A Short Introduction to Marine Parasitology: Marine Parasites of Economic and Medical Importance

Klaus Rohde
Department of Zoology, School of Environmental and Rural Science, University of New England, Armidale, New South Wales, Australia
krohde@une.edu.au

Robin Overstreet
Gulf Coast Research Laboratory, University of Southern Mississippi, Ocean Springs, Mississippi, United States

Introduction

Parasitism, in this chapter, is defined as "a close association of two organisms, in which one—the parasite—depends on the other—the host—deriving some benefit from it. The benefit is often food" (Rohde, 2005b). Many bacteria, viruses, and fungi are parasitic but usually not studied by parasitologists sensu stricto; they are the domain of microbiologists. Parasites as defined here do not always harm their host; the border between so-called genuine parasites and other symbionts such as commensals is often blurred, and investigators who work on disease aspects tend to emphasis the pathogenic aspects and may not consider non-pathogenic species as truly parasitic (see also Shields and Overstreet, 2007). Frequently, species that are harmless under certain conditions become pathogenic under others (see, for example, Overstreet and Lotz, 2016).

There has been much discussion of marine diversity in general and of diversity of marine parasites specifically. Parasite diversity depends on the diversity of their hosts. The more potential hosts, the more parasites can be expected. Appeltans et al. (2012; see also Costello and Chaudhary, 2017) concluded that between one-third and two-thirds of marine species (including both free-living and parasitic ones) had been described already. Rohde (2002a; 2010) emphasized that a very large number of species, particularly of invertebrates and their parasites in the deep sea, and in the meiofauna, remained to be described, a conclusion supported by the finding that there is a vast pool of environmental DNA (eDNA, metabarcoding) in the deep sea benthos (Sinniger et al., 2016), much of which may belong to bacteria but also to protistan and metazoan parasites. Sinniger et al. (2016) conclude that "the data obtained … reveal pronounced heterogeneity and vast amounts of unknown biodiversity in the deep sea."

Concerning beach meiofauna, in the largest study made by many authors over many years, at the North Sea Island of Sylt, and reviewed by Armonies and Reise (2000), 652 species had been recorded, 25 times as many as found in the macrofauna, and an estimated total of about 200 species still had to be described. No systematic survey of these meiofaunal animals for parasites has been made. Surveys (one not published) have shown that the meiofauna in other geographic regions contains many different species, indicating that a large pool of yet undescribed species exists (Rohde, 2016; see also Poulin (2014) for parasite diversity).

Sources of Marine Parasitology Information

Species numbers of some important groups of marine invertebrates can be found in the Catalogue of Life database (https://www.catalogueoflife.org/) and the World Registry of Marine Species (WoRMS, http://www.marinespecies.org).

Some older but still useful comprehensive treatments of disease aspects of marine parasites (including protistan and metazoan ones) are Sindermann (1970; 1990) and the 4 volumes of the important treatise edited by Kinne (1980–1985). Diagnostic methods and symptoms of disease in freshwater and marine fishes are discussed by Ahne (1980), Möller and Anders (1983), Untergasser (1989), Amlacher (1992), Noga (2011), Jeney (2017), and Overstreet (2013) give a comprehensive treatment of waterborne parasitic diseases in the oceans, and farming and husbandry of freshwater and marine organisms including diseases are discussed by Bardach et al. (1974).

Important books that deal with many aspects of marine parasitology are Rohde (1993) and Rohde (2005a). The former concentrates on ecological and zoogeographical aspects, largely or entirely ignored in the above-listed books, but includes brief illustrated discussions of the various parasite groups, as well. The latter has contributions by many authors, in over 80 chapters dealing with the nature of parasitism, protistan parasites and myxozoans, helminths, crustaceans, minor groups and fossils, behavioral aspects of parasitism, ecology, coevolution and speciation, zoogeography, economic and environmental importance, and parasites of medical importance. Rohde (2002a) discusses the ecology and biogeography of marine parasites and Rohde (2016) covers important aspects in the ecology and zoogeography of marine parasites that should be considered in future studies.

Human effects on the environment such as pollution and climate change have increasing significance for the spreading of diseases including parasitic ones and the development of new diseases not only of humans, but also of marine organisms. Aspects dealing with these problems are discussed by Harvell et al. (1999), Lafferty (2009), and Brooks and Hoberg (2013).

Economically Important Marine Parasites

Parasites are not only common and diverse in all seas, they are also of very large ecological and economic importance, the latter particularly in aquaculture. Many species infect humans. Nevertheless, our knowledge is still limited, and many species have not been described. Most invertebrates and even many fish species have never been examined for parasites at all, or only for a few parasite groups.

One important gap in the knowledge concerns the role which parasites play as causes of mass mortalities of marine animals. Best known are parasitic diseases in aquaculture, not surprising considering their great economic importance. Thus, the economic value of mortalities was estimated worldwide at about US $55 billion in 2004, and the greatest losses are due to parasites and viruses, although quantitative, even approximately-accurate statements are difficult to assess. Some estimates showed the following losses due to parasites (various sources in Rohde, 1993): Examination for parasites and their removal can increase the packing costs of fish by about 80%; in spring 1952, 10% of catfish in Hamburg, West Germany were unsuitable for human consumption because of an infection with Microsporidia; in the Netherlands mussel production was reduced from 44.5 million kg in the 1954/1955 season to 23.6 million kg in 1955/1956, at least partly due to an infection of mussels with the copepod *Mytilicola intestinalis*. However, caution is necessary: Stress can increase the likelihood of infection, and for this reason it is often difficult to estimate the relative role of parasites. Therefore, the most important component of the reduction in production in the Netherlands was perhaps not the parasite but deteriorating environmental conditions and the poor quality of the young mussels that were planted, which may have made infection with parasites possible in the first place. For a general discussion of the economic importance of problems relating to marine parasites, see Rohde (1993), the relevant chapters in Rohde (2005a) and Overstreet and Curran (2004) discussed trematodes in cultured catfish from in the United States, some of them using the American white pelican and a cormorant as final hosts.

Finally, ornamental fish kept and bred in aquaculture are economically important. According to Conroy (1976), ornamental marine and freshwater fish kept in aquaculture in the United States during 1972 were valued at US $250 million, and the value of aquaria and accessories at US $350 million, compared with those for cats (US $30 + $55 million) and dogs (US $220 + $300 million). Worldwide, the economic value of ornamental fish and extras was estimated at US $4 billion. Data for 1994 show that 10 million households in the United States-owned aquaria and, in addition, there were others in offices, restaurants, and shops. The estimated value of aquarium fish in 1993 was estimated at US $910 million (over US $350 million of these for the fish themselves; Vieth et al., 1998). By 2007, the United States was the "largest importer of ornamental fish in the world" (Livengood and Chapman, 2007, p. 1) with over 2,000 species traded resulting in over US $1 billion in sales (for example, see Cato and Brown, 2003; AAPMA, 2005). Parasitic diseases are important problems for owners of aquaria.

Examples of economic and medical importance of marine parasites are discussed below. Further detailed examples are available in Rohde (1984; 1993), as well as some relevant chapters in Rohde (2005a).

Marine Parasites in the Free Environment

Not many cases of mass mortalities caused by parasites in the oceans are well documented, mainly because observations in the vast oceans are sporadic and cannot be quantified. A discussion by Jones (2005) shows how little is known. This general ignorance does not only apply to fish parasites. There are indications that some cases of beaching of whales and dolphins can be caused by parasites, but quantitative data are scanty.

Fish Parasites

Some early workers, particularly in the former Soviet Union, have provided convincing evidence for mass mortalities of fish caused by parasites. Large numbers of the mullet *Mugil cephalus* in the Black Sea and the Azov Sea, for example, were killed by the myxozoan *Myxobolus exiguus*. Petrushevski and Shulman (1961) observed 500–600 dead fish per km of coastline. The parasites caused strong damage to the gills, leading to bleeding and secondary infections.

Well documented are mass mortalities of the sturgeon *Accipenser nudiventris* in the Aral Sea in the 1930s, although in this case human influence was decisive. Specimens of the related species *A. stellatus* were introduced into the Aral Sea and with them the monogenean *Nitzschia sturionis,* which had not been known in the Aral Sea previously. It more-or-less eliminated the native species, leading to the collapse of the sturgeon and caviar industry in the Aral Sea. Apparently, the parasite was introduced from the Caspian Sea with fish in 1933 (350,000 fish larvae) and 1934 (7 million larvae and 90 sexually mature fish). For the first time, in 1937, many dying fish were reported, a consequence of infection with the 2 cm-large parasite. Prevalence of infection was 100% in saltwater and almost 100% in parts of the sea with somewhat reduced salt content. Intensity of infection reached 600, and the parasites were now not only on the gills, but also in the mouth cavity and on the lips, and sometimes even the intestine, in which worms survived for some time (references in Rohde, 1984).

