# Chapter 14
# Marine Crustaceans as Potential Hosts and Vectors for Metazoan Parasites

**Markus Wilhelm Busch, Thomas Kuhn, Julian Münster, and Sven Klimpel**

**Abstract** Crustaceans are highly abundant in the marine environment and play a key role as an important source of nutrition for a wide range of marine vertebrates such as fish, birds and mammals (seals, whales). In this context, marine helminth parasites have evolved complex (heteroxenous) life cycles in order to reproduce and use the trophic interactions in the marine food web to facilitate the transmission to the successive hosts. Members of the parasites taxa Digenea, Cestoda, Nematoda and Acanthocephala are common parasites in the marine environment and known to frequently include pelagic and benthic crustaceans of the subgroups Amphipoda, Cirripedia, Copepoda, Decapoda, Euphausiacea, Isopoda and Mysidacea in their life cycle. Infestation data from 52 peer-reviewed publications have been taken into consideration in order to summarize the current knowledge of crustaceans that are known to be the intermediate hosts for marine helminth parasites. This includes the discussion of life cycles, impacts of parasitism on hosts and zoonotical threats (e.g. for the nematode species of the genus *Anisakis*).

**Keywords** Anisakid nematodes • Crustacea • Intermediate host • Life cycle • Metazoan parasites • Vector

---

M.W. Busch (✉) • T. Kuhn • J. Münster • S. Klimpel
Medical Biodiversity and Parasitology, Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

Senckenberg Gesellschaft für Naturforschung (SGN), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

Institute for Ecology, Evolution and Diversity, Goethe-University (GO), Max-von-Laue-Straße 9, 60438 Frankfurt am Main, Germany
e-mail: markus.busch@senckenberg.de; Sven.Klimpel@senckenberg.de

H. Mehlhorn (ed.), *Arthropods as Vectors of Emerging Diseases*,
Parasitology Research Monographs 3, DOI 10.1007/978-3-642-28842-5_14,

## 14.1 Introduction

With approximately 52,000 described species worldwide, the subphylum Crustacea is one of the four most diverse groups within the Metazoa (Martin and Davis 2001). They inhabit especially aquatic (marine, limnic) ecosystems and have gone through a series of behavioural, physiological and morphological adaptations that allow them to colonize virtually any aquatic habitat. The morphological diversity is higher than in any other taxa on earth, and, not surprisingly, the current list of known species is constantly growing while there is still no consensus regarding the number of constituent crustacean classes (e.g. Spears and Abele 1997).

Oceanographers divide the ocean into regions depending on abiotic and biotic conditions of these areas. The benthic zone is the ecological region at the lowest level of a body of water in the ocean, including the sediment surface and some subsurface layers. The pelagic zone includes all open ocean regions and can be divided into further regions categorized by depth and light abundance and is based on the plankton (phytoplankton) which occupy the start of the food chain. The term plankton describes all aquatic organisms including eggs and developmental stages that are drifting passively in the water column (pelagial). Although its distribution and density varies seasonally, horizontally and vertically, it is ubiquitous in both freshwater and marine ecosystems and primarily divided into the functional groups zooplankton and phytoplankton. Crustaceans are the predominant group regarding abundance and biomass in the marine zooplankton and represent an important link between phytoplanktic organisms (primary production) and higher trophic levels (e.g. cephalopods, fish, marine mammals). Due to this key role in the aquatic food webs, the diversity of metazoan parasites utilizing crustaceans as intermediate hosts is comparatively high (Marcogliese 1995). Especially, members of the parasite taxa Digenea, Cestoda, Nematoda and Acanthocephala are known to include invertebrate organisms as intermediate or paratenic hosts to facilitate transmission in the environment even at low densities (Marcogliese 1995).

The following pages summarize the current state of knowledge about the importance of crustaceans in the marine food web and their implications on the transmission of helminth parasites. The diversity of the currently recognized crustacean species that act as intermediate or paratenic hosts for marine helminths is highlighted, and their role in the life cycle of the parasites is discussed. An overall summary of all records of helminth parasites in marine Crustacea is far beyond the scope of this chapter, but it will become apparent that the high density and abundance of marine Crustacea is also reflected in a key position within the life cycle ecology of helminth parasites.

## 14.2 Biodiversity and Distribution of Marine Crustacea

Copepoda with estimated 13,000 morphospecies represents the most species rich taxon of the Crustacea (Boxshall and Defaye 2008). They are highly abundant in almost all aquatic environments (limnic but predominantly marine) and occur from the Arctic to the Southern Ocean (Antarctic waters). Copepods are preyed by small predators (e.g. shrimp, small fishes) and are also on the small end of the food size spectrum of baleen whale species (Mauchline 1998). Due to their dominant part in the marine zooplankton, the calanoid Copepoda are major components of aquatic food webs (Gruner 1993).

With approximately 900 marine species, the subclass Cirripedia is far less diverse. They represent the only sessile group of Crustacea and, with the exception of parasitic forms, live attached to rocks, shells and animals (Newman and Abbott 1980; Ruppert and Barnes 1994).

The pelagic Euphausiacea is the second most common taxon within the Crustacea. They occur in large swarms as permanent members of the zooplankton, and their distribution varies from the neritic epipelagial (e.g. *Meganyctiphanes norvegica*, 100–500 m depth) to the meso- and bathypelagial (e.g. *Bentheuphausia amblyops*, 1,000–5,000 m depth) (Gruner 1993). The most famous species in the Southern Ocean is the vertical migrating Antarctic krill *Euphausia superba*, which has a circumpolar distribution and is the foundation of the Antarctic food web. Antarctic krill is the major link between primary producers and many populations of Antarctic carnivores (e.g. fishes, penguins, seals, whales) (Lascara et al. 1999). Although underlying strong variations, the biomass is estimated at more than 500 million tons (Martin and Davis 2001; Siegel et al. 1998). Investigations between the Antarctic Peninsula and South Georgia in the year 2000 show a mean *E. superba* density of 21.4 g $m^{-2}$ (Hewitt et al. 2002).

The order Amphipoda contains approximately 7,900 species and forms the largest group of the superorder Peracarida (Wirkner and Richter 2007). Most amphipods are marine and have been diversified in pelagic and benthic habitats (Whiteley et al. 2011). Some have been found even in deep-sea trenches of 10,000 m depth (Gruner 1993). The body tends to be laterally compressed and is usually between 5 and 15 mm in length (Ruppert and Barnes 1994). Hyperiid amphipods are exclusively pelagic and distributed from the surface layers to the bathypelagial, whereas members of the Gammaridea are usually benthic, demersal or benthopelagic (Gasca et al. 2009).

The dorsoventrally flattened 4,000 Isopoda species are widely distributed invertebrates that occupy various habitats. Most specimens are between 5 and 15 mm in length and omnivore deposit feeders. They represent the largest group of truly terrestrial crustaceans, and the suborder Paraselloidea forms one of the most abundant components of the deep-sea benthic fauna (Ruppert and Barnes 1994). The probably most famous aquatic parasitic species belong to the Cymothoidae. These parasites are permanent ectoparasites of marine fish and, due to their strategy to attach to external surfaces, gills or in the buccal cavity of their hosts, commonly known as tongue biters (Hadfield et al. 2011).

The order Decapoda comprises approximately 10,000 species. Most of them are marine and colonize the oceans from the supralittoral zone to the deep sea. Specimens are on average bigger sized than all other Crustacea and have a very diverging morphology from shrimp-like elongated to crab-like. Their diet shows a wide range, but most species combine predatory feeding with scavenging (Ruppert and Barnes 1994).

Classification of the Mysidacea includes 160 genera and about 1,000 species. While there is still no consensus about monophyly, the Lophogastrida and Mysida are commonly treated as subgroups of this taxon (Meland and Willassen 2007). They are cosmopolitan and distributed throughout the water column. More than 90% of the mysid species are considered exclusively marine and have adapted to both benthic and pelagic environments (Porter et al. 2008). In addition, they have also been reported from inland fresh and brackish water habitats. Most mysidaceans reach lengths from 2 to 30 mm and live in large swarms where they form an important part of the diet of marine fish. They usually feed as omnivores or scavengers (Ruppert and Barnes 1994).

In general, the distribution of crustaceans and especially zooplankton in the marine environment is heterogenous and depends on different biotic and abiotic factors that determine the vertical and horizontal distribution patterns. Differences in the availability of nutrients as a result of reduced or increased primary production by phytoplanktic organisms often arise through the formation of frontal systems, water column stratification and the course of ocean currents. At the eastern side of the South Atlantic, for example, at the Benguela upwelling region off the coast of Namibia and Angola, zooplankton communities on the shelf across the region are characterized by low diversity and high abundance. These regions contain species which are typical for upwelling areas or cold-temperate shelf waters worldwide (Gibbons and Hutchings 1996). Along fronts primary production of organisms is, due to the permanent upwelling of nutrients, usually higher and has a direct effect on the food chain processes. In the vicinity of these fronts, concentrations of Crustacea and fish are high, and therefore, potential predators and prey organisms are accumulated. This favours the transmission of parasites (Klimpel and Rückert 2005; Munk and Nielsen 1994; Richardson et al. 1998).

## 14.3 Helminth Parasites of Marine Crustacea

Metazoan parasites have evolved complex life cycle strategies in order to reproduce. They can be divided into different types: monoxenous and heteroxenous life cycles. Monogenea and parasitic Crustacea are commonly monoxen. They include a single host group to complete their (direct) life cycle. On the other hand, Digenea, Cestoda, Nematoda and Acanthocephala have to switch between different hosts of various trophic levels (indirect life cycle) and can therefore be designated as heteroxen (Möller and Anders 1983; Rohde 2005). The hosts of parasites can be divided into intermediate, paratenic and final hosts, and consequently, the parasites move from hosts on lower trophic levels to those higher in the food web. In the development and distribution of heteroxen parasites, the intermediate host is a vessel for the transmission to the next host and needed for asexual reproduction (e.g. sporocysts in Digenea) and maturation. Once the parasite has reached a specific level of development or size, it is infectious for the final host in which the parasite changes from the larval stage to sexual maturity (adult stage). Paratenic or transport hosts are special forms of intermediate hosts and incorporated between the propagule stage and the definitive host. They represent an additional host and are not essential for the life cycle (facultative). The larval forms do not undergo further development but accumulate over time and facilitate a successful transmission to the next (obligatory) host (e.g. Chubb et al. 2009). In addition, they can transport and spread a parasite species in order to guarantee a wide geographical dispersal.

Digenean parasites are exclusively endoparasitic with complex indirect life cycles. The marine species commonly occur in the alimentary tract of their final hosts (Mehlhorn 2001). Eggs disperse within the host faeces and contain the miracidium stage that has to be ingested by a mollusc, the obligate first intermediate host. Once incorporated, the miracidium produces asexual sporocysts and rediae that release infectious stages known as cercariae. These will either be ingested by or penetrate actively the second intermediate host, usually a crustacean. Occasionally, the cercariae directly infect the final hosts and grow to the adult stage. If a second intermediate host is included in the life cycle, the trematode develops a metacercariae, which is in case of oral ingestion, infectious for the final host (Marcogliese 1995; Mehlhorn 2001; Möller and Anders 1983). Typical fish parasitic Digenea are represented by the families Derogenidae, Hemiuridae, Lecithasteridae and Lepocreadiidae (Klimpel et al. 2009). *Derogenes varicus* (Derogenidae) is one of the most widespread digenean species and has a distribution between the Subarctic and the Subantarctic as well as in shelf water layers and the deep sea (Klimpel et al. 2006, 2009; Køie 1979; Palm et al. 1999). The parasite utilizes gastropods (e.g. *Natica* spp.) as first intermediate hosts and demersal Decapoda as well as pelagic Copepoda as second intermediate hosts (Køie 1979, 1984). Some digenean parasites are of major medical importance (e.g. Schistosomiasis) as they infest the intestines, bile ducts, lung or blood of their final hosts and cause serious injury in these organs.

