1930s, the decades of the late 1970s, 1990s, and the years after 2000 have been the most productive in terms of new reports. This can be since marine biodiversity, in the early years of research, was performed mostly by expeditions that used to collect within a very large range of distance, in several countries, with the only objective of describing new species but not focusing on a particular place, with little time of sampling effort in each location [10–15]. Research groups that focused more on a particular type of host and in particular locations came to Costa Rica in the 1970s, 1990s, and after, and so made more additions to the marine parasites fauna than in the early years; this is the case of the works by Watson and Thorson with elasmobranchs, Oliveira and collaborators with stranded dolphins, and Santoro and collaborators with sea turtles [19,22–25,33–38,49]. In addition, marine biological sciences in Costa Rica did not begin to develop until around 1971 [70].

Since then, no research group, with its base in Costa Rica, has dedicated systematic efforts to marine wildlife parasitology in this country, and throughout the history of marine parasitology in Costa Rica, it can be concluded that this topic, has been studied mainly by foreign researchers on very specific groups of parasites and hosts (from all the reported species, only 2 out of 146 reports come from a group headed by Costa Rican Scientists). These foreign researchers have made important contributions during limited periods without the emergence or consolidation of an autochthonous marine parasitology research group in the country. Because of the above, in Costa Rica, there is a lack of material deposited in the national scientific collections of parasitology or zoology; most of the comparison material is deposited in other collections, mainly in México, the United States of America, and Switzerland. This is a global problem regarding natural history collections in Latin America, and that continues today, with several groups of researchers that come to Latin American countries, collect biological samples, and take them to other countries, leaving neither specimen deposited in the local biological collections, nor a strengthen capability in Costa Rican researchers to make further advances in the field. Undoubtedly, this harms the pace of progress in the knowledge of the marine parasite biodiversity of Costa Rica [71].

Among the marine parasite groups, helminth parasites have been the most reported parasites in Costa Rica and around the world [2,72]. This can be explained as helminth parasites are more diverse than other marine animal groups that have developed a parasitic style of life [2]. Additionally, their specific identification based on morphology is usually plausible, and sampling methods are easier to gather the specimens; while protozoans, bacteria, and viruses are difficult to sample and identify without using several immunological and molecular techniques.

Most of the parasitic helminths of marine hosts described or reported so far for Costa Rica correspond to trematodes and cestodes, and the identifications were mostly based on the morphology of the adult (for most species, other stages of the life cycle remain undetermined). A simpler morphology-based taxonomy in adult trematodes and cestodes in contrast to nematodes could explain why so few marine parasitic nematodes have been identified in marine environments of Costa Rica, even though parasitic nematodes are very abundant and diverse in vertebrates living in other environments [72–74].

Despite advances in molecular techniques for the identification of nematodes, genetic information for many marine parasitic nematodes is still scarce [73,74]. Only 61 of the nearly 6700 marine species have been reported as hosts for marine parasites in Costa Rica; these are extremely poor numbers in a country with 3.5% of the marine biodiversity of the world [75]. Most marine parasites found in Costa Rica have been collected from relatively near shore habitats, even in brackish waters, so places further from the coast and deeper water environments have been little sampled in search of these organisms. In addition, research has focused on turtles, elasmobranchs, and teleost fish; researchers have found marine parasites only in 35 marine fish of Costa Rica; that number represents very little in comparison to the nearly 800 fish species estimated to be in Costa Rican marine

environments between 0 and 200 m depth [75]. There is lacking a more comprehensive search of parasites in the widest range of hosts. For all the above, the 146 species of marine parasites found so far probably represent a very small percentage of the actual diversity.

The difference in marine parasite species between the Caribbean and the Pacific is remarkable, with 51 species reported for the Caribbean and 101 species reported in the Pacific. This is, in part, a consequence of the lower amount of research carried out in the Caribbean on the subject of marine parasites (11 papers published) in comparison to the Pacific, where 41 papers have been published, 78.4% of the marine parasite species from the Caribbean of Costa Rica have been recorded from one single study with the bull shark *Carcharhinus leucas* [19] and one principal study on the digenean parasites of the green turtle *C. mydas* [33]. The active search for marine parasites is a difficult task, and much of it relay on searching in nesting turtles or stranded mammals. Stranded mammals are more prevalent on the Pacific coast of Costa Rica than on the Caribbean coast and so in other parts of Central America as well [76,77]. In terms of sea turtle nesting sites, the North Caribbean and North Pacific are the sites with the highest numbers of nesting sea turtles, *Lepidochelys olivacea* in the Pacific and *C. mydas* in the Caribbean. However, less research has been done on the rest of the Costa Rican Caribbean coast (e.g., the parasites of the nesting leatherback turtle *Dermochelys coriacea* have not been investigated). In general, in both the Pacific and the Caribbean, the other sea turtle species that nest in much lower numbers in Costa Rica, *Caretta caretta*, *Dermochelys coriacea*, and the Pacific Green Turtle (*Chelonia agazzisi*), have not been investigated for parasites.