Pathological findings are often well documented, but it is not clear whether the symptoms are responsible for mass mortalities and to what degree. Thus, the nematode *Philometra lateolabrasis*, a parasite of the gonads, has negative effects on growth and reproduction. The related species *Philometra bassensis* infects the gonads of the flathead *Platycephalus pellucida* in Australia. Hooper (cited in Rohde, 1984) never found more than one gravid female worm per ovary. Many other fish are infected with unidentified species of this genus, often with high prevalence and sometimes with serious symptoms, especially in female fish. The infection of the nervous system of a fish with a microsporidian is illustrated in Figure 1. Interestingly, in this example is that parasites are restricted to certain nerves, forming cyst-like xenomas with nerve cells.

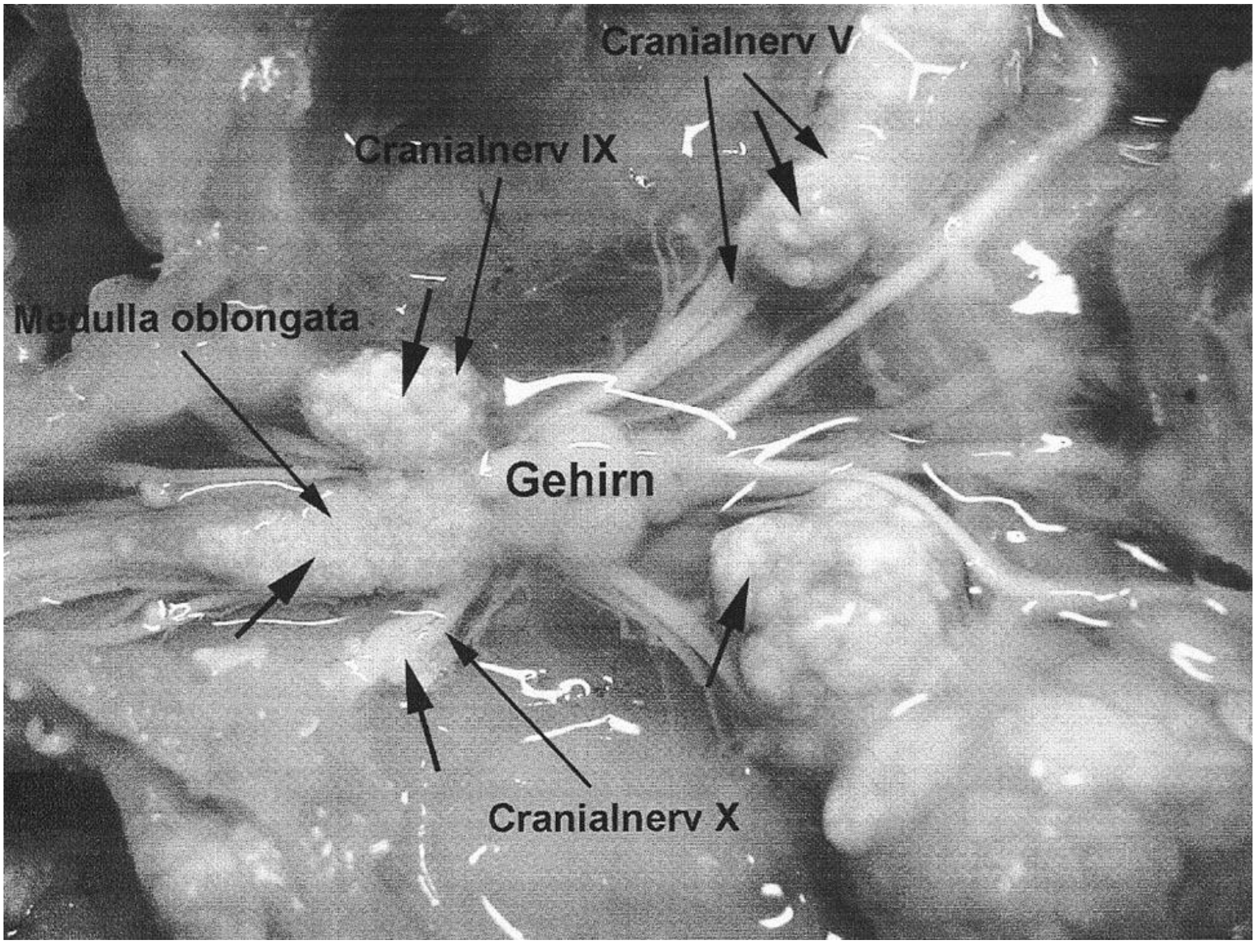

Figure 1. *Spraguea americana* (nicrosporidia) in the nervous system of the Japanese angler fish *Lophius litulon*. The short arrows point to accumulations of up to several mm large cysts (also known as xenomes) consisting of host cells and parasites, or xenoparasitic complexes, in neural ganglia. Sensory nerves are not infected, the infection is restricted to branchial nerves, and foremost to cranial nerves 5, 9, and 10. In infected fish parasites are always located on the dorsal surface of the Medulla oblongata. Gehirn = brain. Source: M. Freeman. License: CC BY-NC-SA 4.0.

Overstreet and Hawkins (2017) discuss parasitic diseases and mortalities of fishes in the Gulf of Mexico.

Parasites of Invertebrates

Many groups of marine invertebrates are exclusively or partly parasitic (relevant chapters in Rohde, 2005a). Parasitic sponges are an example. Many sponges are infected with a variety of parasites (among them parasitic sponges which can surpass the biomass of the infected sponges. The term sponge hotels refers to such cases, although not all inhabitants of such so-called hotels are genuine parasites but may include many symbiotic species not interacting with their host at all. A number of sponge species belonging to several families are obligate parasites. They are of particular importance on coral reefs, where they cause bioerosion of calcium substrates (Figure 2), damaging hosts and even causing their death. According to some estimates 20–40% of all so-called chips (which are calcium splinters) on a coral reef are due to bioerosion. Sponges, therefore, are among the most important causes of recycling of calcium carbonate ($CaCO_3$) on reefs. They are also important as pathogens of oysters and other molluscs, which is particularly important in aquaculture, as discussed below (Hooper, 2005, and further literature therein).

Figure 2. The boring sponge *Coelocarteria singaporensis*. Source: J. Hooper. License: CC BY-NC-SA 4.0.

Parasites of Marine Birds

Hoberg (2005) has reviewed parasites of seabirds. In 2005, from 165 of the more than 300 species of known sea birds, 700 species of helminths had been recorded. Many species of birds have never been examined, and little is known of the pathological effects of parasites. Hoberg (2005) describes one case of mass mortality in the petrel *Pelagodroma marina* which breeds on Chatham Island near New Zealand. About 200,000 birds of a colony of 1 million starved to death after their feet had accidentally become entangled in the filaments of the metacercariae of the trematode *Syncoelium filiferum*. These metacercariae escape from krill (euphausiids), which serve as intermediate hosts and then float in the water, until they get into the mouth cavity of specific fishes where they attach and mature.

Parasites of Marine Mammals

Parasites of marine mammals are better known than those of seabirds. Dailey and Soviet workers (such as Delyamure) have examined them well (Dailey, 2005). Parasites include various protists (Apicomplexa, ciliates, flagellates—many not yet described), helminths (Nematoda, Acanthocephala, Trematoda, Cestoda), insects, mites, and copepods. Concerning the protists, it is of special interest that *Toxoplasma gondii* (Apicomplexa) has been shown to infect dolphins, sea lions, seals, and sea otters (for example, Dubey et al., 2003). The species is one of the most widely spread parasites with low host specificity for intermediate hosts and infects humans with very high prevalence of infection and serious effects. Sexually mature stages are very host specific and infect only felids (cats and related species), which leads to the question of how the parasite gets into the sea; it may be that sea otters ingest oocysts of the parasite in the feces of felids which has been washed into the sea.

Nematodes of marine mammals are widespread and well investigated. All groups of marine mammals carry lungworms (*Parafilaroides*, *Otostrongylus*, Pseudallidae). *Otostrongylus circumlitus*, a large roundworm (nematode), for example, was shown to be the cause of death in 73 beached juvenile elephant seals (*Mirounga augustirostris*). The life cycle of *Parafilaroides decorus* proceeds as follows: The first juvenile stage (J_1) reaches water in the feces or nasal mucus of the final host and is eaten by a fish intermediate host. The second stage (J_2) is found in the stomach wall of the fish, the third (J_3) on the outer surface of the intestine (24–35 days after infection). The fish is eaten by the final host, sea lions, and the larvae migrate into the lung alveoles, where sexual maturity is reached in 21 days (Dailey, 2005, and further references therein).

Other nematodes, of the families Anisakidae (large stomachworms; for a review on molecular differentiation of species within this family see Mattiucci and Nascetti, 2008) and Ancylostomidae (hookworms), infect the digestive tract of marine mammals. Anisakidae are of special interest because some species cause anisakiasis in humans (see below). Eggs are shed by the final host (Pinnipedia or Cetacea) and get into the sea, larvae develop, and are ingested by small crustaceans, for example, krill. Second intermediate hosts (fish and cephalopods) eat the first intermediate hosts; the third juvenile stage (J_3) encysts in their body cavity; sexual maturity is reached in the stomach or intestine of the final host which becomes infected by eating the second intermediate host (Rohde, 1984; Dailey, 2005).