The hermaphroditic Cestoda (subclass Eucestoda, true tapeworms) are endoparasitic in their intermediate and vertebrate final hosts and encompass more than 5,000 known species (Caira and Reyda 2005). Marine cestodes are estimated to more than 1,400 species and include the orders Diphyllobothriidea, Bothriocephalidea (the latter formerly known as Pseudophyllidea), Trypanorhyncha and Tetraphyllidea (Caira and Reyda 2005; Kuchta et al. 2008). These species perform life cycles with three developmental stages. Adult cestodes live in the intestines or nearby organs of their vertebrate final hosts. The excreted egg develops a stage (known as hexacanth embryo) that remains within the egg. Among the Bothriocephalidea, Diphyllobothriidea and Trypanorhyncha, this stage is surrounded by a ciliated membrane and called coracidium (free-swimming stage). These larval stages will be ingested by an appropriate plankton organism where it reaches the so-called procercoid stage that further develops into a worm-like plerocercoid. The plerocercoids occur in the second intermediate host (plankton predator). Fishes (Elasmobranchia and Teleostei) can serve either as intermediate or as final hosts (Palm 2004). An infestation with cestodes is in many cases without serious pathogenetic consequences for the final host. Diphyllobothriasis is the most common cestode zoonosis and transmitted by the genus *Diphyllobothrium* (Diphyllobothriidae). Diarrhoea, abdominal discomfort, fatigue and anorexia are symptoms of an infection with the adult helminths (Blair 2005; Mehlhorn 2001). Copepoda are the first intermediate hosts in this life cycle, whereas fish acquire parasites by preying upon these infested crustaceans. Accumulation can occur in paratenic hosts. Birds and terrestrial mammals are common final hosts (Blair 2005). Humans can get infected by ingesting undercooked, plerocercoid-containing fish (Mehlhorn 2001). While *D. latum* has a freshwater life cycle, *D. pacificum* occurs in the marine environment (Blair 2005).

Nematodes colonize every habitat and ecosystem on earth (terrestrial, limnic, marine). With currently 2,280 known genera in 256 families and estimated 40,000 species worldwide, Nematoda represent probably one of the most species diverse phyla within the metazoan group (Anderson 2000; McClelland 2005). While most nematodes are free-living feeding on decomposing organic material, numerous species are of major significance as parasites of humans, animals and plants and cause massive losses in agriculture and livestock or cause various diseases as human pathogens. Approximately 4% of all known nematode genera are parasitic in limnic and marine fishes. The vast majority of these nematodes use intermediate and paratenic hosts, which enable them to be transferred through the food chain to the fish or mammalian host (Fig. 14.1e, f) (Anderson 1996). They perform a life cycle including four moultings and larval stages before they reach the adult stage and commonly use copepods and amphipods as well as euphausiids as crustacean intermediate hosts (Marcogliese 1995; McClelland 2005). Larvae persist in the haemocoel of their crustacean intermediate hosts and usually in the body cavity, intestines, muscles or alimentary tract of their intermediate hosts (Fig. 14.1a, b, d) (Klimpel and Palm 2011). Marine mammals (Cetacea, Pinnipedia), birds and a wide range of predatory fish species are commonly used as final hosts. As discussed below, several marine nematodes have considerable medical importance. Larvae of the family Anisakidae, for example, can cause severe gastrointestinal diseases (anisakidosis) when ingested alive, and even very small doses of the parasites antigen can be the causative agents of allergic symptoms including anaphylaxis and asthma (Audicana and Kennedy 2008).

The phylum Acanthocephala comprises approximately 1,150 species which are exclusively parasitic (Verweyen et al. 2011). The adults live in the intestine wall of their vertebrate hosts. The marine life cycle involves one or two intermediate hosts with a benthic association (Marcogliese 1995). The eggs, which contain the acanthor larvae, will be released into the water column with the faeces of the final host. Detritus-feeding zooplankton organisms (e.g. Amphipoda) acquire the parasites by oral ingestion (Fig. 14.1c). The acanthor larvae enter the body

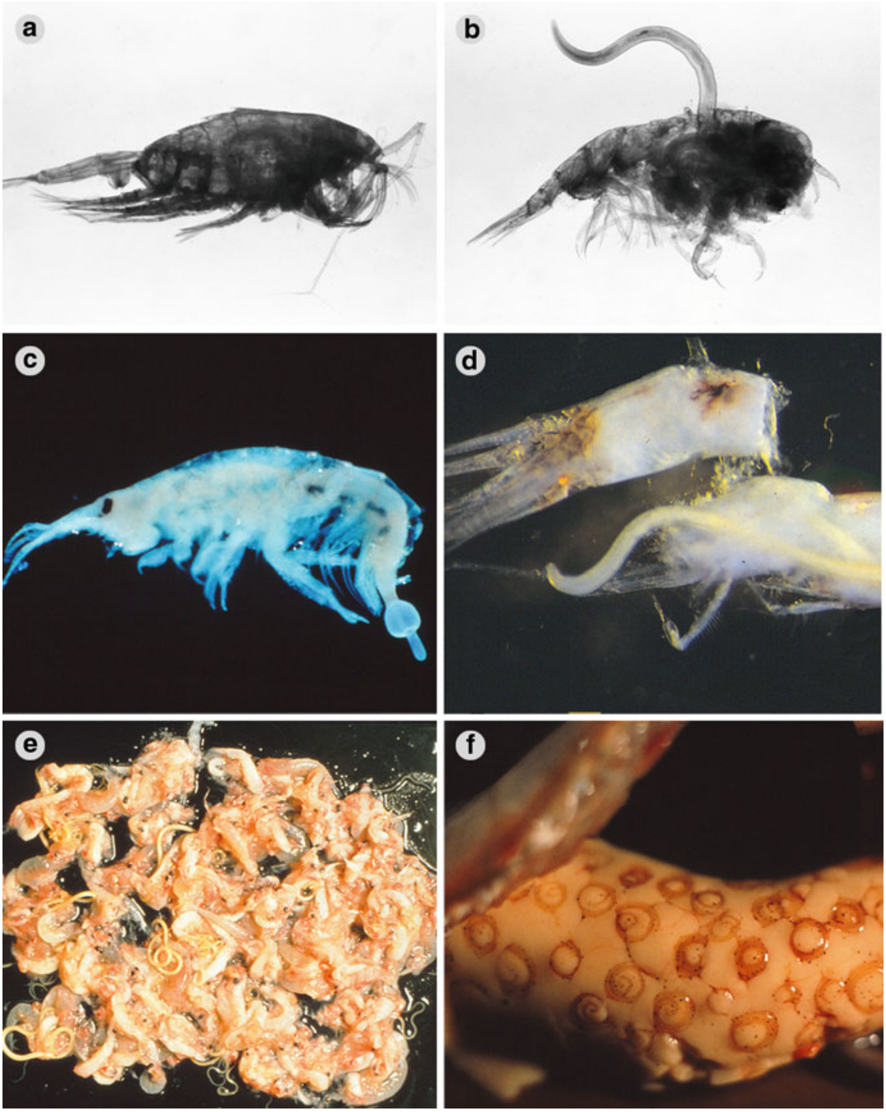

**Fig. 14.1** Marine helminth parasites in intermediate hosts. (**a**) L3 larvae of *Anisakis simplex* in the haemocoel of *Paraeuchaetha norvegica* (Copepoda). (**b**) *Hysterothylacium aduncum* in a hyperiid Amphipoda. (**c**) Amphipod Crustacea hosting a *Pomphorhynchus* larva. (**d**) *Anisakis* sp. in a decapod Crustacea. (**e**) Nematodes and Crustacea in the stomach content of fish. (**f**) Fish liver with *Anisakis* sp. larvae. Photos (**a**), (**b**): Klimpel et al. (2004); (**d**): Klimpel (private property); (**c**), (**e**), (**f**): Möller (private property)

cavity by penetrating the intestinal wall and reach the acanthella stage. Paratenic hosts (e.g. fish) and final hosts (fish, birds, seals, whales) get infected by preying upon the intermediate hosts. In general, Amphipoda serve as main intermediate hosts for marine Acanthocephala (Taraschewski 2005). According to the literature, human pathogenetic species seems to be restricted to terrestrial habitats. Nevertheless, it cannot be excluded that the consumption of marine Acanthocephala in fish food can cause allergic reactions as known from anisakid nematodes (Audicana and Kennedy 2008).

## 14.4 Marine Crustacea in the Life Cycle of Helminth Parasites

Data from 52 peer-reviewed publications have been taken into consideration in order to assess the role of marine crustacean as potential hosts for helminth parasites (Tables 14.1–14.4). A total of 69 different parasites belonging to the Trematoda ($n = 28$), Cestoda ($n = 18$), Nematoda ($n = 10$) and Acanthocephala ($n = 13$) where reported among the crustacean subgroups Copepoda, Euphausiacea, Amphipoda, Decapoda, Mysidacea, Isopoda and Cirripedia (Tables 14.1–14.3). The Acanthocephala have been proven to be parasites of 38 different hosts in three subgroups Euphausiacea, Amphipoda and Decapoda, whereas the Nematoda were reported from 91 different Crustacea in all subgroups. Parasites of the Cestoda and Trematoda have been proven from a total of 27 and 32 crustacean hosts, respectively (Figs. 14.2 and 14.3).

### *14.4.1 Digenea of Marine Crustacea*

Metacercariae of digenetic Trematoda belonging to the families Derogenidae, Hemiuridae, Lecithasteridae, Microphalidae, Opecoelidae and Syncoelidae have been documented in Copepoda, Euphausiacea, Amphipoda and Decapoda. The majority was reported from the families Hemiuridae, Microphalidae and Opecoelidae (Table 14.1). All hemiurid Digenea were detected under natural conditions in copepod Crustacea. In addition, some successful experimental infections have been proven (e.g. Køie 1979, 1989). As described above, *Derogenes varicus* is the most widespread Digenea that utilizes more than 100 teleost fishes as final hosts (Køie 1979). Køie (1979) tested the experimental infection of calanoid Copepoda and Amphipoda with metacercariae of *D. varicus* and identified six species of calanoid copepods to be capable for infection whereas not a single specimen of the Amphipoda was positive. Digenea of the families Syncoeliidae and Opecoelidae have been proven in some euphausiid intermediate hosts (Table 14.1). Adult opecoelids live in the digestive tract of marine and freshwater fishes. Metacercariae from *Opecoeloides collumbellae* have been detected in Decapoda from the species *Hippolyte inermis* (Hippolytidae) at the coast of Corsica and Le Brusc Bay (France) with prevalences between 2.5 and 4.5% (Jousson and Bartoli 2000). Furthermore, Amphipoda seem to be the typical hosts for digenetic trematodes. Most confirmations were detected from the family Microphalidae and less from Opecoelidae (Table 14.1). The common life cycle of the Microphallidae involves Gastropoda as first and intertidal crabs and Amphipoda as

**Table 14.1** Reported marine crustacean intermediate hosts of Digesnea and the respective references

| Host | Parasite | References |
|---|---|---|
| **Copepoda** | | |
| *Acartia clausi* | *Hemiurus communis* | Marcogliese (1995) |
| *A. tonsa* | *Brachyphallus crenatus* | Køie (1992) |
| *Acartia* sp. | *Lecithaster gibbosus*[a], *Lecithaster confusus* | Hunninen and Cable (1943), Køie (1989), Marcogliese (1995) |
| *Centropages abdominalis* | *Lecithaster* sp. | Køie (1989) |
| *C. hamatus* | *Lecithaster gibbosus*[a] | Køie (1989) |
| *Oithona similis* | *Lecithocladium excisum* | Køie (1991), Marcogliese (1995), Reimer et al. (1975) |
| *Pseudocalanus elongatus* | *Lecithaster gibbosus*[a] | Køie (1989) |
| *P. minutus* | *Lecithaster* sp. | Køie (1989) |
| *Tigriopus brevicornis* | *Lecithochirium furcolabiatum* | Marcogliese (2002) |
| Calanoida indet. | *Derogenes varicus*, *Hemiurus luehei*, *Lecithaster gibbosus*, *Lecithocladium excisum* | Køie (1989, 1991), Marcogliese (1995), Reimer et al. (1975), Svendsen (1990) |
| Harpacticoida indet. | *Derogenes varicus* | Marcogliese (2002) |
| **Euphausiacea** | | |
| *Euphausia pacifica* | *Paronatrema* sp. | Marcogliese (1995) |
| *E. similis* | *Neonotoporus trachuri*, *Pseudopecoelus japonicus* | Marcogliese (1995) |
| *Nyctiphanes simplex* | *Paronatrema* sp. | Gómez-Gutiérrez et al. (2010) |
| Euphausiacea indet. | *Syncoelium filiferum* | Marcogliese (1995) |
| **Amphipoda** | | |
| *Calliopius laeviusculus* | *Microphallus papillorobustus* | Zander et al. (1994) |
| *Gammarus duebeni* | *Microphallus claviformes*, *M. papillorobustus* | Zander et al. (1994) |
| *G. finmarchicus* | *Maritrema subdolum*, *Microphallus papillorobustus*, *Podocotyle atomon* | Zander et al. (1994) |
| *G. insensibilis* | *Microphallus papillorobustus* | Brown et al. (2003) |
| *G. locusta* | *Levinseniella brachysoma*, *Maritrema subdolum*, *Microphallus papillorobustus*, *Podocotyle atomon* | Zander et al. (2002) |
| *G. oceanicus* | *Levinseniella brachysoma*, *Maritrema subdolum*, *Microphallus claviformes*, *M. papillorobustus*, *Podocotyle atomon* | Zander et al. (2002) |
| *G. salinus* | *Maritrema subdolum*, *Microphallus claviformes*, *M. papillorobustus*, | Zander et al. (2002) |