Digenean trematodes are diverse in sea turtles; these types of helminths were found in several fish and dolphin species in Costa Rica. Among digenean trematodes, the family Pronocephalidae is diverse in the marine trematode parasitic fauna of Costa Rica. This family of parasites is primarily found in the intestines of marine reptiles, with few species occurring in fish and other marine vertebrates [78]. In Costa Rica, these parasites have been recorded mainly from the green turtle *C. mydas* and the endangered hawkbill turtle *E. imbricata*. Several of the species found in Costa Rica have been previously recorded in the same host species in other studies. In Brazil, species found in hawksbill turtle *E. imbricata*, like *Cricocephalus albus*, *Carettacola stunkardi*, *Hapalotrema postorchis*, and *Monticellius indicum* have been found in the same host [54]. No digenean trematodes have been reported from Costa Rican elasmobranchs; this group is, by far, a less diverse group in this type of host. The extensive adaptive radiation of cestodes in elasmobranchs has "muted" the trematode diversity in this vertebrate group; on the contrary, in fish and sea turtles, trematodes have had a bigger adaptive radiation that exceeds greatly that of cestodes [79,80].

There is little information other than taxonomic about pathology caused by trematodes in marine animal hosts. Regarding spirorchiid-derived pathology in *C. mydas*, one study was the first to investigate parasites in non-stranded Caribbean sea turtles of Costa Rica and the only study in marine turtles of Costa Rica, up to now, revealing the effects of those parasites on the host [37]. In this work, they found the species *Learedius learedi*, *Hapalotrema postorchis*, *Monticellius indicus*, and *Amphiorchis solus* parasitizing the hearth and great vessels of *C. mydas* in the North Caribbean of Costa Rica [37]. The parasites were present in 39 out of 40 turtles in Tortuguero and caused aneurysms, nodular thickening of the vessels' walls, thrombi, and other complications; all these complications are common in the cases of sea turtle spirorchidiasis. All genera found in Costa Rican sea turtles have been found to cause similar pathologies in other studies, being *Learedius* species the most prevalent [81]. In other countries, recent research has determined that heavy helminth infections on *C. mydas* and *E. imbricata* generate significant health complications in individuals with significant intestinal damage, in the case of the microascaphidiid parasite *Octangium* sp., or at the level of other organs such as the myocardium, e.g., the case of spirorchiid trematodes [81,82]. More research is needed to determine other effects of helminth parasitic infestations on turtles in Costa Rica.

Regarding cestodes diversity, most parasites have been reported in the digestive system of elasmobranchs, and most of them are in the family Onchobothriidae [19,22–25]. The fam-

ily Onchobothriidae contains mainly parasitic species of elasmobranchs [83,84]. The genus *Acanthobothrium* is one of the most diverse in the family and is associated with various species, mainly rays [83,84]. Many of the new species described in Costa Rica are cestodes placed in this genus studied in the 1990s. Other cestode species found in the marine fauna of Costa Rica were Tetrabothriid and Phyllobothriid cestodes collected in the digestive system of stranded dolphins; in Central America, the study by Oliveira on parasites of stranded dolphins in the Pacific is the only study that reported parasites of these mammals of Costa Rica [49]. Major tetraphyllidean cestodes that are parasites of dolphins worldwide are *Phyllobothrium delphini* and *Monorygma grimaldi*, both reported by Oliveira in Costa Rica. The role of dolphins in the life cycle of these parasites is as intermediate hosts, no adult stages of these species are known to occur in dolphins. Large sharks that prey on dolphins are thought to be the definitive hosts for these parasites [85]. As there is no data on endoparasites of costarican sharks other than the bull shark, it is not surprising that these parasites in their adult forms have not been reported yet in Costa Rica.