Among the trematodes, *Nasitrema* is of special interest because the species appears to be a significant cause of beaching of whales and dolphins (various sources in Rohde, 1993). The worm (about 1 cm-long) penetrates through the nasal canal into the brain, causing serious symptoms such as imbalance.

The life cycle of the trematode *Philophtalmus zalophi* from the eye of the sea lion *Zalophus wollebaeki* proceeds as follows: Mature worms live under the conjunctiva of the eye lens; the 1st larval stage, the miracidium, is already contained in the egg when it gets into seawater. Sporocysts and rediae develop in the snail intermediate host, the latter producing cercariae which leave the snails and encyst on hard substrates including empty snail shells or shells of the same snail. Metacercariae are infectious immediately after encystation. Only young sea lions, about 2–8 months old, can become infected when they play with hard objects and put them into their mouths. Metacercariae hatch in the mouth, attach to the wall of the oral cavity, and follow the eye secretions produced in the throat, in the ducts that lead to the eyes (personal communication, Murray Dailey).

Marine Parasites in Aquaculture

Marine aquaculture (of fishes, molluscs, and especially oysters, shrimp, prawns, and lobsters) is of very great economic importance and its importance is increasing since it is still underdeveloped in many countries. Thus, in 1994 in Africa, only 76,000 metric tons of freshwater and marine aquaculture were produced and over half of these in Mediterranean countries. The role of disease including parasitic disease in aquaculture has been little studied in these countries (references in Rohde, 2002c). In contrast, aquaculture in Japan is well developed, with an annual production of the marine fish *Seriola* sp., and *Pagrus major* alone, 163,000 and 73,000 tons (Ogawa, 2005). Paperna and Overstreet (1981) give an illustrated account of parasites of cultured mullet.

Aquaculture of Fish

Among cultured fish, Salmonidae (salmon and related species) are of particular importance. Ogawa (2005), referring to the Food and Agriculture Organization of the United Nations (FAO) statistics, states that in 2002, 2.46 million tons of fish were produced, with a value of US $7.38 billion, and over 54% of these were salmonids. The annual production had tripled in the preceding 10 years. Among the important parasitic disease agents of cultured fish are Protista, Myxozoa, various helminths (Figures 3 and 4), copepods and organisms with uncertain taxonomic status (for reviews see the relevant chapters in Rohde, 2005a).

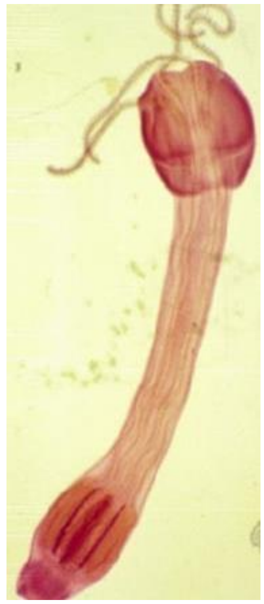

Figure 3. A larva of an unknown species of *Trypanorhyncha* (a cestode) from a teleost fish. Sexual maturity is reached in elasmobranchs (such as sharks and rays) (for example, see Rohde, 1984). Note the 4 tentacles covered with thorns. Source: K. Rohde. License: CC BY.

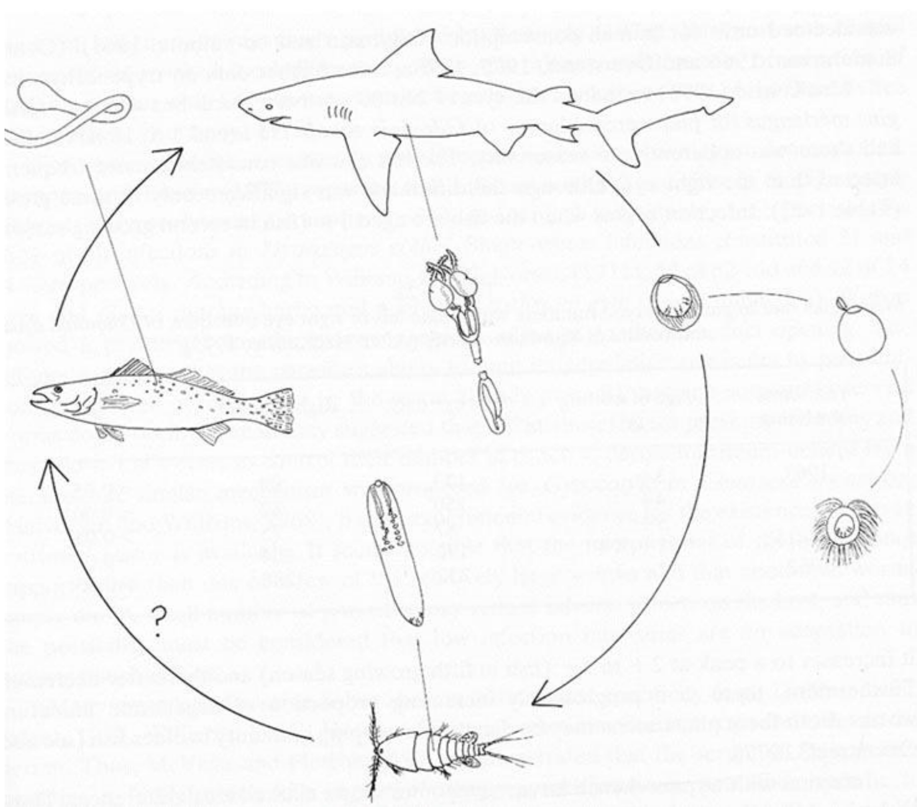

Figure 4. Life cycle of the trypanorhynch tapeworm *Poecilancistrium caryophyllum* which causes so-called wormy trout. The adult develops in sharks, releases proglottids (segments) from the adult, disperses eggs, each with a larva that infects a crustacean which in turn is eaten by a fish. Larvae develop in the flesh and become infective for sharks. Source: Adapted from Overstreet, 1978. License: CC BY.

A few examples will be discussed here. The flagellate *Neoparamoeba pemaquidensis* causes the amoebic gill disease of salmon and trout in various countries. It is possible that a few closely related species are involved. Symptoms are excessive mucus production, hyperplasia of the gill epithelium and fusion, as well as edemas of the gill lamellae.

The ciliate *Cryptocaryon irritans* is the cause of white spot disease which can lead to mass mortalities of fish. Symptoms are 1 mm-large white spots on the skin and gills. In heavy infections, large pieces of skin can be destroyed leading to secondary infections (Möller and Anders, 1983). *Kudoa* (Myxozoa) infects many fish species and can lead to mortalities. Infection causes softening of the muscles and reduces the value of infected fish. Prevalence may be high in several fish species. Thus, practically all *Seriola grandis* exceeding a certain size, caught at Heron Island, Great Barrier Reef, showed the symptoms of muscle softening (Figure 5).

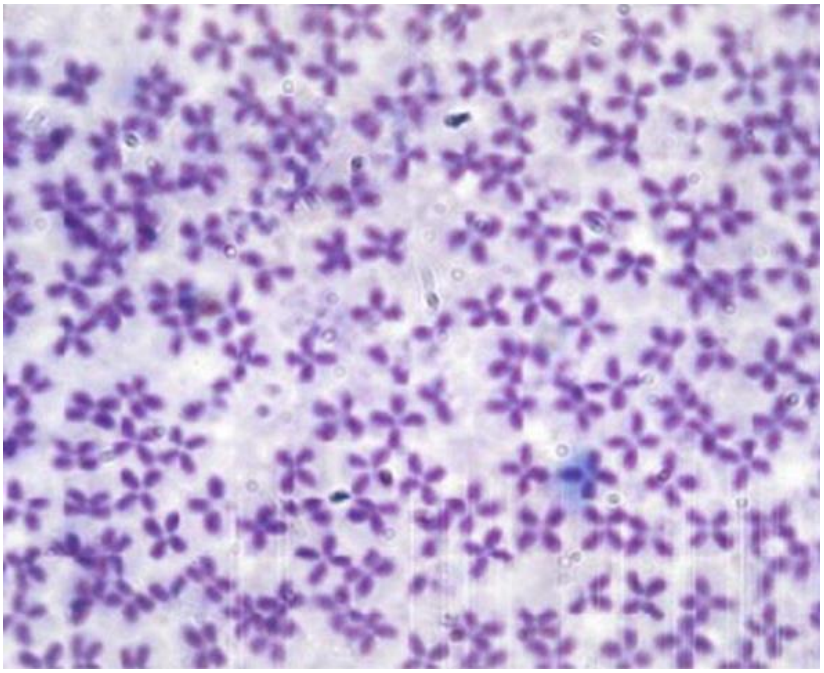

Figure 5. *Kudoa* (Myxozoa) from the muscles of *Seriola grandis* at Heron Island, Great Barrier Reef, Australia. The species leads to muscle softening. Source: K. Rohde. License: CC BY.