(continued)

**Table 14.1** (continued)

| Host | Parasite | References |
|---|---|---|
| | *Levinseniella brachysoma*, *Podocotyle atomon* | |
| *G. tigrinus* | *Microphallus claviformes*, *M. papillorobustus*, *Maritrema subdolum* | Zander et al. (1994) |
| *G. zaddachi* | *Levinseniella brachysoma*, *Maritrema subdolum*, *Microphallus claviformes*, *M. papillorobustus*, *Podocotyle atomon* | Zander et al. (2002) |
| *Paracalliope novizealandiae* | *Maritrema novaezealandensis*[a] | Fredensborg and Poulin (2005), Leung and Poulin (2006) |
| **Decapoda** | | |
| *Farfantepenaeus aztecus* | *Opecoeloides fimbriatus* | Feigenbaum (1975) |
| *F. duorarum* | *Microphallus* sp., *Opecoeloides fimbriatus* | Feigenbaum (1975) |
| *Hemigrapsus crenulatus* | *Maritrema novaezealandensis*, *Microphallus* sp. | Martorelli et al. (2004) |
| **H. penicilliatus** | *Levinseniella conicostoma*, *Maritrema laricola*, *M. setoenesis*, *Microphalloides japonicus*, *Probolocoryphe asadai*, *Microphallus macrorchis* | Blakeslee et al. (2009), McDermott (2011) |
| *H. sanguineus* | *Maritrema jebuensis*, *M. setoenensis*, *Microphalloides japonicus*, *Probolocoryphe asadai*, *Microphallus capellae* | Blakeslee et al. (2009), Chung et al. (2010), McDermott (2011) |
| *H. sexdentatus* | *Maritrema novaezealandensis*, *Microphallus* sp. | Koehler and Poulin (2010) |
| *Hippolyte inermis* | *Opecoeloides collumbellae* | Jousson and Bartoli (2000) |
| *Idotea balthica* | *Maritrema subdolum*, *Podocotyle atomon* | Zander et al. (2002) |
| *I. chelipes* | *Maritrema subdolum*, *Microphallus claviformes*, *M. papillorobustus*, *Levinseniella brachysoma*, *Podocotyle atomon* | Zander et al. (2002) |
| *I. granulosa* | *Maritrema subdolum* | Zander et al. (2000) |
| *Penaeus setiferus* | *Opecoeloides fimbriatus* | Feigenbaum (1975) |

[a] Experimental infection

second intermediate hosts, whereas birds serve as final hosts (Leung and Poulin 2006). The digenean helminth *Maritrema novaezealandensis* induces a behavioural change of its amphipod host *Paracalliope novizealandiae* in order to be more attractive for the final host (Leung and Poulin 2006). Helluy and Thomas (2010) investigated similar consequences for the amphipod species *Gammarus insensibilis* that show an aberrant escape behaviour when infested with larvae of the Digenea *Microphallus papillorobustus* (Microphalidae).

**Table 14.2** Reported marine crustacean intermediate hosts of Cestoda and the respective references

| Host | Parasite | References |
|---|---|---|
| **Copepoda** | | |
| *Acartia clausi* | *Bothriocephalus scorpii* | Solonchenko (1985) |
| *Calanus finmarchicus* | *Aporhynchus norvegicus*, *Scolex pleuronectis* | Klimpel et al. (2003), Marcogliese (1995) |
| *Eurytemora affinis* | *Bothriocephalus scorpii* | Marcogliese (1995) |
| *Mesochra* sp. | *Prochristianella hispida*[a] | Palm (2004) |
| *Tigriopus californicus* | *Lacistorhynchus tenuis*, *Parachristianella monomegacantha*, *Prochristianella hispida*[a] | Palm (2004) |
| Calanoida indet. | *Bothriocephalus barbatus*, *B. gregarius*[b], *Grillotia erinaceus* | Marcogliese (1995) |
| Harpacticoida indet. | *Lacistorhynchus dollfusi* | Marcogliese (1995) |
| **Euphausiacea** | | |
| *Euphausia pacifica* | *Nybelinia surmenicola* | Marcogliese (1995) |
| *E. recurva* | *Pseudonybelinia odontocantha* | Marcogliese (1995) |
| *E. similis* | *Echinobothrium* sp., *Tetrarhynchobothrium* sp. | Marcogliese (1995) |
| *Meganyctiphanes norvegica* | *Aporhynchus norvegicus* | Klimpel et al. (2003) |
| *Nyctiphanes simplex* | *Echinobothrium* sp., *Tetrarhynchobothrium* sp. | Gómez-Gutiérrez et al. (2010) |
| *Thysanoessa inermis* | *Nybelinia surmenicola* | Shimazu (1975) |
| *T. longipes* | *Nybelinia surmenicola*, *Pelichnibothrium caudatum* | Marcogliese (1995), Shimazu (1975) |
| *T. raschii* | *Nybelinia surmenicola* | Shimazu (1975) |
| Euphausiacea indet. | *Nybelinia surmenicola* | Shimazu (1975) |
| **Decapoda** | | |
| *Callianassa* sp. | *Parachristianella monomegacantha* | Palm (2004) |
| *Callichirus islagrande* | *Prochristianella hispida* | Palm (2004) |
| *Callinectes sapidus* | *Polypocephalus* sp. | Hutton (1964) |
| *Farfantepenaeus aztecus* | *Parachristianella dimegacantha*, *Prochristianella hispida* | Feigenbaum (1975) |
| *F. brasiliensis* | *Mecistobothrium penaeus*, *Parachristianella monomegacantha*, *P. heteromegacantha*, *Polypocephalus* sp., *Prochristianella hispida* | Feigenbaum (1975), Hutton (1964) |
| *F. duorarum* | *Parachristianella dimegacantha*, *P. monomegacantha*, *Polypocephalus* sp., *Prochristianella hispida* | Feigenbaum (1975), Hutton (1964) |
| *F. setiferus* | *Polypocephalus* sp. | Hutton (1964) |
| *Penaeus setiferus* | *Prochristianella hispida* | Feigenbaum (1975) |
| *Sicyonia dorsalis* | *Polypocephalus* sp. | Hutton (1964) |

(continued)

**Table 14.2** (continued)

| Host | Parasite | References |
|---|---|---|
| *Solenocera atlantidis* | *Polypocephalus* sp. | Hutton (1964) |
| *Squilla empusa* | *Polypocephalus* sp. | Hutton (1964) |
| *Trachypeneus constrictus* | *Polypocephalus* sp. | Hutton (1964) |
| *T. similis* | *Polypocephalus* sp. | Hutton (1964) |
| *Xiphopenaeus kroyeri* | *Polypocephalus* sp. | Hutton (1964) |

[a] Experimental infection
[b] Nomen nudum

### 14.4.2 Cestoda of Marine Crustacea

Larvae of nine cestode families have been documented in crustacean intermediate hosts from the Copepoda, Euphausiacea and Decapoda (Table 14.2). Most parasites belong to the order Trypanorhyncha, including the families Aporhynchidae (e.g. *Aporhynchus norvegicus*), Eutetrarhynchidae (e.g. *Prochristianella hispida*), Lacisthorhynchidae (e.g. *Lacistorhynchus dollfusi*), Tentaculariidae (e.g. *Nybelinia surmenicola*) and Paranybeliniidae (e.g. *Pseudonybelinia odontocantha*). A minority of the reported larvae belong to the families Bothriocephalidae, Echinobothriidae and Polypocephalidae. Trypanorhynch cestodes mature in the lumen of the spiral intestine of an elasmobranch definitive host. The eggs are dispersed within gravid segments into the seawater as part of the host faeces (Palm 2004). The coracidium stage is ingested by a Copepoda, whereupon it penetrates the intestinal wall and develops in the haemocoel to the procercoid. This stage is infective for larger invertebrates or small fish and further develops to the plerocercoid. In some cases, a second intermediate host or paratenic host, for example, larger fishes, is required (Palm 2004).

The life cycle of *Aporhynchus norvegicus* (Aporhynchidae) has been proposed by Klimpel et al. (2003). It includes three hosts with calanoid Copepoda (e.g. *Calanus finmarchicus*) as first and pelagic Euphausiacea (e.g. *Meganyctiphanes norvegica*) as second intermediate hosts. Potential final hosts are dogfish sharks such as *Etmopterus spinax* (Etmopteridae). In the Norwegian Deep, *C. finmarchicus* is the main prey of *M. norvegica*, while stomach content analyses of *E. spinax* show that *M. norvegica* is the main prey of this shark species (Klimpel et al. 2003). The life cycle of *Parachristianella monomegacantha* (Eutetrarhynchidae) includes invertebrates as obligatory second intermediate hosts. Copepoda (e.g. *Tigriopus californicus*) directly ingest the eggs. A free-swimming coracidium does not occur. Second intermediate hosts are decapod penaeid crustaceans such as the mud shrimp (*Callianassa* sp.). Elasmobranch fish like the guitarfish *Rhinobatos productus* harbour the adult helminths (Palm 2004). The cosmopolitan genus *Bothriocephalus* (Bothriocephalidae) comprises approximately 80 species that use one or two intermediate hosts in their life cycles (Blend and Dronen 2003).

**Table 14.3** Reported marine crustacean intermediate hosts of Nematoda and the respective references

| Host | Parasite | References |
|---|---|---|
| **Copepoda** | | |
| *Acartia bifilosa* | *Hysterothylacium* sp. | Lick (1991) |
| *A. longiremis* | *Hysterothylacium* sp.[a] | Lick (1991) |
| *A. tonsa* | *Anisakis simplex*[a], *Hysterothylacium aduncum*[a] | Køie (1993, 2001) |
| *Acartia* sp. | *Contracaecum osculatum*[a] | Køie and Fagerholm (1995) |
| *Calanus finmarchicus* | *Hysterothylacium* sp. | Lick (1991), Marcogliese (1995), Svendsen (1990) |
| *Calanus* sp. | *Hysterothylacium* sp. | Lick (1991) |
| *Centropages hamatus* | *Contracaecum osculatum*[a] | Køie and Fagerholm (1995) |
| *C. typicus* | *Hysterothylacium* sp. | Svendsen (1990) |
| *Euchoeta* sp. | *Hysterothylacium* sp. | Lick (1991) |
| *Eurytemora affinis* | *Hysterothylacium* sp. | Lick (1991) |
| *Microsetella norvegica* | *Hysterothylacium* sp.[a] | Lick (1991) |
| *Oithona similis* | *Anisakis simplex*[a] | Køie (2001) |
| *Paracalanus parvus* | *Contracaecum osculatum*[a] | Køie and Fagerholm (1995) |
| *Paraeuchaeta norvegica* | *Anisakis simplex* | Klimpel et al. (2004) |
| *Pseudocalanus elongatus* | *Hysterothylacium* sp. | Lick (1991) |
| *Pseudocalanus* sp. | *Hysterothylacium* sp. | Lick (1991) |
| *Temora longicornis* | *Contracaecum osculatum*[a], *Hysterothylacium* sp.[a] | Køie and Fagerholm (1995), Lick (1991) |
| Calanoida indet. | *Hysterothylacium aduncum* | Hurst (1984), Køie (1993), Marcogliese (1995), Svendsen (1990) |
| Harpacticoida indet. | *Hysterothylacium aduncum*[a] | Klimpel et al. (2004), Køie (1993) |
| **Cirripedia** | | |
| *Balanus* sp. | *Anisakis simplex*[a], *Contracaecum osculatum*[a] | Køie (2001), Køie and Fagerholm (1995) |
| **Mysidacea** | | |
| *Erythrops erythrophthalma* | *Hysterothylacium* sp. | Lick (1991) |
| *Mesopodopsis slabberi* | *Anisakis* sp., *Hysterothylacium* sp., *Pseudoterranova decipiens* | Lick (1991) |
| *Mysis gaspensis* | *Paracuaria adunca* | Jackson et al. (1997) |
| *M. mixta* | *Hysterothylacium* sp. | Lick (1991) |
| *M. stenolepis* | *Paracuaria adunca*, *Pseudoterranova decipiens* | Jackson et al. (1997) |
| *Neomysis americana* | *Hysterothylacium* sp., *Paracuaria adunca*, *Pseudoterranova decipiens* | Jackson et al. (1997), Lick (1991) |
| *N. integer* | *Contracaecum osculatum*[a], *Hysterothylacium aduncum*, *Hysterothylacium* sp., *Pseudoterranova decipiens* | Klimpel and Rückert (2005), Køie and Fagerholm (1995), Lick (1991) |

(continued)