Monogenean parasites of Costa Rica have been found mostly on the gills of several species of carangid fish, tuna, and puffer fish. Mazocraeidan monogeneans are common in fish as ectoparasites that feed on mucus and epithelial cells on the surface of the body of the fish hosts, causing morbidity and mortality usually when they are in great numbers in the gills. Some studies have hypothesized the possibility that these parasites could also act as vectors of viruses [86]. The species found so far in Costa Rica have been reported previously in South America [87]. In lists published about marine monogeneans of Asia (China, Japan), several families of monogeneans are represented [88,89]. It would be expected a high diversity of monogeneans in tropical marine environments as predicted by a greater diversity of hosts [90]. However, the search for this type of parasite in Costa Rica is also scarce; they have been searched only in a limited group of hosts, mainly carangid fishes.

Marine biologists have also made important contributions to the knowledge of Costa Rican marine parasites belonging to several groups of crustaceans. After the 1990s, a greater number of reports of parasitic or epibiont crustacean species have been made for Costa Rica [29–31]. Bopyrid isopods are a well-represented isopod family around the world. *Probopyrus pandalicola* had been previously reported in the Eastern Pacific from the branchial cavity of several species of decapods, including the genus *Palaemon*; in Costa Rica, it was found in the branchial cavity of *Palaemon hiltoni* [29]. In the Gulf of California, this species was registered as a parasite of *Palaemon pandaliformis*, *Palaemon ritteri*, and *Palaemon nortropi* [91]. *Aporobopyrus trilobatus* was previously known from the Caribbean and Pacific coast of Mexico, and *Petrholistes edwardsi* was already known to be a host of *A. bourdonis* from the Pacific of Mexico [31,45,92].

The role of some crustacean species as parasites or simply epibionts is still difficult to establish. For some families, such as the Caligidae copepods, their role as ectoparasites is clearer [93]; also, for some large cirripedes [94], that can cause certain limitations to their hosts if they are small, but for others, it is not yet clear if they cause any harm to the host. Whatever the case, research on marine metazoans parasites other than helminths is still widely an unexplored terrain, as is the search for marine parasites in invertebrate hosts; in Costa Rica, this is not an exception.

Basic questions like the richness and abundance of parasites in a given marine zone in Costa Rica cannot be answered yet, nor how these species interact with other community components or how those interactions between different hosts can favor the transmission of a given group of parasites. For many marine parasites, their specific role as parasites in the health and sickness of the host has not been determined. Of course, sampling some alive marine hosts is very challenging. For example, feces or serum samples, even today, are not very useful in the morphological identification of most marine parasites (because eggs or larval stages that can be found in those samples have not been described), and molecular identification is not available for most of them, and very few sequences of the Costa Rican marine parasites are deposited in the main genetic databases.

Additionally, maintaining living individuals from the marine environment in controlled conditions to study their parasites employing experimental infections to describe their life cycles and pathology is hardly possible because of numerous technical difficulties, research permits, and several other ethical and technical issues.

The last checklist of the helminth fauna of Costa Rica was published in 2004 [46], and after that, only a few additions have been made to the list, and the Colección Helmintológica de Costa Rica [47]. Only four holotypes out of the 32 marine parasite species described from material of Costa Rica are deposited in Costa Rican Collections, and, in the case of voucher specimens, only 32% of the reported species of marine parasites of Costa Rica have voucher specimens deposited in local biological collections (Supplementary Table S1).

There is a need for more research on marine wildlife parasites in Costa Rica. Research lines followed by new parasitologists in Costa Rica have focused mostly on human parasitology and molecular diagnosis of medical and veterinary important parasites with a clinical and epidemiological approach, while other basic research on wildlife parasitology has been left behind for several years. Since the diversity and other aspects of the ecology of the parasites in the marine environment are important indicators of the ecosystem's health, it is necessary that the interest in basic research in marine parasitology arises again in the country and that this is supported by the sources of the research funding of public universities, research institutions, and other entities inside and outside of Costa Rica.