Many monogeneans infect fish, and they—jointly with copepods—are indeed the most diverse group of multicellular parasites of fish (Figure 6, see for example the 2 relevant chapters in Rohde, 2005a). They infect the gills or the fins and body surface. Some species are very pathogenic and are among the most important disease agents in aquaculture. An example is *Benedenia seriolae* from the body surface of some marine fish. It feeds on the epidermis and causes serious wounds and bleeding. The condition worsens when fish kept in aquaculture rub their bodies on the nets used in aquaculture. Another example is *Gyrodactylus* spp. Mackenzie (1970) reports that young *Pleuronectes platessa* are hardly infected in nature, but adult fish kept captive in aquaculture may be heavily infected. *Gyrodactylus* is also responsible for mass mortalities of ornamental fish in aquaculture (Rohde, 1993).

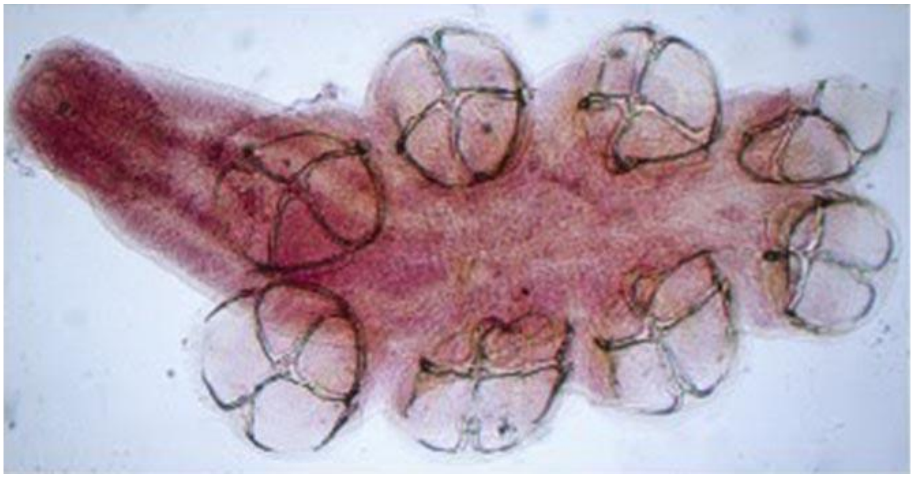

Figure 6. *Eurysorchis australis* (Monogenea, Polyopisthocotylea) from the mouth cavity of *Seriolella bramis* in New Zealand. Monogenea are, jointly with Copepoda, the most diverse group of fish ectoparasites (for example, see Rohde, 1984). Note the 8 ventral suckers (clamps). Source: K. Rohde. License: CC BY.

Among endoparasites, digenetic trematodes are as important as monogeneans and copepods among the endoparasites. They are among the most diverse groups of multicellular endoparasites in freshwater and the oceans. Some blood flukes with unknown life cycles infect the blood vessels, among others in the gills, of the yellowtail *Seriola dumerili*. The parasite's eggs accumulate in the fish's afferent gill arteries and block them, often leading to death (see, for example, Bullard and Overstreet, 2004).

Of special importance among the copepods are *Lepeophtheirus salmonis* and *Caligus elongatus*, parasites of salmon and related species (Ogawa, 2005; see also Johnson et al. (2004) for infections in Canada). In his review, Ogawa (2005) concludes that new diseases of fish appear continuously and that—at this time, at least—it is impossible to predict outbreaks of such infections. In particular, globalization and the increasing fish trade have contributed to the introduction of pathogens into countries where they previously had been unknown. The development of preventive and combative measures is important.

Aquaculture of Molluscs

Carnegie (2005), on the basis of a FAO report, states that the 3 most important molluscs in aquaculture are the Pacific oyster *Crassostrea gigas*, the Manila mussel *Ruditapes philippinarum*, and the Japanese mussel *Pationpecten yessoensi*, with an annual economic value of US $7.4 billion, that is, 13.3% of the entirety of global aquaculture. Because of their importance, the effects of parasitic infections are particularly well documented. In some cases, parasites have led to the complete collapse of mollusc aquaculture, not always because of the great mortality of infected animals, but also because investments in the industry stopped, due to the high risk involved. In the following, only a few well documented examples are described. Further examples can be found in Rohde (1993) and Carnegie (2005).

Oyster production in Delaware Bay, New Jersey, United States was approximately 6 million pounds of oyster meat annually in the late 1940s and early 1950s until 1955. In 1960, it decreased to 167,000 pounds as a consequence of infection with *Haplosporidium nelsoni* (Haplosporidia). Twenty years later production had not recovered. The same parasite led to the complete collapse of oyster culture in Virginia in 1959. The related species *Haplosporidium costale* caused epidemics among oysters in Virginia, with losses of 12–14% in 1959 and 36–44% in 1990 (references in Rohde, 1993). Figure 7 illustrates mass mortality of oysters due to 2 species of Haplosporidia, *Haplosporidium nelsoni* and *Perkinsus marinus*, in Virginia, United States. Some recent reviews of work on haplosporidian parasites of molluscs are Carnegie and Cochennec-Laurean (2004), Burreson and Ford (2004), and Arzul and Carnegie (2015).

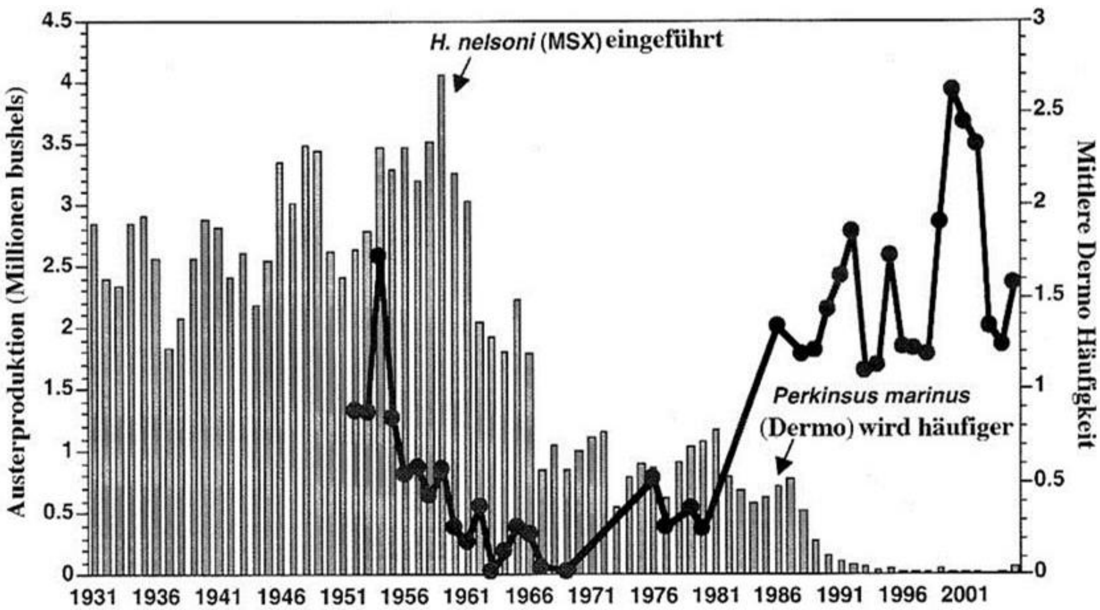

Figure 7. Effects of 2 species of Haplosporidia (Protista), *Haplosporidium nelsoni* and *Perkinsus marinus* (black dots and line), on oyster production (columns) in Virginia, United States. Abundance (frequency) of infection with *Perkinsus marinus* for each population was calculated as 5 × heavy infections, 3 × light infections and 1 × rare infections; the sum divided by total number of oysters examined. Bushels are Virginia bushels of oyster meat. 1 US bushel = 0.716 Virginia bushel; 1 Virginia bushel = approximately 4.2 kg. Source: R. Carnegie. License: CC BY-NC-SA 4.0.

Aquaculture of Prawns/Shrimp and Lobsters

Overstreet (2005a) stresses the importance of disease in prawn cultures. Microorganisms are the main culprits, but parasites can also lead to high mortality. Among parasites, various protistans such as flagellates and ciliates, diatoms, gregarines, and microsporidians play a role, and also hydrozoans, hirudineans, isopods, and helminths, like nematode, trematode, and cestode larvae. Some of these species are not parasitic sensu stricto; rather, they are epizoans, which for example grow in masses on the gills or body surface, interfering with swimming and orientation. Cestode larvae can infect the nervous system and affect the behavior of hosts. Numerous Microsporidia infect prawns, and all either make the sale of hosts impossible or reduce their value.

Cawthorn (2005) discusses diseases of the American lobster *Homarus americanus* and concludes that there are many ecto- and endoparasites, but that most do not cause significant disease. Important for lobsters is the ciliate *Anophrydoides haemophilia*, responsible for bumper car disease. Some Protists are responsible for shell disease, probably jointly with bacteria, diatoms, and other factors. Furthermore, the amoeba *Neoparamoeba pemaquidensis* causes the amoebic gill disease of salmon, lobsters, and other crustaceans.