**Table 14.3** (continued)

| Host | Parasite | References |
|---|---|---|
| *N. intermedia* | *Hysterothylacium* sp.[a] | Lick (1991) |
| *Praunus flexuosus* | *Paracuaria adunca* | Jackson et al. (1997) |
| **Amphipoda** | | |
| *Americorchestia megalophthalma* | *Pseudoterranova decipiens* | Jackson et al. (1997) |
| *Amphiporeia virginiana* | *Paracuaria adunca*, *Pseudoterranova decipiens* | Jackson et al. (1997) |
| *Calliopius laeviusculus* | *Hysterothylacium* sp. | Zander et al. (1994) |
| *Caprella septentrionalis* | *Anisakis* sp., *Hysterothylacium* sp., *Pseudoterranova decipiens* | Lick (1991) |
| *Echinogammarus obtusatus* | *Paracuaria adunca*, *Pseudoterranova decipiens*, *Tetrameres* sp. | Jackson et al. (1997) |
| *Eogammarus kygi* | *Hysterothylacium* sp. | Moravec and Nagasawa (1986) |
| *Gammarus duebeni* | *Hysterothylacium* sp. | Lick (1991) |
| *G. finmarchicus* | *Hysterothylacium* sp. | Zander et al. (1994) |
| *G. inaequicauda* | *Hysterothylacium* sp. | Lick (1991) |
| *G. lawrencianus* | *Ascarophis* sp., *Hysterothylacium* sp., *Paracuaria adunca*, *Pseudoterranova decipiens*, *Tetrameres* sp. | Jackson et al. (1997), Lick (1991) |
| *G. locusta* | *Ascarophis arctica*, *Hysterothylacium* sp. | Lick (1991), Zander et al. (2002) |
| *G. oceanicus* | *Ascarophis arctica*, *Hysterothylacium* sp., *Paracuaria adunca*, *Tetrameres* sp. | Jackson et al. (1997), Lick (1991), Svendsen (1990), Zander et al. (2002) |
| *G. salinus* | *Ascarophis arctica* , *Hysterothylacium* sp. | Lick (1991), Zander et al. (2002) |
| *G. zaddachi* | *Ascarophis arctica* , *Hysterothylacium* sp. | Lick (1991), Zander et al. (2002) |
| *Gammarus* spp. | *Hysterothylacium aduncum* | Klimpel and Rückert (2005) |
| *Hyperia galba* | *Hysterothylacium aduncum* | Klimpel and Rückert (2005) |
| *Themisto abyssorum* | *Ascarophis* sp., *Hysterothylacium aduncum* | Jackson et al. (1997), Klimpel and Rückert (2005), Køie (1993), Marcogliese (1995) |
| *T. gaudichaudii* | *Hysterothylacium aduncum* | Klimpel and Rückert (2005) |
| *Unciola irrorata* | *Hysterothylacium* sp., *Pseudoterranova decipiens* | Lick (1991) |
| **Isopoda** | | |
| *Edotia triloba* | *Hysterothylacium* sp. | Lick (1991) |
| *Idotea neglecta* | *Pseudoterranova decipiens* | Lick (1991) |
| *Idotea* spp. | *Hysterothylacium aduncum* | Klimpel and Rückert (2005) |
| *Jaera albifrons* | *Hysterothylacium* sp. | Zander et al. (1994) |
| **Euphausiacea** | | |
| *Euphausia krohnii* | *Anisakis* sp. | Smith and Snyder (2005) |
| *E. nana* | *Anisakis simplex*, *Anisakis* sp. | Lick (1991) |

(continued)

**Table 14.3** (continued)

| Host | Parasite | References |
|---|---|---|
| *E. pacifica* | *Anisakis simplex*, *Anisakis* sp., *Contracaecum osculatum*, *Hysterothylacium* sp. | Lick (1991), Marcogliese (1995), Smith and Snyder (2005) |
| *E. similis* | *Philometra* sp. | Marcogliese (1995) |
| *E. vallentini* | *Anisakis* sp. | Hays et al. (1998) |
| *Meganyctiphanes norvegica* | *Anisakis simplex*, *Hysterothylacium* sp. | Hays et al. (1998), Lick (1991), Smith and Snyder (2005) |
| *Nyctiphanes australis* | *Anisakis simplex* | Marcogliese (1995) |
| *N. couchii* | *Anisakis simplex*, *Hysterothylacium* sp. | Hays et al. (1998), Lick (1991) |
| *N. simplex* | *Anisakis simplex* | Gómez-Gutiérrez et al. (2010) |
| *Thysanoessa inermis* | *Anisakis simplex*, *Hysterothylacium* sp. | Lick (1991), Marcogliese (1995), Smith (1971) |
| *T. longicaudata* | *Anisakis simplex* | Smith (1971) |
| *T. longipes* | *Anisakis simplex* | Marcogliese (1995) |
| *T. raschii* | *Anisakis simplex*, *Hysterothylacium aduncum*, *Hysterothylacium* sp. | Lick (1991), Marcogliese (1995), Smith and Snyder (2005), Svendsen (1990) |
| *Thysanoessa* spp. | *Ascarophis* sp., *Hysterothylacium* sp. | Marcogliese (1995) |
| Euphausiacea indet. | *Anisakis simplex*, *Hysterothylacium aduncum* | Hurst (1984), Køie (1993), Marcogliese (1995), Svendsen (1990) |
| **Decapoda** | | |
| *Alpheus heterochaelis* | *Pseudoterranova decipiens* | Hutton and Sogandares-Bernal (1960) |
| *Artemesia longinaris* | *Ascarophis marina* | Martorelli et al. (2000) |
| *Carcinus maenas* | *Ascarophis morrhuae* | Moravec et al. (2003) |
| *Clibanarius vittatus* | *Hysterothylacium* sp. | Lick (1991) |
| *Emerita talpoida* | *Hysterothylacium* sp. | Lick (1991) |
| *Farfantepenaeus aztecus* | *Contracaecum* sp., *Hysterothylacium* sp. | Feigenbaum (1975), Lick (1991) |
| *F. brasiliensis* | *Hysterothylacium* sp. | Lick (1991) |
| *F. californiensis* | *Hysterothylacium* sp. | Lick (1991) |
| *F. duorarum* | *Contracaecum* sp., *Hysterothylacium* sp. | Lick (1991) |
| *Fenneropenaeus indicus* | *Hysterothylacium* sp. | Lick (1991) |
| *Hemigrapsus crenulatus* | *Ascarophis* sp. | McDermott (2011) |
| *H. oregonensis* | *Ascarophis* sp. | Moravec et al. (2003) |
| *H. sexdentatus* | *Ascarophis* sp. | McDermott (2011) |
| *Hemiplax hirtipes* | Acuariidae gen. sp., *Ascarophis* sp. | Moravec et al. (2003) |
| *Homarus americanus* | *Ascarophis* sp., *Hysterothylacium* sp. | Lick (1991), Moravec et al. (2003) |
| *Hyas araneus* | *Anisakis* sp. | Lick (1991) |
| *Litopenaeus setiferus* | *Contracaecum* sp., *Hysterothylacium* sp. | Feigenbaum (1975), Lick (1991) |

(continued)

**Table 14.3** (continued)

| Host | Parasite | References |
|---|---|---|
| *L. stylirostris* | *Contracaecum* sp., *Hysterothylacium* sp. | Lick (1991) |
| *Litopenaeus vannamei* | *Ascarophis* sp., *Hysterothylacium* sp. | Feigenbaum (1975), Lick (1991) |
| *Marsupenaeus japonicus* | *Hysterothylacium* sp. | Lick (1991) |
| *Munida gregaria* | *Hysterothylacium aduncum* | Hurst (1984), Køie (1993), Marcogliese (1995), Svendsen (1990) |
| *Pachycheles rudis* | *Ascarophis* sp. | Poinar and Kuris (1975) |
| *Pandalus borealis* | *Anisakis* sp., *Hysterothylacium* sp. | Lick (1991) |
| *P. latirostris* | *Anisakis* sp. | Lick (1991) |
| *Peisos petrunkevitchi* | *Ascarophis marina* | Martorelli et al. (2000) |
| *Rimapenaeus constrictus* | *Contracaecum* sp., *Hysterothylacium* sp. | Lick (1991) |
| *Sclerocrangon boreas* | *Pseudoterranova decipiens* | Lick (1991) |
| *Sicyonia dorsalis* | *Contracaecum* sp., *Hysterothylacium* sp. | Lick (1991) |
| *S. typica* | *Contracaecum* sp., *Hysterothylacium* sp. | Lick (1991) |
| *Solenocera atlantidis* | *Contracaecum* sp., *Hysterothylacium* sp. | Lick (1991) |
| *Trachypeneus similis* | *Contracaecum* sp., *Hysterothylacium* sp. | Hutton et al. (1962), Lick (1991) |
| *Xiphopenaeus kroyeri* | *Hysterothylacium* sp. | Lick (1991) |

[a] Experimental infection

First intermediate hosts are copepod Crustacea (e.g. *Eurytemora affinis*) (Marcogliese 1995). Experimental infections succeeded to infest the Copepoda species *Acartia clausi* (Solonchenko 1985).

## *14.4.3 Nematoda of Marine Crustacea*

Larvae of ten different nematode genera have been found in marine Crustacea distributed within all major groups, whereas Copepoda, Amphipoda, Euphausiacea and Decapoda seem to be the most important intermediate hosts (Table 14.3). Mostly parasites of the family Anisakidae (order Ascaridida) are included (*Anisakis*, *Contracaecum*, *Hysterothylacium*, *Pseudoterranova*), but members of the Cystidicolidae (*Ascarophis* sp.), Acuariidae (*Paracuaria* sp.), Tetrameridae (*Tetrameres* sp.) and Philometridae (*Philometra* sp.) (order Spirurida) have also been recognized. In addition to the naturally occurring infestations, experimental infections of the anisakids *Anisakis simplex* s.l., *Contracaecum osculatum* and

**Table 14.4** Reported marine crustacean intermediate hosts of Acanthocephala and the respective references

| Host | Parasite | References |
|---|---|---|
| **Euphausiacea** | | |
| *Euphausia krohnii* | *Echinorhynchus* sp. | Marcogliese (1995) |
| *Nyctiphanes simplex* | *Polymorphidae* sp. | Gómez-Gutiérrez et al. (2010) |
| *Microdeutopus gryllotalpa* | *Bolbosoma caenoforme* | Marcogliese (1995) |
| *Thysanoessa raschii* | *Bolbosoma caenoforme* | Marcogliese (1995) |
| *Thysanoessa* sp. | *Bolbosoma caenoforme* | Marcogliese (1995) |
| **Amphipoda** | | |
| *Aeginina longicornis* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *Ampithoe rubricata* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *Calliopius laeviusculus* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *C. rathkii* | *Echinorhynchus gadi*[a] | Marcogliese (1994) |
| *Caprella septentrionalis* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *Cyphocaris challengeri* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *Gammarellus angulosus* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *Gammarus duebeni* | *Echinorhynchus gadi* | Marcogliese (1994) |
| *G. locusta* | *Echinorhynchus gadi* | Zander et al. (2000) |
| *G. oceanicus* | *Echinorhynchus gadi* | Zander et al. (2002) |
| *G. salinus* | *Echinorhynchus gadi* | Zander et al. (2002) |
| *G. tigrinus* | Acanthocephala indet. (Acanthella) | Zander et al. (1994) |
| *G. zaddachi* | *Echinorhynchus gadi* | Zander et al. (2002) |
| *Microdeutopus gryllotalpa* | Acanthocephala indet. (Acanthella) | Zander et al. (1994) |
| *Pontoporeia femorata* | *Echinorhynchus gadi* | Marcogliese (1994) |
| **Decapoda** | | |
| *Brachynotus spinosus* | *Polymorphus sphaerocephalus* | Pichelin et al. (1998) |
| *Cancer irroratus* | *Polymorphus major* | Schmidt and MacLean (1978) |
| *Cyclograpsus granulosus* | *Polymorphus sphaerocephalus* | Pichelin et al. (1998) |
| *Emerita analoga* | *Polymorphus kenti*, *Profilicollis altmani* | Nickol et al. (1999) |
| *E. talpoida* | *Profilicollis altmani* | Nickol et al. (2002) |
| *Hemigrapsus crenulatus* | *Profilicollis antarcticus*, *P. novaezelandensis* | Latham and Poulin (2003), McDermott (2011) |
| *H. oregonensis* | *Profilicollis botulus* | McDermott (2011) |
| *H. sexdentatus* | *Profilicollis antarcticus*, *P. novaezelandensis* | Latham and Poulin (2002, 2003), McDermott (2011) |
| *Hemiplax hirtipes* | *Profilicollis antarcticus*, *P. novaezelandensis*, *Profilicollis* spp.[a] | Fredensborg and Poulin (2005), Latham and Poulin (2002) |

(continued)