Scientific knowledge on marine parasites of Costa Rica, other than taxonomic, is very scarce. Many of the reports have depended upon the finding of stranded dead or nearly dead hosts. That situation, together with the scarcity of voucher specimens that represent our metazoan marine parasite fauna, does not allow us to infer the dynamics of parasites at the population level and higher, given that systematic research has not been carried out to fully understand the diversity of marine parasites in Costa Rica, and little work have been done regarding the parasite communities and their interactions. Climate change and macroenvironmental disturbances could be making many parasite species silently disappear. In some contexts, the biological traits of some parasite species make them highly vulnerable to these disturbances, e.g., complex life cycles, host specificity, and narrow climatic tolerances [95]. Conversely, in other contexts, pollution and climate change are making parasites more abundant and a cause of important diseases for their hosts [96].

4. Materials and Methods

An exhaustive search of publications about metazoan marine parasite species reported in Costa Rica was performed. The keywords "Costa Rica" and "Central America" were used together with the words "marine parasites", "marine helminths", "marine acanthocephalan", "marine trematodes", "marine fish parasites", "marine turtle parasites", "parasitic copepods", "parasitic crustaceans", "monogenean", "marine epibionts", "marine parasitic Mollusca" in the scientific search engines Google Scholar, Microsoft Academic, and BASE. Additionally, the "Colección Helmintológica de Costa Rica" databases and archives were analyzed to supplement the information. The WORMS database was also consulted to guarantee the accepted names are being used. The list of species of metazoan marine parasites known for Costa Rica was obtained, along with other information about the research that has been carried out on some of these species as well as the expeditions and history of the collections of marine parasites in different species since the first quarter of the twentieth century. All metazoan marine or brackish water parasites reported for Costa Rica were included, and protozoans and other microorganisms were excluded from this review. Figures were elaborated using the software Microsoft PowerBI and Microsoft Excel, while the map was created using QGIS 3.0 and Google Earth Pro applications.

5. Conclusions

A total of 146 species of marine parasites have been reported in Costa Rica; of them, 32 new species were described from Costa Rica material. Three species of sea turtles and elasmobranchs (mainly rays) have been the hosts most thoroughly studied in the search

for parasites in Costa Rica, in total 61 marine species have been recorded as hosts of at least one metazoan marine parasite, which is very few compared to the enormous diversity of marine wildlife. Helminths from the Trematoda and Cestoda constitute the groups better represented, in inside these groups, few families are associated mainly with the most sampled hosts. Studies other than taxonomic about marine parasites in Costa Rica are also lacking, as well as ecological studies. This review points out the importance of enhancing the science of marine parasitology in Costa Rica because of its implications for the knowledge of marine biodiversity, the ecological importance of parasites in marine biological communities, and conservation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/parasitologia3020014/s1, Figure S1: Number of voucher specimens and country where they have been deposited, Figure S2: Number of type specimens and country where they have been deposited, Table S1: Open database of the list of metazoan marine parasites reported for Costa Rica from 1937 to 2022.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. List of marine parasites reported for Costa Rica from 1937 to 2022.

Parasite Species	Class/Order	Host Species	Reporting Reference	Location
Acanthobothrium nicoyaense[a]	Cestoda: Tetraphyllidea	*Aetobatus narinari*	[22]	Punta Morales, Pacific Coast
Acanthobothrium costarricense[a]	Cestoda: Tetraphyllidea	*Dasyatis longus*	[23]	Punta Morales, Pacific Coast
Acanthobothrium cimari [a]	Cestoda: Tetraphyllidea	*Dasyatis longus*	[23]	Punta Morales, Pacific Coast
Acanthobothrium puntarenasense [a]	Cestoda: Tetraphyllidea	*Dasyatis longus*	[23]	Punta Morales, Pacific Coast
Acanthobothrium vargasi [a]	Cestoda: Tetraphyllidea	*Dasyatis longus*	[23]	Punta Morales, Pacific Coast
Acanthobothrium campbelli [a]	Cestoda: Tetraphyllidea	*Urotrygon chilensis*	[23]	Punta Morales, Pacific Coast
Acanthobothrium franus [a]	Cestoda: Tetraphyllidea	*Narcine entemedor*	[25]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Acanthobothrium inbiorium [a]	Cestoda: Tetraphyllidea	*Narcine entemedor*	[25]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Acanthobothroides pacificus [a]	Cestoda: Tetraphyllidea	*Himantura pacifica*	[24]	Playa Panamá, Guanacaste
Scalithrium geminum [a]	Cestoda: Tetraphyllidea	*Himantura pacifica*	[24]	Playa Panamá, Guanacaste
Cylindrophorus hypoprioni	Cestoda: Tetraphyllidea	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Triloculatum triloculatum	Cestoda: Tetraphyllidea	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast

Table A1. *Cont.*

Parasite Species	Class/Order	Host Species	Reporting Reference	Location
Escherbothrium molinae [a,b]	Cestoda: Tetraphyllidea	*Urotrygon chilensis*	[57]	Punta Morales, Puntarenas
Anthobothrium pristis	Cestoda: Tetraphyllidea	*Pristis perotteti*	[19]	Barra del Colorado, Caribbean Coast
Anthobothrium laciniatum	Cestoda: Tetraphyllidea	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Pterobothrioides carvajali [a,b]	Cestoda: Trypanorhyncha	*Dasyatis longus*	[26]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Dasyrhynchus variocinnatus	Cestoda: Trypanorhyncha	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Callitetrarhynchus gracilis	Cestoda: Trypanorhyncha	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Heteronybelinia estigmena	Cestoda: Trypanorhyncha	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Otobothrium penetrans	Cestoda: Trypanorhyncha	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Cathetocephalus thatcheri	Cestoda: Cathetocephalidea	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Tetrabothrius forsteri	Cestoda: Tetrabothriidea	*Stenella coeruleoalba* *Stenella attenuata*	[49]	Playa hermosa, Guanacaste
Strobilocephalus triangularis	Cestoda: Tetrabothriidea	*Stenella coeruleoalba*	[49]	undefined location
Trigonocotyle sp.	Cestoda: Tetrabothriidea	*Stenella longirostris*	[49]	Tamarindo, Guanacaste
Phyllobothrium delphini	Cestoda: Phyllobothridea	*Stenella coeruleoalba*	[49]	undefined location
Phyllobothrium pristis [a]	Cestoda: Phyllobothridea	*Pristis perotteti*	[19]	Barra del Colorado, Caribbean Coast
Paraorygmatobothrium nicaraguensis [a]	Cestoda: Phyllobothridea	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Monorygma grimaldii	Cestoda: Phyllobothridea	*Stenella coeruleoalba* *Stenella attenuata* *Tursiops truncatus*	[49]	undefined location
Scyphophyllidium leuci [a]	Cestoda: Phyllobothridea	*Charcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Hargicola oligoplites	Monogenea: Mazocraeidea	*Oligoplites altus*	[50]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Mazocraes sp.	Monogenea: Mazocraeidea	*Anchovia macrolepidota*	[50]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Neohexostoma euthynni	Monogenea: Mazocraeidea	*Euthynnus lineatus*	[50]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Ahpua piscicola	Monogenea: Mazocraeidea	*Caranx Caballus,* *Oligoplites altus*	[32]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Pseudomazocraes monsivaisae	Monogenea: Mazocraeidea	*Selene peruviana*	[32]	Puntarenas
Cemocotylella elongata [a]	Monogenea: Mazocraeidea	*Caranx caballus*	[12]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Hargicotyle louisianensis	Monogenea: Mazocraeidea	*Menticirrhus* sp.	[32]	Puntarenas
Heterobothrium ecuadori	Monogenea: Mazocraeidea	*Sphoeroides* sp.	[18]	Puntarenas
Polymicrocotyle manteri	Monogenea: Mazocraeidea	*Lutjanus colorado*	[32]	Puntarenas
Jaliscia caballeroi	Monogenea: Mazocraeidea	*Lepidochelys olivacea*	[46,47]	undefined location
Dermophthirius maccallumi [a]	Monogenea: Mazocraeidea	*Carcharhinus leucas*	[19]	Barra del Colorado, Caribbean
Neomicrocotyle pacifica	Monogenea: Mazocraeidea	*Caranx sexfasciatus*	[14]	Bahía Culebra, Guanacaste
Heteronchocotyle leucas [a]	Monogenea: Diclybothriidea	*Carcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast

Table A1. *Cont.*

Parasite Species	Class/Order	Host Species	Reporting Reference	Location
Erpocotyle carcharhini [a]	Monogenea: Diclybothriidea	*Carcharhinus leucas*	[19]	Barra del Colorado, Caribbean Coast
Alloinfundiburictus costaricae [a]	Trematoda: Plagiorchiida	*Haemulopsis axillaris*	[13]	Bahía Culebra, Guanacaste
Bucephalus gorgon [a]	Trematoda: Plagiorchiida	*Caranx hippos and Seriola*	[13]	Bahía Culebra, Guanacaste
Prosorhynchoides sp.	Trematoda: Plagiorchiida	*Caranx caballus*	[46,47]	undefined location
Manteria brachyderus	Trematoda: Plagiorchiida	*Caranx caballus/Oligoplites altus*	[21]	undefined location
Brachycladium palliatum	Trematoda: Plagiorchiida	*Stenella coeruleoalba*	[49]	undefined location
Brachycladium pacificum	Trematoda: Plagiorchiida	*Stenella longirostris*	[49]	undefined location
Nasitrema globicephalae	Trematoda: Plagiorchiida	*Stenella attenuata*	[49]	undefined location
Oschmarinella albamarina	Trematoda: Plagiorchiida	*Ziphius cavirostris*	[49]	undefined location
Homalometron lesliorum [a]	Trematoda: Plagiorchiida	*Eucinostomus currani*	[28]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Theletrum lamothei [a]	Trematoda: Plagiorchiida	*Echidna nocturna*	[27]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Ectenurus virgula	Trematoda: Plagiorchiida	*Fistularia commersonii*	[27]	Ocotal, Guanacaste
Lecithochirium microstomum	Trematoda: Plagiorchiida	*Fistularia commersonii*	[27]	Ocotal, Guanacaste
Lecithochirium monticelli	Trematoda: Plagiorchiida	*Syhodus* sp.	[18]	Ocotal, Guanacaste
Mecoderus oligoplitis	Trematoda: Plagiorchiida	*Oligoplites altus, Oligoplites refulgens, Oligoplites* sp.	[21]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Ekuarhuni papillatus [a,b]	Trematoda: Plagiorchiida	*Mugil curema*	[52]	Punta Dominical, Puntarenas
Forticulcita isabelae [a]	Trematoda: Plagiorchiida	*Mugil curema*	[52]	Punta Dominical, Puntarenas
Trifoliovarium sp.	Trematoda: Plagiorchiida	*Echidna nocturna*	[27]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Bianium plicitum	Trematoda: Plagiorchiida	*Arothron hispidus, Sphoeroides* sp.	[16]	Bahía prieta, Guanacaste and Mata de Limón, Puntarenas
Hypocreadium myohelicatum	Trematoda: Plagiorchiida	*Epinephelus itajara*	[27]	Cuajiniquil, Gulf of Santa Elena, Guanacaste
Stephanostomum casum	Trematoda: Plagiorchiida	*Caranx caballus*	[27]	Playa Ocotal, Guanacaste, Pacific Coast
Tergestia laticollis	Trematoda: Plagiorchiida	*Caranx caballus*	[27]	Playa Ocotal, Guanacaste, Pacific Coast
Plesiochorus cymbiformis	Trematoda: Plagiorchiida	*Lepidochelys olivacea*	[38]	Ostional National Wildlife Refuge, Nicoya Peninsula, North Pacific Coast
Enodiotrema megachondrus	Trematoda: Plagiorchiida	*Lepidochelys olivacea*	[38]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Enodiotrema reductum	Trematoda: Plagiorchiida	*Eretmochelys imbricata*	[41]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Pachypsolus irroratus	Trematoda: Plagiorchiida	*Lepidochelys olivacea*	[38]	Ostional National Wildlife Refuge, Nicoya Peninsula
Microscaphidium reticulare	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Microscaphidium warui	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Deuterobaris intestinalis	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Polyangium linguatula	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast

Table A1. *Cont.*

Parasite Species	Class/Order	Host Species	Reporting Reference	Location
Octangium hyphalum	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Schizamphistomum scleroporum	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Schizamphistomum erratum	Trematoda: Plagiorchiida	*Chelonya mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Helicometra fasciata	Trematoda: Plagiorchiida	*Muraena* sp.	[13]	Bahía Culebra, Guanacaste
Cricocephalus resectus	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Cricocephalus megastomus	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Cricocephalus albus	Trematoda: Plagiorchiida	*Chelonia mydas*, *Eretmochelys imbricata*	[33,41]	Tortuguero National Park, North Caribbean Coast, Gulf of Nicoya
Desmogonius desmogonius	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pronocephalus obliquus	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Charaxicephaloides polyorchis	Trematoda: Plagiorchiida	*Chelonia mydas*	[36]	Tortuguero National Park, North Caribbean Coast
Charaxicephalus robustus	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pleurogonius longiusculus	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pleurogonius sindhii	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pleurogonius sp.	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pleurogonius tortugueroi [a]	Trematoda: Plagiorchiida	*Chelonia mydas*	[34]	Tortuguero National Park, North Caribbean Coast
Pleurogonius linearis [c]	Trematoda: Plagiorchiida	*Chelonia mydas*, *Eretmochelys imbricata*	[33]	Tortuguero National Park, North Caribbean Coast, Gulf of Nicoya
Pleurogonius solidus	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pleurogonius lobatus	Trematoda: Plagiorchiida	*Chelonia mydas*, *Eretmochelys imbricata*	[33,41]	Tortuguero National Park, North Caribbean Coast, Gulf of Nicoya
Pleurogonius trigonocephalus [c]	Trematoda: Plagiorchiida	*Eretmochelys imbricata*	[41]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Rameshwarotrema uterocrescens	Trematoda: Plagiorchiida	*Chelonia mydas*	[35]	Tortuguero National Park, North Caribbean Coast
Adenogaster serialis [c]	Trematoda: Plagiorchiida	*Eretmochelys imbricata*	[41]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Pyelosomum crassum [c]	Trematoda: Plagiorchiida	*Eretmochelys imbricata*	[41]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Pyelosomum cochlear	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Pyelosomum posterorchis [c]	Trematoda: Plagiorchiida	*Eretmochelys imbricata*	[41]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Rhytidodoides similis	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Rhytidodoides intestinalis	Trematoda: Plagiorchiida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Clinostomum complanatum	Trematoda: Diplostomida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast

Table A1. *Cont.*

Parasite Species	Class/Order	Host Species	Reporting Reference	Location
Learedius learedi	Trematoda: Diplostomida	*Chelonia mydas*	[33,37]	Tortuguero National Park, North Caribbean Coast
Hapalotrema postorchis	Trematoda: Diplostomida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Monticellius indicus	Trematoda: Diplostomida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Amphiorchis solus	Trematoda: Diplostomida	*Chelonia mydas*	[33]	Tortuguero National Park, North Caribbean Coast
Carettacola stunkardi [c]	Trematoda: Diplostomida	*Eretmochelys imbricata*	[41]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Neospirorchis sp.	Trematoda: Diplostomida	*Chelonia mydas*	[37]	Tortuguero National Park, North Caribbean Coast
Halocercus lagenorhynchi	Nematoda: Strongylida	*Stenella coeruleoalba*	[49]	Playa Panamá, Guanacaste
Halocercus sp.	Nematoda: Strongylida	*Stenella attenuata* *Stenella longirostris*	[49]	undefined location
Echinocephalus janzeni [a]	Nematoda: Rabditida	*Himantura pacifica*	[59]	undefined location
Crassicauda anthonyi	Nematoda: Rhabditida	*Ziphius cavirostris*	[49]	Matapalo, Puntarenas, Pacific Coast
Anisakis spp.	Nematoda: Rhabditida	*Stenella coeruleoalba* *Stenella attenuata* *Stenella longirostris* *Ziphius cavirostris*	[49]	undefined location
Koronacantha pectinaria	Palaeoacanthocephala: Echinorhynchida	*Microlepidotus brevipinnis*	[60]	Bahía Culebra, Guanacaste
Floridosentis pacifica	Eoacanthocephala: Neoechinorhynchida	*Mugil curema*	[51]	Punta Dominical, Puntarenas and Gulf of Nicoya
Neoechinorhynchus mamesi	Eoacanthocephala: Neoechinorhynchida	*Dormitator maculatus*, *Dormitator latifrons*	[62]	Playa Grande, Guanacaste
Ozobranchus branchiatus	Hirudinea: Rhynchobdellida	*Chelonia mydas*, *Lepidochelys olivacea*	[37,39,40]	Tortuguero National Park, North Caribbean Coast, Ostional wildlife refuge, Nicoya penninsula, north Pacific coast
Ozobranchus margoi	Hirudinea: Rhynchobdellida	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Cymothoa exigua	Crustacea: Isopoda	*Lutjanus colorado*, *L. jordani and L. peru*	[44]	undefined location
Probopyrus pandalicola	Crustacea: Isopoda	*Palaemon hiltoni*	[29]	Gulf of Nicoya, Puntarenas, North Pacific Coast
Aporobopyrus bourdonis [a]	Crustacea: Isopoda	*Petrolisthes edwardsii*	[45]	Junquillal, Area of conservation, Guanacaste
Aporobopyrus aduliticus	Crustacea: Isopoda	*Petrolisthes* sp.	[31]	Punta Dominical, Puntarenas and Gulf of Nicoya
Aporobopyrus trilobatus	Crustacea: Isopoda	*Petrolisthes ortmanni*	[45]	Punta Dominical, Puntarenas and Gulf of Nicoya
Podocerus chelonophilus	Crustacea: Amphipoda	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Planes sp.	Crustacea: Decapoda	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Anelasma squalicola [c]	Crustacea-Cirripedia: Pollicipedomorpha	*Etmopterus benchleyi*	[53]	Off Pacific Coast
Paralepas quadrata	Crustacea-Cirripedia: Scalpellomorpha	*Panulirus penicillatus*	[30]	Chatam Bay, Isla del Coco
Conchoderma auritum	Crustacea: Cirripedia:Scalpellomorpha	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula

Table A1. *Cont.*

Parasite Species	Class/Order	Host Species	Reporting Reference	Location
Conchoderma virgatum	Crustacea: Cirripedia:Scalpellomorpha	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Lepas hilli	Crustacea: Cirripedia:Scalpellomorpha	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Ptychascus barnwelli [a]	Crustacea: Cirripedia:Kentrogonidae	*Minuca burgersi, Minuca mordax & Minuca vocator*	[67]	Limón, Moin.
Stephanolepas muricata	Crustacea: Cirripedia:Balanomorpha	*Eretmochelys imbricata, Chelonya mydas*	[63]	Golfo Dulce, Pacific Coast and Gulf of Nicoya
Chelonibia testudinaria	Crustacea: Cirripedia:Balanomorpha	*Lepidochelys olivacea*	[39,40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Platylepas decorata	Crustacea: Cirripedia:Balanomorpha	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Platylepas hexastylos	Crustacea: Cirripedia:Balanomorpha	*Lepidochelys olivacea*	[40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Stomatolepas elegans	Crustacea: Cirripedia:Balanomorpha	*Lepidochelys olivacea*	[39,40]	Ostional National Wildlife Refuge, Nicoya Peninsula
Xenobalanus globicipitis	Crustacea: Cirripedia:Balanomorpha	*Stenella attenuata*	[49]	Bajamar Puntarenas
Pandarus satyrus	Crustacea: Copepda: Siphonostomatoida	*Prionace glauca*	[43]	undefined location
Pennella instructa	Crustacea: Copepda: Siphonostomatoida	*Conchoderma virgatum*	[15]	Chatam Bay, Isla del Coco
Gloiopotes ornatus	Crustacea: Copepda: Siphonostomatoida	sailfish (SNI)	[15]	Chatam Bay, Isla del Coco
Caligus mutabilis	Crustacea: Copepda: Siphonostomatoida	*Scomberomorus brasiliensis*	[20]	undefined location
Caligus omissus [a]	Crustacea: Copepda: Siphonostomatoida	*Scomberomorus sierra*	[20]	undefined location
Caligus chorinemi	Crustacea: Copepda: Siphonostomatoida	*Seriola lalandi*	[20]	Bahía Culebra, Guanacaste
Lepeophtheirus alvaroi [a]	Crustacea: Copepda: Siphonostomatoida	Unknown	[65]	Bahía Wafer, Isla del Coco
Unicolax collateralis [a]	Crustacea: Copepda: Siphonostomatoida	*Euthynnus lineatus*	[20]	undefined location
Pseudocycnus appendiculatus	Crustacea: Copepda: Siphonostomatoida	*Thunnus albacares*	[20]	undefined location
Cybicola buccatus	Crustacea: Copepda: Siphonostomatoida	*Scomberomorus sierra, Scomberomorus brasiliensis*	[20]	undefined location
Lernanthropus micropterygis	Crustacea: Copepda: Siphonostomatoida	*Seriola sp.*	[11]	Bahía Culebra, Guanacaste
Balaenophilus manatorum	Crustacea: Copepoda:Harpacticoida	*Lepidochelys olivacea*	[39]	Ostional National Wildlife Refuge, Nicoya Peninsula

[a] was reported as a new species (sp.nov), [b] was described as a new genus, and [c] report is new for the Eastern Tropical Pacific.

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