Cleaning Symbiosis

A considerable range of behavioral patterns leading to (or thought to lead to) the removal of parasites has been observed. They include preening and bathing of birds in dust and water, passive and active anting (where ants are allowed to passively crawl over the body, or where ants are actively squeezed over the plumage). Also, rubbing of dogs against rough surfaces, jumping of fish out of the water, and so on, may have a cleaning function. Best known is cleaning symbiosis in which one animal (the cleaner) cleans another (the host or client) from parasites and diseased (necrotic) tissues. For example, cleaning behavior has been observed in birds which remove ectoparasites from cattle, hippopotamus, and large marine fish floating on the ocean surface, in several species of shrimps, and in many species of fish. Hosts are freshwater and marine fishes, whales and dolphins, and invertebrates, among others. Many cleaner fish possess special morphological adaptations which enable them to pick up parasites (the mouth is located terminally to facilitate picking up of parasites, the anterior teeth are fused to form cutting plates, and color patterns are conspicuous, useful in signaling to hosts: "I am a cleaner!"). The marine cleaner fish *Labroides dimidiatus* (Figure 8) even performs a cleaning dance to attract host fish. Invitation postures of hosts, in turn, signal to the cleaner that they are ready to be cleaned. Some fish mimic cleaners and approach host fish to bite off scales and tissues, or in order to avoid being eaten by predators.

The widespread occurrence of cleaning symbioses indicates that they are of great ecological importance. They have been best examined in the sea, in particular in tropical waters (Grutter, 2005).

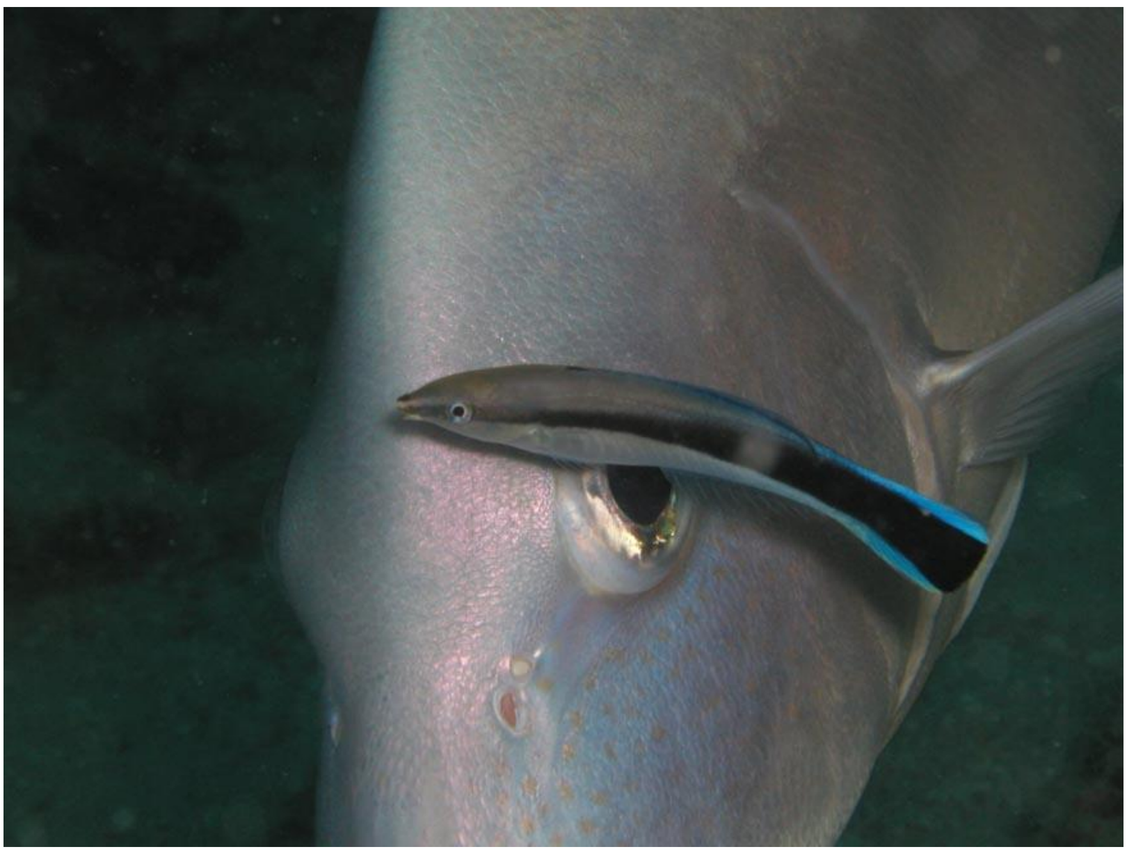

Figure 8. The cleaner wrasse *Labroides dimidiatus* cleaning a host, the marine fish *Diagramma pictum*. Note the conspicuous color pattern of the cleaner fish and its terminal mouth. Source: A. Grutter. License: CC BY-NC-SA 4.0.

Future Perspectives in Research

Rohde (2016) has discussed aspects that need attention in future research (see also Leung et al., 2015). Foremost, many species remain to be described from all habitats, but particularly poorly known are the deep sea fauna and meiofauna. Estimates of expected species numbers from these habitats vary widely, but it is likely that a vast number of free-living species remains to be described, and there is no reason why many of these should not have parasites. Is niche space in such parasite systems largely non-saturated, that is, are there many empty niches (Rohde, 2005c). Knowledge of biogeographical patterns of marine parasites, such as latitudinal gradients in species diversity, niche width and reproductive strategies, as well as longitudinal gradients, is poor. Useful in such studies is the application of agent-based models, but very few such studies have been made (for example, Rohde and Stauffer, 2005).

How do parasites locate their hosts? Many mechanisms are probably involved in each case, such as chemical and behavioral ones, but one aspect has been particularly little studied, that is, magnetic orientation which is important in orientation for many animals such as birds. There is just a single study in which magnetic orientation in marine parasites (in parasitic marine larval copepods and monogeneans) has been demonstrated (Rothsey and Rohde, 2002). An amazing variety of sensory receptors has been demonstrated by transmission electron microscopy in some parasite species, for example, in aspidogastreans and polyopistocotylean monogeneans (see Figure 9), but practically nothing is known about their function in host, niche and mate finding (for example, see Rohde, 2002b; 2013).

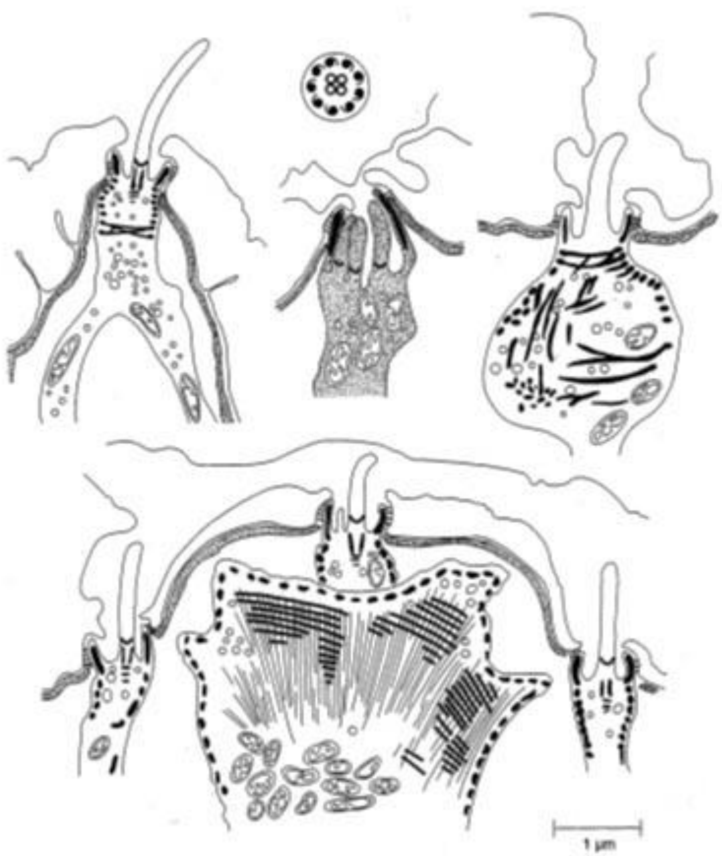

Figure 9. Diagrams of non-pharyngeal sensory receptors. A) Small uniciliate receptor; B) multiciliate receptor; C) large uniciliate receptor; D) receptor complex with large non-ciliate receptor and some small uniciliate receptors. Source: Rohde and Watson, 1996. License: CC BY-NC-SA 4.0.

Not only description of species, but of their life cycles is important. Here, the knowledge is even more limited than for taxonomy. For example, of the many hundreds of trematode species on the Great Barrier Reef, the life cycles of only 2 had been studied up to 2014 (Cribb et al., 2014).

In total, the oceans present vast scope for future taxonomic, ecological, zoogeographical, and experimental work.

Marine Parasites Infecting Humans

Background

Far more than 100 (and actually probably more than 200) species of eukaryotes infect humans. By far the most important are parasites with terrestrial or freshwater life cycles. Nevertheless, there are many marine species found in humans, although none needs humans as obligate hosts. The various infections including symptoms are discussed in the standard work, edited by Rohde (2005a), and Overstreet (2013) gave a comprehensive and well-illustrated account of marine parasitic diseases. A few examples are discussed here.