**Table 14.4** (continued)

| Host | Parasite | References |
|---|---|---|
| *Homarus americanus* | *Polymorphus botulus* | Nickol et al. (1999) |
| *Macrobrachium* sp. | *Polymorphus formosus* | Nickol et al. (1999) |
| *Nectocarcinus integrifrons* | *Polymorphus sphaerocephalus* | Pichelin et al. (1998) |
| *Neohelice granulata* | *Polymorphus chasmagnathi* | Nickol et al. (1999) |
| *Pagurus longicarpus* | *Polymorphus* sp. | Nickol et al. (1999) |
| *Paragrapsus gaimardii* | *Polymorphus sphaerocephalus* | Pichelin et al. (1998) |
| *P. laevis* | *Polymorphus sphaerocephalus* | Pichelin et al. (1998) |
| *P. quadridentatus* | *Polymorphus sphaerocephalus* | Pichelin et al. (1998) |
| *Uca rapax* | *Arhythmorhynchus frassoni* | Nickol et al. (2002) |
| *U. spinicarpus* | *Hexaglandula corynosoma* | Nickol et al. (2002) |

[a] Experimental infection

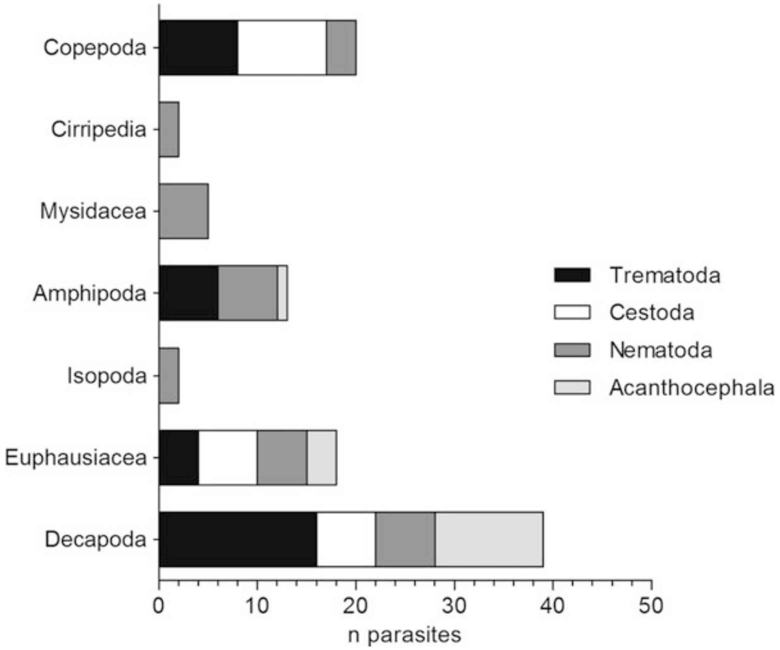

**Fig. 14.2** Numbers of parasites species that have been reported in the crustacean subgroups (see Tables 14.1–14.4)

*Hysterothylacium aduncum* in some copepods, cirripeds and mysidacea have also been reported (Table 14.3).

The family Cystidicolidae includes some 23 genera that are considered valid (Moravec and Klimpel 2009). While they are usually found in the intestine,

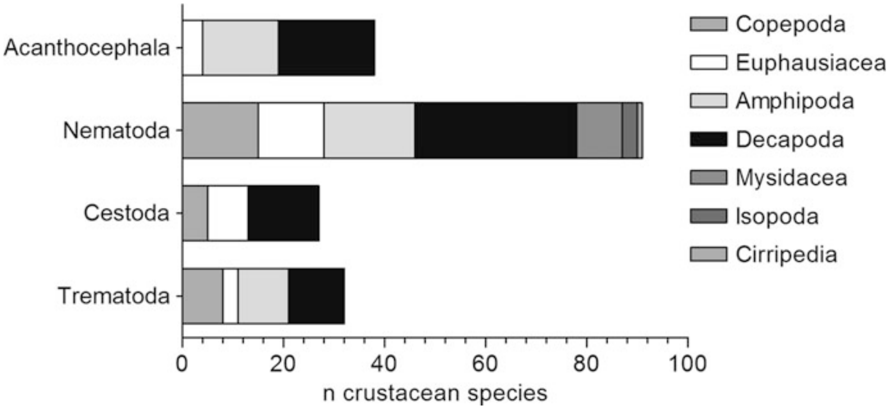

**Fig. 14.3** Numbers of crustacean species that have been reported to be intermediate hosts for marine helminth parasites (see Tables 14.1–14.4)

stomach and pyloric caeca of marine and freshwater fishes, some have adapted to the swim bladder of physostomous fishes (Anderson 2000). According to Anderson (2000), the life cycle includes aquatic insects and crustaceans that serve as intermediate hosts whereas marine fish are used as final hosts. The eggs are released into the water with the faeces of the final host and are ingested by aquatic insects or crustaceans where they remain in the haemocoel or host tissue. The definitive hosts get infected by preying upon arthropods containing third stage larvae. The cosmopolitan *Ascarophis* sp. is the largest genus within this family, worldwide distributed from littoral and demersal to pelagic waters, and parasitic in the digestive tract of marine and estuarine fishes (Muñoz and George-Nascimento 2007). While *Ascarophis* has been recognized in various marine crustaceans, there is no evidence that the parasites are able to switch from one to another intermediate host (Anderson 2000).

Members of the Tetrameridae include the genera *Tetrameres* and *Microtetrameres* which are, as adults, parasites of the proventriculus of waterfowls and terrestrial birds. The larvae are not known to be very host specific regarding the intermediate hosts and include either aquatic crustaceans (aquatic species) or terrestrial insects and isopods (terrestrial species) in their life cycle, respectively. Encapsulated in the haemocoel of the arthropod host, they are infective for the definitive host within a few days (Anderson 2000).

With the exception of *Paracuaria* spp. that mainly occur in the hosts intestines, parasites of the only family of the Acuarioidea (Acuariidae) are found in the upper alimentary tract (crop, gizzard, oesophagus) of piscivorous birds (e.g. Procellariiformes, Pelecaniformes, Falconiformes). Very similar to the Tetrameridae, it is likely that two general life cycles exist, one in the terrestrial and one in the aquatic environment. The definitive avian hosts acquire their infection from ingesting larvae in the haemocoel of aquatic, arthropods or sometimes fish paratenic hosts that have preyed upon infected intermediate hosts (Anderson 2000).

The Philometridae contain a large number of species that are exclusively parasitic in various ray-finned freshwater, brackish water and marine fishes. Very similar to anisakid nematodes, parasites of the genus *Philometra* are pathogenic and very common in commercially available fish species (McClelland 2005; Moravec et al. 2010). According to Anderson (2000), philometrids utilize crustaceans as intermediate hosts, and the predatory fish hosts get infected by feeding either on infested copepods or by paratenesis. Once ingested, the parasites migrate into the serosa of the swim bladder where they grow to the adult stage. The inseminated females migrate to the definitive site (e.g. gill arteries, body cavity, subcutaneously in fins and cheek pouches) where they become gravid, break the host's tissue and burst-release the numerous larvae into the surrounding water.

The members of the Ascaridida are probably the most important marine zoonotic pathogens and exclusively parasites of the gastrointestinal tract of various classes of vertebrates, including birds and mammals. In combination with the Spirurida, they are responsible for the vast majority of nematode infections in marine fish (Rohde 2005). The family Anisakidae represents the largest group within the Ascaridoidea and can be split into the subfamilies Anisakinae (*Anisakis*, *Contracaecum*), Goeziinae and Raphidascaridinae (*Hysterothylacium*, *Pseudoterranova*) (Hartwich 1974).

The Anisakidae perform an indirect life cycle in the aquatic environment and utilize hosts on different trophic levels to be transferred through the marine food web. A wide range of marine mammals (Cetacea, Pinnipedia) and piscivorous birds are utilized as final hosts, whereas invertebrates (e.g. Crustacea) and sometimes Cephalopoda as well as a variety of fish are included as intermediate and/or paratenic hosts.

The eggs of the nematodes are released into the water column within the faeces of the respective final hosts where they are ingested by either pelagic (e.g. *Anisakis*) or benthic (e.g. *Pseudoterranova*) crustaceans. The parasites are transferred along the food chain to larger macroinvertebrates in which they reach the length and developmental stage to be infective to fish and their respective final hosts (Klimpel et al. 2004, 2008; Klimpel and Rückert 2005; Mattiucci and Nascetti 2008; McClelland 2005). These larger invertebrates as well as smaller sized schooling fish are thought to be important second intermediate hosts, whereas predatory fish serve as paratenic hosts. The capability of re-infecting larger piscivorous fish hosts without further moulting is an essential adaptation in order to accumulate enormous numbers of larvae and enhance the transmission to the successive final hosts (Klimpel and Palm 2011; Lile 1998). Due to their high prevalence in commercially available fish species, the genera *Anisakis*, *Contracaecum* and *Pseudoterranova* are probably the most important anisakid nematodes (e.g. Hochberg and Hamer 2010; Karl et al. 2010). These genera are comparatively well known and have evolved various adaptations in order to utilize a wide range of marine organisms as intermediate and final hosts. In the case of the whale worm *Anisakis* spp., marine mammals such as toothed and baleen whales of the families Delphinidae, Kogiidae, Physeteridae and Ziphiidae are considered the main definitive hosts, but members of the Balaenopteridae, Pontoporidae, Monodontidae, Phocoenidae and Neobalaenidae

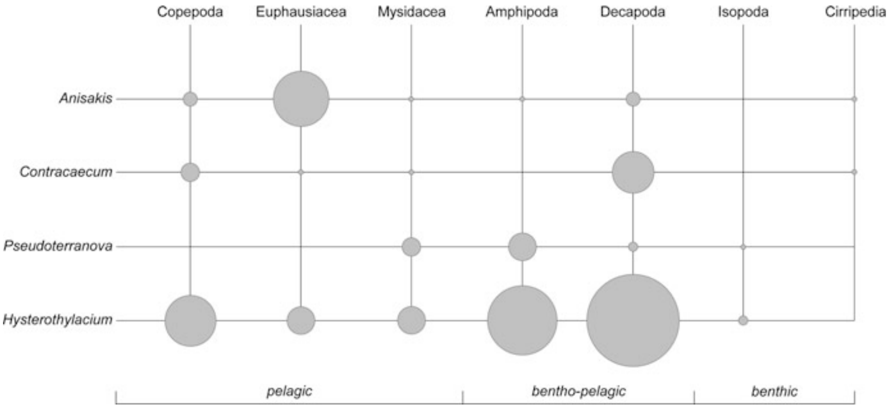

**Fig. 14.4** Relative importance and pelagic, benthopelagic and benthic association, respectively, of marine crustacean intermediate hosts that have been reported for anisakid nematodes of the genera *Anisakis*, *Contracaecum*, *Pseudoterranova* and *Hysterothylacium*. Circle size reflects the number of reported hosts in the respective crustacean subgroups

have also been parasitized (e.g. Klimpel et al. 2004, 2010; Mattiucci and Nascetti 2008). The life cycle of *Anisakis* is considered to take place in the pelagic environment which is also reflected in the use of Copepoda and especially Euphausiacea as crustacean intermediate host (Fig. 14.4). The sealworm *Pseudoterranova* sp. is known to utilize a variety of ten different marine seals belonging to Otariidae and Phocidae as final hosts and is thought to perform a benthic life cycle including benthic invertebrates, teleosts and larger demersal fish species (Klimpel and Palm 2011; Mattiucci and Nascetti 2008). Very similar to *Anisakis* sp., larger piscivorous fish may serve as successive intermediate or paratenic hosts (Anderson 2000; McClelland 2005). The life cycle of the members of the genus *Contracaecum* is equally complex and includes benthic and pelagic invertebrates and fish as intermediate hosts, as well as marine mammals of the families Otariidae and Phocidae as final hosts (Fig. 14.4) (Klimpel and Palm 2011). However, in contrast to *Pseudoterranova*, *Contracaecum* is able to infect different fish-eating birds of various genera (e.g. *Larus*, *Pelecanus*) as well. The species of the raphidascarine *Hysterothylacium* are typically found as adults in the digestive tract of fishes but have although been reported from a very wide range of aquatic invertebrates including gastropods, cephalopods, chaetognaths, echinoderms and cnidarians serving as intermediate hosts (Fig. 14.4) (Anderson 2000; Klimpel and Rückert 2005; McClelland 2005). *Hysterothylacium* is therefore probably the most abundant anisakid fish parasites and extremely common throughout the marine food web.