Helminths (Parasitic Worms)

The largest number of marine parasite species found in humans are helminths, that is, parasitic worms, such as nematodes (roundworms), trematodes (flukes), and cestodes (tapeworms). Characteristics of the groups, important for understanding the discussion below are as follows.

Most nematodes have separate sexes and pass through 4 juvenile stages (J_1–J_4), until sexual maturity is reached in the fifth stage. These stages are transformed into each other by 4 molts, that is, the loss of the old cuticle and formation of a new one. In some cases, the cuticle of the preceding stage remains as a sheath of the new stage.

Adult trematodes are usually hermaphroditic (that is, the same individual has both male and female reproductive organs, which however may mature at different times), and they produce eggs in which the first larval stage, the ciliated miracidium, develops. This larva must get into the first intermediate host, almost always a mollusc, for further development to the sporocyst. Sporocysts produce daughter sporocysts or rediae, in which tailed cercariae are formed, which leave the host and either encapsulate outside the host or infect a second intermediate host, becoming metacercariae. Development of the sexually mature worm occurs after a final (definitive) vertebrate host has become infected. Species of the family Schistosomatidae have separate sexes and their cercariae penetrate actively through the skin of a vertebrate host.

All marine cestodes infecting humans belong, with one exception, to the Pseudophyllidea (families Diphyllobothriidae and Bothriocephalidae) which normally mature in marine mammals. Eggs are shed in the feces. The first larval stage, the ciliated coracidium, develops in them. The coracidium hatches and penetrates into a copepod for further development, where it is transformed to the procercoid. In the muscles of fish which become infected by eating infected copepods, the next larva, the plerocercoid, develops. Mammals become infected by eating infected fish. Not rarely there are additional transport (paratenic) hosts, where larvae survive but do not grow and develop further.

Anisakiasis

Nematodes are of particular importance, as they cause the most severe symptoms. Thus, species of the family Anisakidae (Figures 10–12) cause the syndrome (= complex of symptoms) of anisakiasis. Infection occurs by eating insufficiently cooked fish and invertebrates (cephalopods). The species complex most frequently encountered is *Anisakis simplex* (consisting of 3–5 species). *Pseudoterranova decipiens*, also a species complex consisting of several species, also is not rare. *Anisakis physeteris*, *Contracaecum osculatum*, and *Hysterothylacium aduncum*, on the other hand, are rare in humans (Nagasawa, 2005). Morphological differences between the different genera of Anisakidae and life cycles are discussed and illustrated in Rohde (1984). Overstreet (2013) discusses anisakids infecting humans in greater detail.

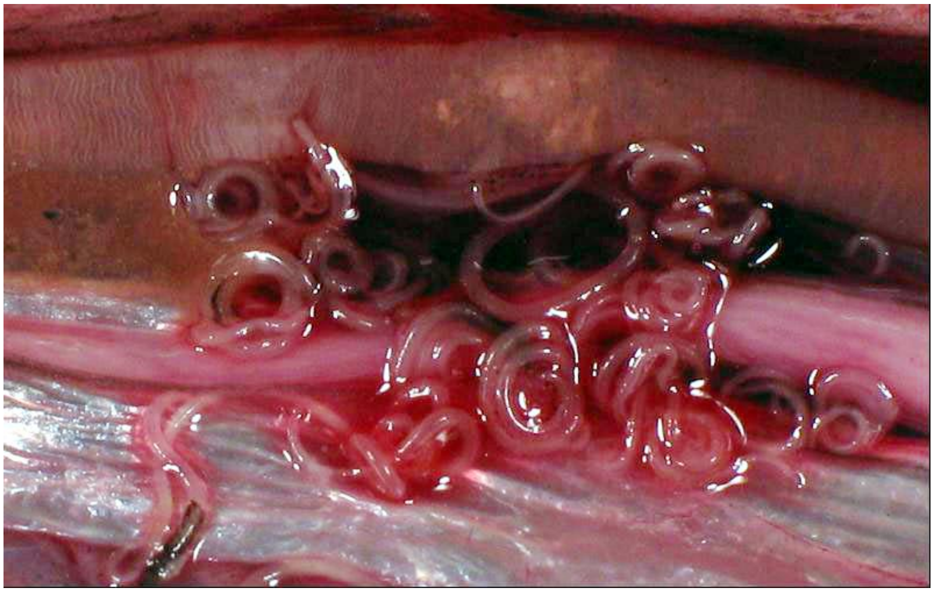

Figure 10. Anisakidae juveniles. Source: Anilocra. Dedicated to the public domain.

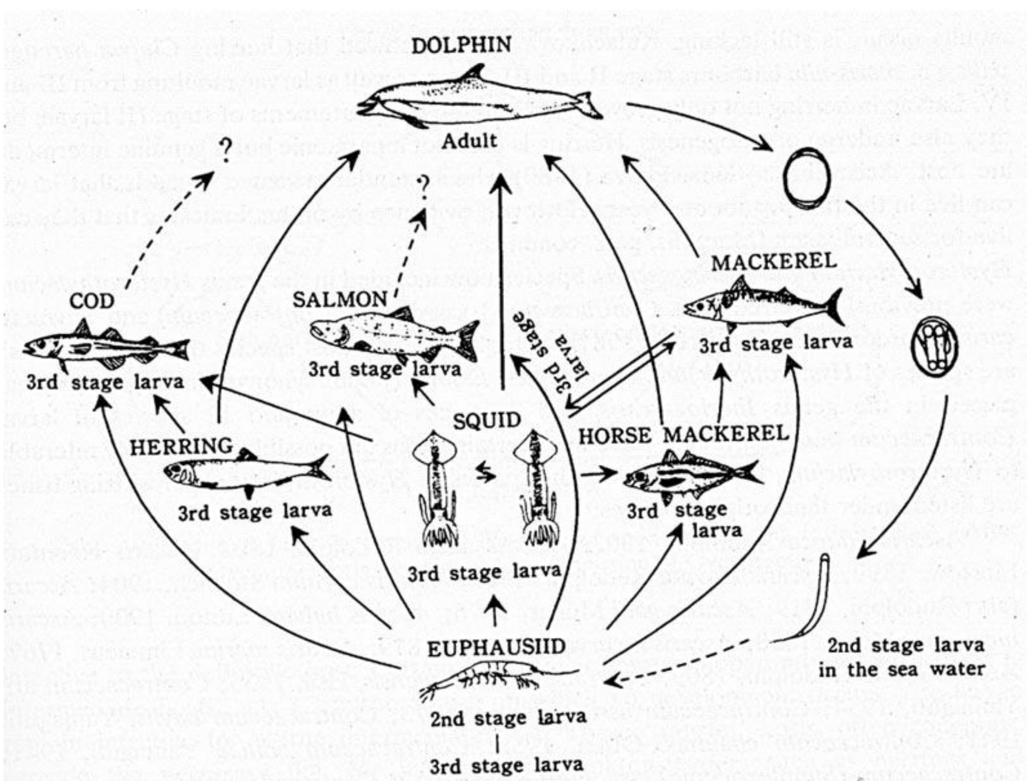

Figure 11. Life cycle of *Anisakis simplex*. Source: Adapted from Oshima, 1972. License: CC BY.

The life cycle of *Pseudoterranova decipiens* (seal worm) is as follows. Adult worms live in the intestine of seals. Eggs are shed in the feces and sink to the seafloor. Development in the eggs proceeds to the third juvenile (J_3) stage (0.2 mm-long), which leaves the egg, remaining, however, in the cuticle of the second juvenile (J_2) stage which serves as a sort of sheath. Juveniles attach with their tail end to the substratum and are ingested by various small crustaceans (copepods, juvenile amphipods, and mysids). The juveniles then break through the sheath and penetrate into the haemocoel of the host. Copepods are eaten by larger macro-invertebrates (adult amphipods, mysids, or polychaetes), in which larvae can reach a length of more than 8 mm. Small fish become infected by eating infected macro-invertebrates. Large fish, in turn, become infected by eating invertebrates or small fish. Juveniles (still in the third stage) penetrate through the intestinal wall of fish and grow in their musculature to a length of about 30–60 mm. Finally, seals become infected by eating infected fish or macro-invertebrates. The last 2 molts occur in the intestine of seals. Humans are not necessary for the completion of the life cycle; they play the role of transport hosts for the third juvenile (McClelland, 2005). (For a discussion of anisakids, see also Smith and Wootten, 1978). Species of the genus *Anisakis* do not use seals, but instead whales and dolphins, as final hosts, known at times as "whale worms" (for example, Dailey, 2005) (Figure 12).

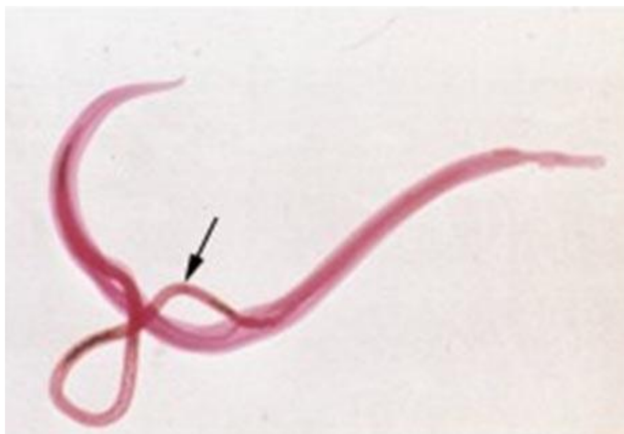

Figure 12. *Austrobilharzia terrigalensis* (Trematoda, Schistosomatidae) from the blood vessels of the gull *Larus novaehollandiae* at Heron Island, Great Barrier Reef, Australia. The thin male (arrow) lies in a fold of the much broader female. Cercariae of this species cause cercarial dermatitis. Source: K. Rohde. License: CC BY.

The symptoms of anisakiasis vary considerably, depending on which organs or tissues are infected (namely, stomach, intestinal, or extraintestinal). Acute and chronic forms can also be distinguished. The former is mainly characterized by fast-developing abdominal pains, as fast as 2 hours after infection, often accompanied by nausea and vomiting. In the mild, chronic stomach anisakiasis, pains are often subacute and can last for more than 2 years (if the parasites are not removed by surgery). Almost all cases of intestinal anisakiasis are acute, usually with severe abdominal pains, nausea, constipation, and diarrhea. In most extraintestinal cases, symptoms are localized and mild (Nagasawa, 2005).

Infections are easily preventable by cooking of hosts, or by freezing at −20 ºC for 1 or more days (Nagasawa, 2005). The probability of acquiring an infection can be reduced by removal of the viscera of fish a short time after capture, which prevents migration of juveniles from the intestine into the tissues, although some juveniles are already in the tissues (Williams and Jones, 1976). The effectiveness of control measures has been demonstrated by the fact that no new cases of human infections occurred after the Netherlands government had introduced a law that made it compulsory to freeze fish before sale as green herring (which is raw herring) (Rae, 1972). However, in many countries fresh fish are preferred over frozen ones.

Trichinosis

Trichinosis is caused by infections with species of the nematode *Trichinella*. Heavy infections can cause death and were, for example, quite common in Europe in the 19th century, until strict inspections radically reduced the prevalence of infection. The most widespread infection mechanism is eating undercooked pork. Mature worms live only for a short time in the host's duodenum, where they copulate and produce live juveiles, which migrate into the blood system. Juveniles of the first stage (J_1; that is, before molting) encapsulate in the striated muscles. Some genotypes live freely in the muscles without forming capsules. Marine mammals are infected with several species of *Trichinella* including *Trichinella nativa* and *T. britovi*. Cases of *Trichinella* in marine mammals are restricted to the circumpolar arctic, where 60% of polar bears are infected in some regions. Walrus (also up to 60%), and more rarely whales and seals also serve as hosts. *Trichinella* acquired from marine mammals is an important source of human infection. Walrus and polar bears are the most important sources. Symptoms depend on infection intensity. Importantly, even freezing at −20 ºC for 4 years did not kill all juveniles (Forbes, 2005). A more detailed discussion of genotypes of *Trichinella* infecting humans can be found in Overstreet (2013).

Angiostrongylosis

Normal final hosts of the rat lungworm *Angiostrongylus cantonensis* are various rodents, including rats, among others. The parasite is not a genuine marine parasite but uses terrestrial and freshwater animals in its life cycle. However, some marine invertebrates are transport (paratenic) hosts which can transmit the infection to other hosts. Humans are abnormal hosts who contain the third juvenile stage when infected. The worms do not mature in humans. Originally the species was restricted to the Indo-Pacific region but has been introduced into other tropical and subtropical regions.

Mature worms live in the lung arteries of rodents (and at high infection intensities, also in the right ventricle). They produce eggs from which larvae hatch in the lung arteries and capillaries. They migrate up the trachea, are swallowed and shed in the feces. Terrestrial and freshwater molluscs eat the larvae or are infected by external penetration of the juveniles. The juveniles develop within a few weeks to the third stage (J_3), which is infective to rodents. In the rodents, the juveniles reach the surface of the brain via the blood or nervous system. After a few weeks they migrate into the lung arteries (Overstreet, 2005b).

Various brackish water and marine fish as well as invertebrates can be experimentally infected (see, for example, Cheng, as cited in Rohde, 1993). Shrimps of the families Palaemonidae and Penaeidae in aquaculture are probably the most important transport hosts, and oysters and marine mussels (*Mercenaria*) are suitable intermediate hosts (Overstreet, 2005b).

The syndrome caused by the worms is eosinophilic meningoencephalitis (or eosinophilic meningitis), an inflammation of the cerebral membranes with an accumulation of eosinophilic white blood cells. In extreme cases there may even be mental disturbances and death. Very strong headaches, paralysis, vomiting, and fever are only some of the other possible symptoms. Freezing and heating kills the juveniles (Overstreet, 2005b).

Schistosome Dermatitis (Cercarial Dermatitis)

Larvae of several species of the trematode family Schistosomatidae, which normally infect birds and non-human mammals, attempt, and sometimes succeed, in penetrating through the skin of humans in certain waters. Since humans are an abnormal host, the parasites die without obtaining sexual maturity, but can cause often severe inflammatory reactions of the skin. In the sea, species of *Austrobilharzia* (Figure 13), *Ornithobilharzia*, and *Gigantobilharzia*, probably as well as other genera, are responsible. They all use birds as the normal, final hosts. Of special interest is *Austrobilharzia* (for example, *A. terrigalensis* and *A. variglandis*) which use many species of molluscs as intermediate hosts.

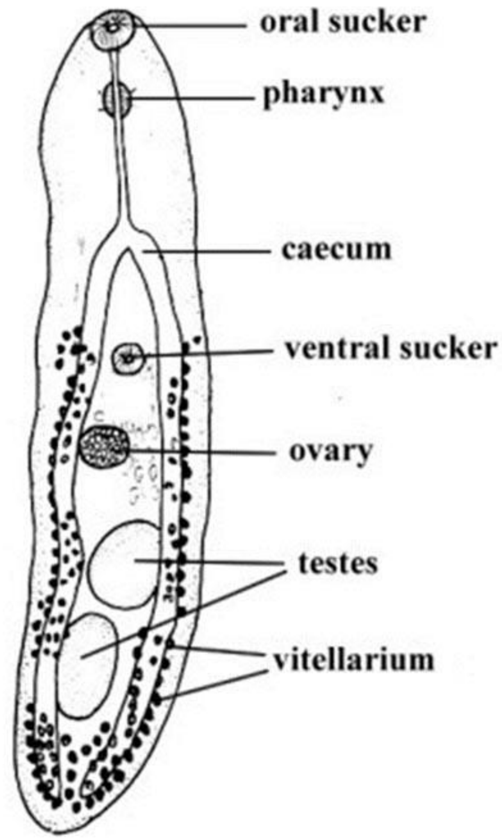

Figure 13. Heterophyid trematode. Source: K. Rohde. License: CC BY.

Infections occur especially in calm coastal waters like lagoons or estuaries, which can be explained by the behavior of schistosome larvae. They swim to the surface of the water and wait there until a suitable host appears. They then penetrate into the skin, where they cause prickling irritations, lasting for about an hour. Urticaria and other skin reactions which can develop to liquid-filled bladders, are characteristic. Secondary infections may occur, and lesions are often pigmented and can last for 10 days or even weeks or months. A first infection generally leads to only weak reactions, though repeated infections lead to much stronger reactions, including general symptoms such as fever and edemas (Walker, 2005; Rohde, 1993). Contact with larvae of species known to cause dermatitis, sometimes causing no symptoms, which was demonstrated by experiments with cercariae of *Austrobilharzia terrigalensis* (Rohde, 1993).

Other Helminths

Humans may be infected with a large number of helminth species by ingesting larvae (such as plerocercoids of tapeworms or metacercariae of flukes) in insufficiently cooked marine animals. Raw, salted, marinated, or undercooked fish and invertebrates, such as molluscs, are traditional delicacies in many countries (among others Korea, Japan, Hawaii, and other Pacific islands). Widespread are sushi and sashimi (raw fish), originally Japanese delicacies, but now popular worldwide. In Polynesia, freshly caught fish, such as tuna or bonito, are cut into small pieces, washed in seawater and eaten with freshly pressed lemon juice. Laird (1961) and Chai et al. (2009), for example, have shown that human infections with numerous trematodes are frequent in Japan, the Philippines, Polynesia, and Southeast Asia.