Besides their role as important parasites of marine organisms, the anisakid nematodes have achieved a notorious dubiety as causative agents of the zoonotic disease anisakidosis when ingested alive by humans. With estimated 20,000 cases of human infections every year, this foodborne infection is of major medical importance and the result of the ingestion of larvae in raw or insufficient cooked fish products (Hochberg and Hamer 2010; Kuhn et al. 2011). The disease is predominantly reported from a wide range of coastal regions primarily along Japan and Europe and associated with major clinical symptoms such as abdominal pain, vomiting, nausea and fever as consequence of a penetration of the alimentary tract of the human accidental host. Several studies have also revealed that even small doses of the nematodes antigens can cause severe immunological reactions in humans (e.g. Audicana and Kennedy 2008). In addition to the seal worms *Pseudoterranova* spp. and *Contracaecum* spp. (birds, seals), the species of the genus *Anisakis* are considered the most common cause for human infections (disease anisakiasis). By analysing various coding and non-coding molecular markers in the last decades, it has become apparent that a few anisakid morphospecies (e.g. *Anisakis simplex*, *Pseudoterranova decipiens*) are not only single species but a complex of several sibling species distinguishable only by their genetic structure and ecological traits (e.g. Kuhn 2010; Mattiucci and Nascetti 2008). In addition, it is still unclear whether all species cause clinical symptoms in humans.

### 14.4.4 Acanthocephala of Marine Crustacea

Larvae of two Acanthocephala families have been documented in Euphausiacea, Amphipoda and Decapoda (Table 14.4). The acanthocephalan parasites belong to the families Echinorhynchidae (e.g. specimens of the genus *Echinorhynchus*) and Polymorphidae (e.g. specimens of the genus *Polymorphus*). All larvae that have been reported in the crustacean intermediate hosts belong to the class Palaeacanthocephala, the largest taxon within the Acanthocephala that has also been documented in limnic environments (Kennedy 2006; Klimpel et al. 2009; Moravec et al. 1999). Their general life cycle is characterized by a wide range of crustacean (first) intermediate hosts, whereas the final host specificity can be either narrow or wide (Taraschewski 2005). *Echinorhynchus gadi*, frequently occurring in North Atlantic marine hosts, uses benthic Crustacea from the families Gammaridae (e.g. specimens of the genus *Gammarus*) and Caprelidae as obligatory first intermediate hosts (Marcogliese 1994; Zander 1998) and follows a benthic life cycle strategy. Teleost fish are considered final hosts for *E. gadi* (Marcogliese 1994, 2002; Zander and Reimer 2002).

All Acanthocephala larvae documented in decapods were isolated from the family Polymorphidae (Table 14.4). Latham and Poulin (2002) investigated the impact of the Acanthocephala species *Profilicollis antarcticus* and *P. novaezelandensis* on the shore crabs of the genus *Hemigrapsus* on the coast of New Zealand. After ingestion of the parasite eggs, the acanthocephalan larvae encyst in the decapod's haemocoel and develop to the cystacanth stage. Shore-associated bird species are considered final hosts (Latham and Poulin 2002).

## 14.5 Impact of Parasitism on Hosts Behaviour and Viability

The infection of an organism by parasites is usually a trade-off between effective utilization of the host as a biosphere and facilitating the transmission to the next eligible host at each stage of the life cycle. Impacts on the hosts morphology, health and body condition or behavioural changes are regular phenomena during parasites infestations.

Digenean parasites have different effects on the health of their hosts. The consequences for the first intermediate host can be serious (e.g. castration) (Cribb 2005). Investigations have documented a reduced reproduction rate or an increased change of behaviour during heavy infestations of second intermediate hosts (Crustacea) (Cribb 2005). Metacercariae of the digenean family Microphalidae, for example, encyst in the protocerebrum, leading to conspicuous escape behaviour of their amphipod and decapod host, which results in an increased likelihood to be fed by a predator (Cribb 2005).

The study of the consequences of cestode infections is depending on the intensity, and research has mainly been focused on the fish host (Williams and Jones 1994). Loss of weight, anaemia, physiological stress, growth reduction and reproduction has been observed (Caira and Reyda 2005). The pathogenicity for the crustacean host is hitherto quite unknown.

Nematodes of marine Crustacea (Ascaridida, Spirurida) usually occur in the coelom of their invertebrate host either free in the haemocoel or closely associated with internal organs. Poinar and Kuris (1975) described the effects of *Ascarophis* parasitizing intertidal decapods (*Hemigrapsus oregonensis*, *Pachycheles rudis*) and indicated a decrease of growth and increase of mortality among older and larger crabs. Experiments have shown that Crustacea infected with *Hysterothylacium aduncum* demonstrate erratic behaviour and mortality (McClelland 2005). The consequences for the fish host range from mechanical compression or necrosis of the liver to lesions in the gut wall, viscera and musculature, depletion of lipids and mortality (Rohde 1984; Williams and Jones 1994). Infections with nematode larvae of the family Anisakidae have been also described to cause gastritis, ulcers, diarrhoea, dehydration and anaemia in their mammalian and avian definitive hosts (e.g. McClelland 2005).

Acanthocephalan parasites have different effects on the health of their hosts. The consequences range from change of the hosts behaviour (intermediate hosts) to serious damage of their tissue (final hosts). Studies of the effects of acanthocephalans on intermediate hosts have focused mainly on small crustaceans (Bakker et al. 1997; Hindsbo 1972). The results indicate that even an infestation with a small intensity can induce a change of behaviour or colour. Shore crabs infected with *Profilicollis* species cause alteration in the burrowing behaviour, with the consequence of elevated mortality rates due to the predation by shorebirds (Latham and Poulin 2002). The pathogenicity for the final hosts depends on the mode of attachment. As longer the presoma as higher is usually the damage of the host's intestine wall (Taraschewski 2005). Due to the short length of *Corynosoma* species and their short presoma, the infestation of seals and whales has no serious consequences. On the other hand, an infestation of sea otters and eider ducks with polymorphid Acanthocephala can have much more consequences. After perforation of the intestine wall, the adult parasites attain to the body cavity causing peritonitis and possibly mortality (Taraschewski 2005). However, it is known that acanthocephalan parasites influence host populations by affecting fitness and act as regulatory factors. The influence on the crustacean first intermediate host still needs some clarification.

## 14.6 Concluding Remarks

The marine environment is a large scale three-dimensional habitat, and the likelihood of finding an eligible successive intermediate or final host in a life cycle is far lower compared to the terrestrial realm. In order to ensure transmission and guarantee survival and dispersal in the aquatic environment, parasites have evolved a variety of different (highly effective) mechanisms. While distribution and dispersal of parasites is often closely related to the distribution of the respective final hosts (spread the eggs with their faeces), infection of the successive host in a life cycle is usually linked with trophic interactions within the marine food web (Klimpel et al. 2011; Kuhn et al. 2011). The parasites live in a highly diluted environment and the free-living stages are typically short-lived and have to find a suitable host within 24–48 h (Marcogliese 2005). Some parasitic larvae can actively search and penetrate the next host (e.g. cercariae of Digenea), while others have to be passively ingested (e.g. larvae of Nematoda). A successful transmission is depending on the longevity of the intermediate host, but Copepoda, for example, are short-lived organisms and their infection rates are usually very low (see Table 14.5) (Marcogliese 2005). Klimpel et al. (2004) reported *Paraeuchaetha norvegica* at the Norwegian Deep to be infected with *Anisakis simplex* s.l. third stage larvae (L3) with a prevalence of 0.26% and *Hysterothylacium aduncum* in hyperiid Amphipoda with a prevalence of 1.95%. It is very likely that even small infestation rates in crustacean intermediate hosts are sufficient to ensure high infection rates of final hosts. For example, the stomach content of a north Pacific fin whale (*Balaenoptera physalus*) contains approximately 340 kg of the Euphausiacea *Thysanoessa raschii* (Nemoto 1970). This equates to approximately 234,000 individuals of this crustacean species (Falk-Petersen 1981). With consideration of an infection rate of 0.019% (*A. simplex* s.l.), the final host would acquire at least 45 parasitic nematodes with each feeding event (Smith and Snyders 2005). This is equivalent with an weekly uptake of more than 300 infective nematode larvae (L3).

The addition of an extra intermediate or paratenic host seems to ensure the transmission and maintain parasites in a dilute environment (Marcogliese 2002). The integration of arthropod vectors is largely restricted to the terrestrial system, and only a few exceptions are reported from the marine environment

**Table 14.5** Reported prevalences (min/max/mean) of parasitic helminth groups and genera in crustacean intermediate hosts

| Hosts | P% min/max/mean | | | | | |
|---|---|---|---|---|---|---|
| | Copepoda | Mysidacea | Amphipoda | Isopoda | Euphausiacea | Decapoda |
| **Parasite** | | | | | | |
| Digenea | | | 0.30/100/28.05 | 0.20/76.00/16.68 | | |
| Cestoda | | | | | 0.10/100/33.40 | |
| Nematoda | 0.26/1.95/1.10 | 0.02/0.59/0.25 | 0.10/18.70/4.51 | 0.90/1.00/1.03 | 0.001/0.49/0.12 | 0.09/100/20.75 |
| Acanthocephala | | | 0.50/16.70/4.55 | | 3.10/3.10/3.10 | 1.00/91.00/25.80 |
| Isopoda | | | | | | 91.10/100/95.55 |
| **Digenea** | | | | | | |
| *Levinseniella* | | | 0.20/70.90/28.42 | | | |
| *Maritrema* | | | 2.50/63.00/31.62 | 1.36/76.00/32.00 | | |
| *Microphallus* | | | 0.30/100/19.82 | 2.40/8.10/5.25 | | |
| *Podocotyle* | | | 7.50/67.40/32.94 | 6.70/18.70/12.70 | | |
| **Cestoda** | | | | | | |
| *Aporhynchus* | 100/100/100 | | | | | |
| *Echinobothrium* | | | | | 0.10/0.10/0.10 | |
| *Tetrarhynchobothrium* | | | | | 0.10/0.10/0.10 | |
| **Nematoda** | | | | | | |
| *Anisakis* | 0.03/0.03 | | 0.11/0.16/0.11 | | 0.007/0.49/0.04 | 0.09/0.27/0.15 |
| *Hysterothylacium* | 1.95/1.95/1.95 | 0.23/0.59/0.41 | 0.32/18.20/5.10 | 0.90/0.90/0.90 | | 0.15/100/22.39 |
| *Contracaecum* | | | | | 0.001/0.001/0.001 | 27.27/37.50/32.38 |
| *Ascarophis* | | | 1.00/18.70/6.07 | | | |
| *Pseudoterranova* | | 0.01/0.35/0.16 | 0.09/0.28/0.20 | 1.19/1.19/1.19 | | |
| *Thynnascaris* | | | | | | 3.05/3.05/3.05 |
| **Acanthocephala** | | | | | | |
| *Echinorhynchus* | | | 0.50/6.60/3.54 | | | |
| *Polymorphus* | | | | | 3.10/3.10/3.10 | 1.00/91.00/25.80 |

References: Brattey et al. (1985), Brown et al. (2003), Fredensborg and Poulin (2005), Gómez-Gutiérrez et al. (2010), Hurst (1984), Hutton et al. (1962), Jackson et al. (1997), Klimpel et al. (2004), Klimpel and Rückert (2005), Lick (1991), Marcogliese (1994, 1995), Martorelli et al. (2000), Moravec and Nagasawa (1986), Nickol et al. (1999), Smith and Snyder (2005), Voigt (1986), and Zander et al. (1994, 2000, 2002) (e.g. hirudineans using isopods as vectors, McCallum et al. 2004). Complex helminth parasite life cycles develop either “upwards” by adding new hosts after the definitive host, which subsequently becomes an intermediate host (terminal addition/horizontal incorporation), or “downwards” by adding a new host, for example, Crustacea, before the definitive host (non-terminal addition/vertical incorporation) (O’Grady 1985; Parker et al. 2003). Because most helminth life cycles follow a basic scheme and often are restricted to three or a maximum of four hosts including obligate crustacean intermediate hosts, many incorporation events must have occurred long time ago. The involvement of further host species at a particular stage in the life cycle (lateral incorporation) is depending on actual niche overlap between the existing and the new host (in many helminths, via the food web) and requires generalistic parasites. Any successful mutant surviving in an extra host spreads and fixates. Though lateral incorporation does not add to helminth life cycle length, it clearly contributes to the variety of different helminth life cycles that we can observe to date. It consequently adds to the pool of helminth species available that are able to infest potential marine hosts, thus contributing to the mixture of highly specific or non-specific parasites within the various taxa and increasing metazoan parasite diversity. Palm and Klimpel (2007) suggested for marine cestodes and nematodes, lateral (involvement of alternative hosts) instead of vertical incorporation to be responsible for the recorded species biodiversity within the marine environment. So the evolution of marine fish parasites and species diversity can be driven by the parasite and its life cycle adaptation or the peculiarities of the ecosystem, leading to a better exploitation of the available ecological niches. Host–parasite interactions, however, are ubiquitous in real systems and are known to affect community structure, trophic relationships and energy flow (e.g. Lafferty 1999; Marcogliese 2002; Poulin and Morand 2000, 2004). Food web context is also thought to have been important in the evolution of many of the characteristics observed in marine parasites, including heteroxenous life cycles. Food web context has been hypothesized to have an influence on transmission rates and pathways of some parasite species in aquatic systems (Marcogliese 2002), and food webs have exerted strong selective pressures on the evolution of parasite transmission strategies, parasites are now shaping some of the ecological properties of existing food webs. Our present review shows that parasites in the marine environment are a natural component and may be viewed as an biological indicator of the relative health of the ecosystem inhabitants. The majority of metazoan parasite species present on and within invertebrates (especially Crustacea) and fish are only in some cases hazardous to human health. There are a moderate number of trematodes, cestodes and nematodes which have been reported in humans, but only a few cause serious diseases. In consideration of the biodiversity of marine Crustacea, it is not surprising that this group of invertebrates play a key role as potential hosts and vectors for metazoan parasites. The high abundance of key species in nearly all marine habitats favours the transmission potential and the maintenance of helminth life cycles. This is especially important for the distribution of zoonotic parasite species (e.g. anisakid nematodes).