Trematodes transmitted by marine or brackish water animals to humans use molluscs as first intermediate hosts, and many invertebrates and fish containing the metacercariae as second intermediate hosts. Infections are restricted to estuaries and coastal regions, and all species are small. With few exceptions, species belong to the family Heterophyidae (Figure 14) (or, more rarely, to the Echinostomatidae and Gymnophallidae families). Prevalence of infection can be very high. For example, in a Korean village, 75% of the population was infected (see the references in Blair, 2005). Infections with such flukes are probably much more common than usually assumed, because symptoms, if they are present at all, are often minor with little specificity, in spite of the often enormous infection intensities. Thus, almost 70,000 worms of 3 species were demonstrated in a Korean patient who had relatively minor symptoms, such as occasionally light pains in the stomach region, diarrhea, and bad digestion. On the other hand, worms were also found in patients with serious symptoms like pancreatitis (inflammation of the pancreas), although it is not clear whether the parasites were the causes of the symptoms. In rare cases, the small worms may leave the intestinal canal and they, or more frequently their eggs, may cause embolisms in the brain, spinal cord, and heart, sometimes with fatal consequences (Blair, 2005). Of special interest is that the fluke *Nanophyetus salmincola* contains a hyperparasitic microorganism, *Neorickettsia helminthoeca*, which causes a lethal infection in canids (dogs and related species), salmon poisoning disease. Although human infections with this trematode are not known, a related species in Siberia, Russia infects almost 100% of humans in some regions. Infection is acquired in freshwater, but metacercariae have been found in marine fish (salmonids), where they can survive for several years (references in Rohde, 1984; 2005a). Greiman et al. (2016) found *Neorickettsia* sp. in various larval stages of the trematode *Plagiorchis elegans* but not in the ovarian tissue. This suggests that vertical transmission of *Neorickettsia* within adult digeneans occurs by incorporation of infected vitelline cells into the egg rather than direct infection of the ooplasm as known for other bacteria of invertebrates.

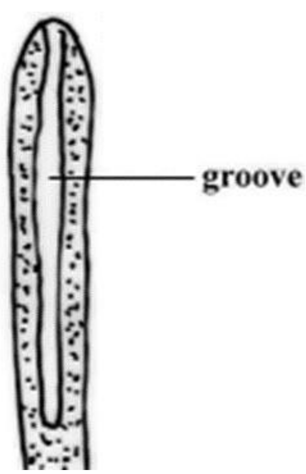

Figure 14. Anterior end of a pseudophyllidean tapeworm. Note the simple scolex with a groove. Source: K. Rohde. License: CC BY.

Tapeworms, with one exception (a trypanorhynch, Figure 3), belong either to the genus *Diphyllobothrium* or to *Diplogonoporus* (Figure 15). Natural final hosts are whales and seals. Life cycles include copepods as first intermediate hosts, and fish (containing the plerocercoid larva infective to humans) as second intermediate hosts. Transport hosts may also be included. Most important for humans are *Diphyllobothrium pacificum* and *Diplogonoporus* spp. Symptoms are diarrhea, abdominal pain, anorexia, and general weakness. Kikuchi et al. (cited in Rohde, 1993) report an accidental infection with a larval trypanorhynch in Japan, apparently acquired by ingestion of a raw cephalopod. Overstreet (2013) gives a detailed discussion of human infections with marine tapeworms.

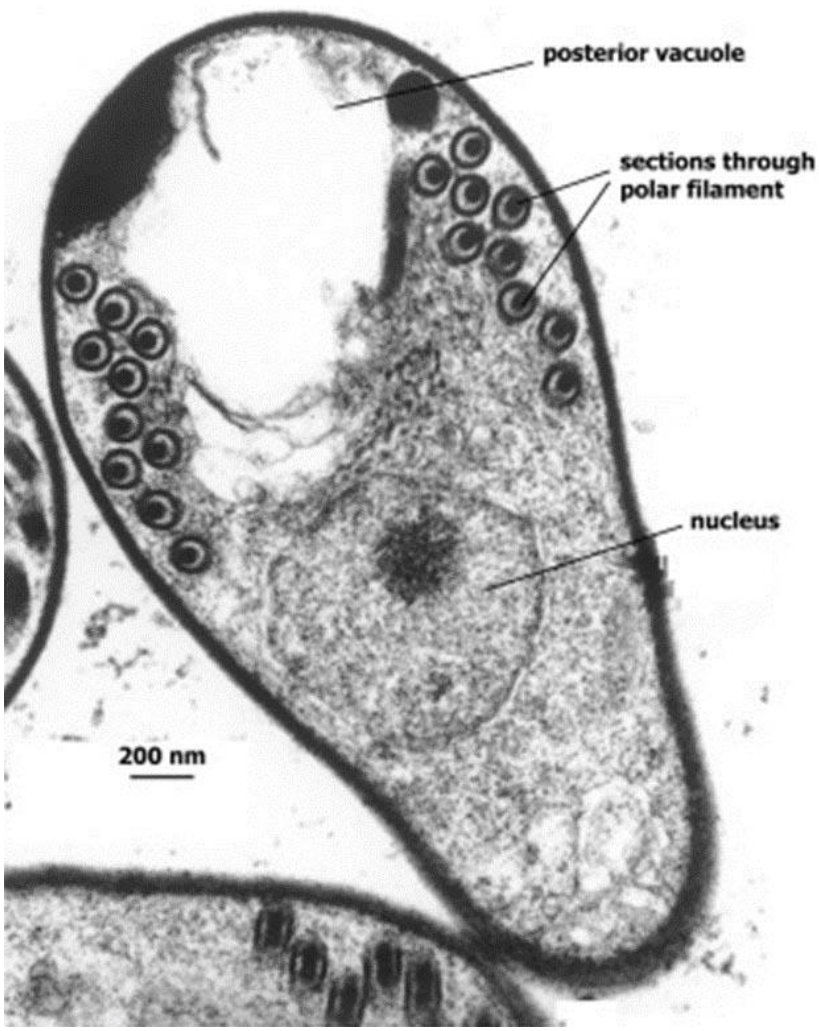

Figure 15. Mature spore of *Vairimorpha cheracis*, a microsporidian parasite of the Australian yabby *Cherax destructor*, transmission electron micrograph. Note the nucleus, posterior vacuole, and sections through 11 coils of polar filament. A new host cell is infected by extrusion of the spore's content into the cell through the everted filament. Source: E. Moodie. License: CC BY-NC-SA 4.0.

Furthermore, ingested acanthocephalans and nematodes (in addition to those causing anisakiasis) may occasionally infect humans (for details and references, see Rohde, 1993). Deardorff et al. (1986) describe a case of human infection with a sexually mature female roundworm *Philometra* sp. which had penetrated through the wound of the hand of a fisherman.

Unicellular Eukaryotes (Protista)

Marine species infecting humans belong to the Microsporidia and Apicomplexa, and possibly to the flagellates. Microsporidia are found in almost all phyla of invertebrates and in 5 classes of vertebrates. To date, more than 1,300 species have been described, but this is only a small proportion of the extant species, since most potential hosts have never been examined. Microsporidia are intracellular parasites and form infective spores (Figure 15). At least 14 species in 6 genera (only some of them in the sea) infect humans, most however only immune-deficient individuals, such as AIDS patients. *Pleistophora*, for example, parasitizes poikilothermic animals, especially marine and freshwater fish, but it was also found in a human with weakened immunity. An increasing number of species resembling species in fish are found in immunocompromised humans. Fish, as well as crustaceans, must be considered to be possible sources of infection (Freeman, 2005).

Marine Apicomplexa belong exclusively to the Coccidia. Infection occurs by ingestion of oocysts. Again, mainly immune-defective persons become infected. The species *Cryptosporidium parvum* (and related species of the same genus) cause cryptosporidiosis in humans. Oocysts are ingested in polluted water and cause serious diarrhea. Although the species are typical freshwater organisms, infective oocysts can be washed into coastal waters and survive there for up to a year. Marine mussels and oysters can accumulate oocysts and ingestion of such potential carriers should therefore be avoided by immunocompromised persons (Freeman, 2005). Gómez-Bautista et al. (2000), for example, have shown that mussels (*Mytilus gallo-provincialis)* and cockles (*Cerastoderma edule*) on the coast of northwestern Spain contained oocysts of this species which were infective to newly born mice.

The primitive protistan (flagellate) *Giardia* infects various vertebrates, among them humans, usually in freshwater. However, resistant resting stages were isolated from marine mussels. The possibility can therefore not be excluded that humans can become infected by eating infected marine molluscs (Freeman, 2005). One symptom of giardiasis is serious diarrhea.

Arthropods

Webb et al. (1985) described a case of human infection with the mite *Orthohalarachne attenuata*, which normally occurs in the nostrils of walrus. In humans, the iris of the eye becomes infected, leading to damage to the cornea, and eye irritation. Apparently, infection can be acquired by close contact with walruses.

Vertebrates

Among the fishes, the eel-like Cyclostomata (lampreys) occasionally attack humans as temporary parasites; that is, they attach themselves by means of their oral disc covered with many horny teeth-like structures to the body and ingest the host’s blood and other tissue (Figure 16).

Figure. 16. Oral disk of the sea lamprey *Petromyzon marinus* from Aquarium Finisterrae in A Coruña, Galicia, Spain. Source: F. Losada Rodríguez, 2007. License: CC BY-SA 4.0.

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