**Acknowledgements** The present study was financially supported by the German Research Council (DFG KL 2087/1-1, 1-2).

# References

Anderson RC (1996) Why do fish have so few roundworm (nematode) parasites? Environ Biol Fishes 46:1–5

Anderson RC (2000) Nematode parasites of vertebrates – their development and transmission. CAB, Wallingford, pp 650

Audicana MT, Kennedy MW (2008) *Anisakis simplex*: from obscure infectious worm to inducer of immune hypersensitivity. Clin Microbiol Rev 21:360–379

Bakker TCM, Mazzi D, Zala S (1997) Parasite-induced changes in behavior and color make *Gammarus pulex* more prone to fish predation. Ecology 78:1098–1104

Blair D (2005) Cestode and trematode infections. In: Rohde K (ed) Marine parasitology. CSIRO, Collingwood, pp 427–430

Blakeslee AMH, Keogh CL, Byers JE, Kuris AM, Lafferty KD, Torchin ME (2009) Differential escape from parasites by two competing introduced crabs. Mar Ecol Prog Ser 393:83–96

Blend CK, Dronen NO (2003) *Bothriocephalus gadellus* n. sp. (Cestoda: Bothriocephalidae) from the beardless codling *Gadella imberbis* (Vaillant) (Moridae) in the southwestern Gulf of Mexico, with a review of species of *Bothriocephalus* Rudolphi, 1808 reported from gadiform fishes. Syst Parasitol 54:33–42

Boxshall GA, Defaye D (2008) Global diversity of copepods (Crustacea: Copepoda) in freshwater. Hydrobiologia 595:195–207

Brattey J, Elner RW, Uhazy LS, Bagnall AE (1985) Metazoan parasites and commensals of five crab (Brachyura) species from eastern Canada. Can J Zool 63:2224–2229

Brown SP, De Lorgeril J, Joly C, Thoma F (2003) Field evidence for density-dependent effects in the trematode *Microphallus papillorobustus* in its manipulated host, *Gammarus insensiblis*. J Parasitol 89:668–672

Caira JN, Reyda FB (2005) Eucestoda (true tapeworms). In: Rohde K (ed) Marine parasitology. CABI, Wallingford, pp 92–104

Chubb JC, Ball MA, Parker GA (2009) Living in intermediate hosts: evolutionary adaptions in larval helminths. Trends Parasitol 26:93–102

Chung OS, Lee HJ, Sohn WM, Lee SH, Park IY, Oh SA, Chai JY, Seo M (2010) Discovery of *Maritrema jebuensis* n. sp. (Digenea: Microphallidae) from the Asian Shore Crab, *Hemigrapsus sanguineus*, in Korea. Korean J Parasitol 48:335–338

Cribb TH (2005) Digenea (endoparasitic flukes). In: Rhode K (ed) Marine parasitology. CABI, Wallingford, pp 76–87

Falk-Petersen S (1981) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: Seasonal changes in body weight and the main biochemical composition of *Thysanoessa inermis* (Krøer), *T. raschii* (M. Sars) and *Meganyctiphanes norvegica* (M. sars) in relation to environmental factors. J Exp Biol Ecol 49:103–120

Feigenbaum DL (1975) Parasites of the commercial shrimp *Penaeus vannamei* Boone and *Penaeus brasiliensis* Latreille. Bull Mar Sci 25:491–514

Fredensborg BL, Poulin R (2005) Larval helminths in intermediate hosts: does competition early in life determine the fitness of adult parasites? Int J Parasitol 35:1061–1070

Gasca R, Manzanilla H, Suárez-Morales E (2009) Distribution of hyperiid amphipods (Crustacea) of the southern Gulf of Mexico, summer and winter, 1991. J Plankton Res 31:1493–1504

Gibbons MJ, Hutchings L (1996) Zooplankton diversity and community structure around the southern Africa, with special attention to the Benguela upwelling system. S Afr J Sci 92:63–76

Gómez-Gutiérrez J, Robinson CJ, Kawaguchi S, Nicol S (2010) Parasite diversity of *Nyctiphanes simplex* and *Nematoscelis difficilis* (Crustacea: Euphausiacea) along the northwestern coast of Mexico. Dis Aquat Org 88:249–266

Gruner HE (1993) Crustacea. In: Gruner HE (ed) Lehrbuch der speziellen Zoologie. Band I: Wirbellose Tiere, 4. Teil: Arthropoda (ohne Insecta). Gustav Fischer, Jena, pp 448–1030

Hadfield KA, Bruce NL, Smit NJ (2011) *Cymothoa hermani* sp. nov. (Isopoda, Cymothoidae, Crustacea), a parasitic isopod, collected off the Zanzibar coast, Tanzania from the mouth of a parrotfish (Scaridae). Zootaxa 2876:57–68

Hartwich G (1974) Keys to genera of the Ascaridoidea. In: Anderson RC, Chabaud AG, Wilmott S (eds) CIH Keys to the nematode parasites of vertebrates. Farnham Royal, Commonwealth Agriculture Bureau, Richmond, pp 1–15

Hays R, Measures LN, Huot J (1998) Euphausiids as intermediate hosts of *Anisakis simplex* in the St. Lawrence estuary. Can J Zool 76:1226–1235

Helluy S, Thomas F (2010) Parasitic manipulation and neuroinflammation: evidence from the system *Microphallus papillorobustus* (Trematoda) – *Gammarus* (Crustacea). Parasit Vectors 3(38):1–11

Hewitt RP, Watkins JL, Naganobu M, Tshernyshkov P, Brierley AS, Demed DA, Kasatkina S, Takao Y, Goss C, Malyshk A, Brandon MA, Kawaguchi S, Siegel V, Trathan PN, Emery JH, Everson I, Milled DGM (2002) Setting a precautionary catch limit for Antarctic Krill. Oceanography 15:26–33

Hindsbo O (1972) Effects of *Polymorphus* (Acanthocephala) on colour and behaviour of *Gammarus lacustris*. Nature 238:333

Hochberg NS, Hamer DH (2010) Anisakidosis: perils of the deep. Clin Infect Dis 51:806–812

Hunninen AV, Cable RM (1943) The life history of *Lecithaster confusus* Odhner (Trematoda: Hemiuridae). J Parasitol 29:71–79

Hurst RJ (1984) Marine invertebrate hosts of New Zealand Anisakidae (Nematoda). N Z J Mar Freshwat Res 18:187–196

Hutton RF (1964) A second list of parasites from marine and coastal animals of Florida. Trans Am Microsc Soc 83:439–447

Hutton RF, Sogandares-Bernal F (1960) A list of parasites from marine and coastal animals of Florida. Trans Am Microsc Soc 79:287–292

Hutton RF, Ball T, Eldred B (1962) Immature nematodes of the genus *Contracaecum* Railliet and Henry, 1912, from shrimps. J Parasitol 48:327–332

Jackson CJ, Marcogliese DJ, Burt MDB (1997) Role of hyperbenthic crustaceans in the transmission of marine helminth parasites. Can J Aquat Sci 54:815–820

Jousson O, Bartoli P (2000) The life cycle of *Opecoeloides columbellae* (Pagenstecher, 1863) n. comb. (Digenea, Opecoelidae): evidence from molecules and morphology. Int J Parasitol 30:747–760

Karl H, Baumann F, Ostermeyer U, Kuhn T, Klimpel S (2010) *Anisakis simplex* (s.s.) larvae in wild Alaska salmon: no indication of post migration from viscera into flesh. Dis Aquat Org 94:201–209

Kennedy CR (2006) Ecology of the *Acanthocephala*. Cambridge University Press, New York, pp 240

Klimpel S, Palm HW (2011) Anisakid nematode (Ascaridoidea) life cycles and distribution: increasing zoonotic potential in the time of climate change? In: Mehlhorn H (ed) Progress in parasitology, vol 2, Parasitology research monographs. Springer, Heidelberg, pp 201–222

Klimpel S, Rückert S (2005) Life cycle strategies of *Hysterothylacium aduncum* to become the most abundant anisakid fish nematode in the North Sea. Parasitol Res 97:141–149

Klimpel S, Palm HW, Seehagen A (2003) Metazoan parasites and food composition of juvenile *Etmopterus spinax* (L., 1758) (Dalatiidae, Squaliformes) from the Norwegian Deep. Parasitol Res 89:245–251

Klimpel S, Palm HW, Rückert S, Piatkowski U (2004) The life cycle of *Anisakis simplex* in the Norwegian Deep (northern North Sea). Parasitol Res 94:1–9

Klimpel S, Palm HW, Busch MW, Kellermanns E, Rückert S (2006) Fish parasites in the Arctic deep-sea: poor diversity in pelagic fish species vs. heavy parasite load in a demersal fish. Deep Sea Res I 53:1167–1181

Klimpel S, Kellermanns E, Palm HW (2008) The role of pelagic swarm fish (Myctophidae: Teleostei) in the oceanic life cycle of *Anisakis* sibling species at the Mid-Atlantic Ridge, Central Atlantic. Parasitol Res 104:43–53

Klimpel S, Busch MW, Kellermanns E, Kleinertz S, Palm HW (2009) Metazoan deep-sea fish parasites. ACTA Biologica Benrodis, Supplementband 11. Verlag Natur & Wissenschaft, Solingen, pp 384

Klimpel S, Busch MW, Kuhn T, Rohde A, Palm HW (2010) The *Anisakis simplex* complex off the South Shetland Islands (Antarctica): endemic populations versus introduction through migratory hosts. Mar Ecol Prog Ser 403:1–11

Klimpel S, Kuhn T, Busch MW, Karl H, Palm HW (2011) Deep-water life cycle of *Anisakis paggiae* (Nematoda: Anisakidae) in the Irminger Sea indicates kogiid whale distribution in north Atlantic waters. Polar Biol 34:899–906

Koehler AV, Poulin R (2010) Host partitioning by parasites in an intertidal crustacean community. J Parasitol 96:862–868

Køie M (1979) On the morphology and life-history of *Derogenes varicus* (Müller, 1784) Loss, 1901 (Trematoda, Hemiuridae). Parasitol Res 59:67–78

Køie M (1984) Digenetic trematodes from *Gadus morhua* L. (Osteichthyes: Gadidae) from Danish and adjacent waters, with special reference to their life-histories. Ophelia 23:195–222

Køie M (1989) On the morphology and life history of *Lecithaster gibbosus* (Rudolphi, 1802) Lühe, 1901 (Digenea, Hemiuroidea). Parasitol Res 75:361–367

Køie M (1991) Aspect of the morphology and life cycle of *Lecithocladium excisum* (Digenea, Hemiuridae), a parasite of *Scomber* spp. Int J Parasitol 21:597–602

Køie M (1992) Life cycle and structure of the fish digenean *Brachyphallus crenatus* (Hemiuridae). J Parasitol 78:338–343

Køie M (1993) Aspects of the life cycle and morphology of *Hysterothylacium aduncum* (Rudolphi, 1802) (Nematoda, Ascaridoidea, Anisakidae). Can J Zool 71:1289–1296

Køie M (2001) Experimental infections of copepods and stickelbacks *Gasterosteus aculeatus* with small ensheathed and large third-stage larvae of *Anisakis simplex* (Nematoda, Ascaridoidea, Anisakidae). Parasitol Res 87:32–36

Køie M, Fagerholm HP (1995) The life cycle of *Contracaecum osculatum* (Rudolphi, 1802) sensu stricto (Nematoda, Ascaridoidea, Anisakidae) in view of experimental infection. Parasitol Res 81:481–489

Kuchta R, Scholz T, Brabec J, Bray RA (2008) Suppression of the tapeworm order Pseudophyllidea (Platyhelminthes: Eucestoda) and the proposal of two new orders, Bothriocephalidea and Diphyllobothriidea. Int J Parasitol 38:49–55

Kuhn T (2010) Molecular studies on marine ascaridoid nematodes. Diploma thesis, Heinrich Heine University, Düsseldorf, pp 100

Kuhn T, García-Màrquez J, Klimpel S (2011) Adaptive radiation within marine anisakid nematodes: a zoogeographical modeling of cosmopolitan, zoonotic parasites. PLoS One 6(12):e28642

Lafferty KD (1999) The evolution of trophic transmission. Parasitol Today 15:111–115

Lascara CM, Hofmann EE, Ross RM, Quetin LB (1999) Seasonal variability in the distribution of Antarctic Krill, *Euphausia superba*, west of the Antarctic Peninsula. Deep Sea Res I 46:951–984

Latham ADM, Poulin R (2002) Field evidence of the impact of two acanthocephalan parasites on the mortality of three species of New Zealand shore crabs (Brachyura). Mar Biol 141:1131–1139

Latham ADM, Poulin R (2003) Spatiotemporal heterogeneity in recruitment of larval parasites to shore crab intermediate hosts: the influence of shorebird definitive hosts. Can J Zool 81:1282–1291

Leung TLF, Poulin R (2006) Effects of the trematode *Maritrema novaezealandensis* on the behaviour of its amphipods host: adaptive or not? J Helminthol 80:271–275

Lick R (1991) Untersuchungen zu Lebenszyklus (Krebse-Fische-marine Säuger) und Gefrierresistenz anisakider Nematoden in Nord- und Ostsee. Ber Inst Meereskd Kiel 218:1–195

Lile NK (1998) Alimentary tract helminths of four pleuronectid flatfish in relation to host phylogeny and ecology. J Fish Biol 53:945–953

Marcogliese DJ (1994) *Aeginina longicornis* (Amphipoda: Caprellidea), new intermediate host for *Echinorhynchus gadi* (Acanthocephala: Echinorhynchidae). J Parasitol 80:1043–1045

Marcogliese DJ (1995) The role of zooplankton in the transmission of helminth parasites to fish. Rev Fish Biol Fish 5:336–371

Marcogliese DJ (2002) Food webs and the transmission of parasites to marine fish. Parasitology 763(124):83–99

Marcogliese DJ (2005) Parasites of the superorganism: Are they indicators of ecosystem health?. Int J Parasitol 35:705-716

Martin JW, Davis GE (2001) An updated classification of the recent Crustacea, Science series 39. Natural History Museum of Los Angeles County, California, pp 124

Martorelli SR, Navone GT, Ivanov V (2000) Proposed life cycle of *Ascarophis marina* (Nematoda: Cystidicolidae) in Argentine waters. J Parasitol 86:1047–1050

Martorelli SR, Fredensborg BL, Mouritsen KN, Poulin R (2004) Description and proposed life cycle of *Maritrema novaezealandensis* n. sp. (Microphallidae) parasitic in red-billed gulls, *Larus novaehollandiae scopulinus*, from Otago Harbor, South Island, New Zealand. J Parasitol 90:272–277

Mattiucci S, Nascetti G (2008) Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host–parasite co-evolutionary processes. Adv Parasitol 66:47–148

Mauchline J (1998) The biology of calanoid copepods. In: Blaxter JHS, Southward AJ, Tyler PA (eds) Advances in marine biology. Academic, San Diego, pp 710

McCallum HI, Kuris A, Harvell CD, Lafferty KD, Smith GW, Porter J (2004) Does terrestrial epidemiology apply to marine systems. Trends Ecol Evol 19:585–591

McClelland G (2005) Nematoda (roundworms). In: Rhode K (ed) Marine parasitology. CABI, Collingwood, pp 104–115

McDermott JJ (2011) Parasites of shore crabs in the genus *Hemigrapsus* (Decapoda: Brachyura: Varunidae) and their status in crabs geographically displaced: a view. J Nat Hist 45:2419–2441

Mehlhorn H (2001) Encyclopedic reference of parasitology: Diseases, treatment, therapy. Springer, Berlin, pp 676

Meland K, Willassen E (2007) The disunity of “Mysidacea” (Crustacea). Mol Phylogenet Evol 44:1083–1104

Möller H, Anders K (1983) Krankheiten und Parasiten der Meeresfische. Verlag Heino Möller, Kiel, pp 258

Moravec F, Klimpel S (2009) Two new species of cystidicolid nematodes from the digestive tract of the deep-sea fish *Coryphaenoides mediterraneus* (Gilioi) (Macrouridae) from the Mid-Atlantic Ridge. Syst Parasitol 73:37–47

Moravec F, Nagasawa K (1986) New records of amphipods as intermediate hosts for salmonid nematode parasites in Japan. Folia Parasitol 33:45–49

Moravec F, Wolter J, Körting W (1999) Some nematodes and acanthocephalans from exotic ornamental and freshwater fishes imported to Germany. Folia Parasitol 46:296–310

Moravec F, Fredensborg BL, Latham ADM, Poulin R (2003) Larval Spirurida (Nematoda) from the crab *Macrophthalmus hirtipes* in New Zealand. Folia Parasitol 50:109–114

Moravec F, Bakenhaster M, Fajer-Avila EJ (2010) New philometrids (Nematoda: Philometridae) from head tissues of two serranid fishes (*Epinephelus morio* and *Mysteroperca microleis*) off Florida, northern Gulf of Mexcio. Acta Parasitol 55:359–368

Munk P, Nielsen TG (1994) Trophodynamics of the plankton community at Dogger Bank: predatory impact by larval fish. J Plankton Res 16:1225–1245

Muñoz G, George-Nascimento M (2007) Two new species of *Ascarophis* (Nematoda: Cystidicolidae) in marine fishes from Chile. J Parasitol 93:1178–1188

Nemoto T (1970) Feeding pattern of baleen whales. In: Steele JH (ed) Marine food chains. University of California Press, Berkeley, pp 241–252

Newman WA, Abbott DP (1980) Cirripedia: the barnacles. In: Morris RH, Abbott DP, Haderlie EC (eds) Intertidal invertebrates of California. Stanford University Press, Stanford, pp 504–536

Nickol BB, Crompton DWT, Searle DW (1999) Reintroduction of *Profiliocollis* Meyer, 1931, as a genus in Acanthocephala: significance of the intermediate host. J Parasitol 85:716–718

Nickol BB, Heard RW, Smith NF (2002) Acanthocephalans from crabs in the southeastern U.S. with the first intermediate hosts known for *Arhythmorhynchus frassoni* and *Hexaglandula corynosoma*. J Parasitol 88:79–83

O'Grady RT (1985) Ontogenetic sequences and the phylogenetics of parasitic flatworm life cycles. Cladistics 1:159–170

Palm HW (2004) The Trypanorhyncha Diesing, 1863. PKSPL-IPB, Bogor, pp 710

Palm HW, Klimpel S (2007) Evolution of parasitic life in the ocean. Trends Parasitol 23:10–12

Palm HW, Klimpel S, Bucher C (1999) Checklist of metazoan fish parasites of German coastal waters. Ber Inst Meereskd Kiel 307:1–148

Parker GA, Chubb JC, Ball MA, Roberts GN (2003) Evolution of complex life cycles in helminth parasites. Nature 425:480–484

Pichelin S, Kuris AM, Gurney R (1998) Morphological and biological notes on *Polymorphus (Profilicollis) sphaerocephalus* and *Corynosoma stanleyi* (Polymorphidae: Acanthocephala). J Parasitol 84:798–801

Poinar GO, Kuris AM (1975) Juvenile *Ascarophis* (Spirurida: Nematoda) parasitizing intertidal decapod Crustacea in California: with notes on prevalence and effects on hosts growth and survival. J Invertebr Pathol 26:375–382

Porter ML, Meland K, Price W (2008) Global diversity of mysids (Crustacea-Mysida) in freshwater. Hydrobiologia 595:213–218

Poulin R, Morand S (2000) The diversity of parasites. Q Rev Biol 75:277–293

Poulin R, Morand S (2004) Parasite diversity. Smithsonian Institute Press, Washington, DC

Reimer L, Hnatiuk S, Rochner J (1975) Metacercarien in Planktontieren des mittleren Atlantik. Wiss Z Paedagog Hochsch Güstrow (Math Nat Fak) 2(75):239–358

Richardson K, Nielsen TG, Bo Pedersen F, Heilmann JP, Lokkegaard B, Kaas H (1998) Spatial heterogeneity in the structure of the planktonic food web in the North Sea. Mar Ecol Prog Ser 168:197–211

Rohde K (1984) Diseases caused by metazoans: helminths. In: Kinne O (ed) Diseases of marine animals, vol iv, part 1. Biologische Anstalt, Helgoland, pp 193–319

Rohde K (2005) Definitions, and adaptations to a parasitic way of life. In: Rohde K (ed) Marine parasitology. CABI, Wallingford, pp 1–6

Ruppert EE, Barnes RD (1994) Invertebrate zoology. Saunders College Publishing, Orlando, pp 1056

Schmidt GD, MacLean SA (1978) *Polymorphus (Profilicollis) major* Lundström 1942 juveniles in Rock Crabs, *Cancer irroratus*, from Maine. J Parasitol 64:953–954

Shimazu T (1975) Some cestode and acanthocephalan larvae from euphausiid crustaceans collected in the northern North Pacific Ocean. Bull Jpn Soc Sci Fish 41:813–821

Siegel V, Loeb V, Gröger J (1998) Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977 to 1997. Polar Biol 19:393–398

Smith JW (1971) *Thysanoessa inermis* and *T. longicaudata* (Euphausiidae) as first intermediate hosts of *Anisakis* sp. (Nematoda: Ascaridata) in the northern North Sea, to the North of Scotland and at the Faroe. Nature 234:478

Smith JW, Snyder JM (2005) New locality for third-stage larvae of *Anisakis simplex* (sensu lato) (Nematoda: Ascaridoidea) in euphausiids *Euphausia pacifica* and *Thysanoessa raschii* from Prince William Sound, Alaska. Parasitol Res 97:539–542

Solonchenko AI (1985) Development of larval stages of *Bothriocephalus scorpii.* In: Hargis WJ Jr (ed) Parasitology and pathology of marine organisms of the world ocean. NOAA Technical Reprot NMFS 25, pp 83–84

Spears T, Abele LG (1997) Crustacean phylogeny inferred from 18S rDNA. In: Fortey RA, Thomas RH (eds) Arthropod relationships. Chapman & Hall, London, pp 169–187

Svendsen YS (1990) Hosts of third stage larvae of *Hysterothylacium* sp. (Nematoda, Anisakidae) in zooplankton from outer Oslofjord, Norway. Sarsia 75:161–167

Taraschewski H (2005) Acanthocephala (thorny or spiny-headed worms). In: Rohde K (ed) Marine parasitology. CABI, Collingwood, pp 116–121

Verweyen L, Klimpel S, Palm HW (2011) Molecular phylogeny of the Acanthocephala (Class Palaeacanthocaphala) with a paraphyletic assemblage of the orders Polymorphida and Echinorhynchida. PLoS One 6(12):e28285

Voigt M (1986) Gammariden (Crustacea: Amphipoda) als Zwischenwirte von Fischparasiten in Schleswig-Holsteinischen Küstengewässern. Diploma thesis, Christian-Albrechts University, Kiel, pp 63

Whiteley NM, Rastrick SPS, Lunt DH, Rock J (2011) Latidudinal variations in the physiology of marine gammarid amphipods. J Exp Mar Biol Ecol 400:70–77

Williams H, Jones A (1994) Parasitic worms of fish. Taylor & Francis, London, p 593

Wirkner CS, Richter S (2007) Comparative analysis of the circulatory system in Amphipoda (Malacostraca, Crustacea). Acta Zool 88:159–171

Zander CD (1998) Ecology of host parasite relationships in the Baltic Sea. Naturwissenschaften 85:426–436

Zander CD, Reimer LW (2002) Parasitism at the ecosystem level in the Baltic Sea. Parasitology 124:119–135

Zander CD, Groenewold S, Strohbach U (1994) Parasite transfer from crustacean to fish hosts in the Lübeck Bight, SW Baltic Sea. Helgoländer Meeresunters 48:89–105

Zander CD, Reimer LW, Barz K, Dietel G, Strohbach U (2000) Parasite communities of the Salzhaff (Northwest Mecklenburg, Baltic Sea) II. Guild communities, with special regard to snails, benthic crustaceans, and small-sized fish. Parasitol Res 86:359–372

Zander CD, Koçoglu Ö, Skroblies M (2002) Parasite populations and communities from the shallow littoral of the Orther Bight (Fehmarn, SW Baltic Sea). Parasitol Res 88:734–744