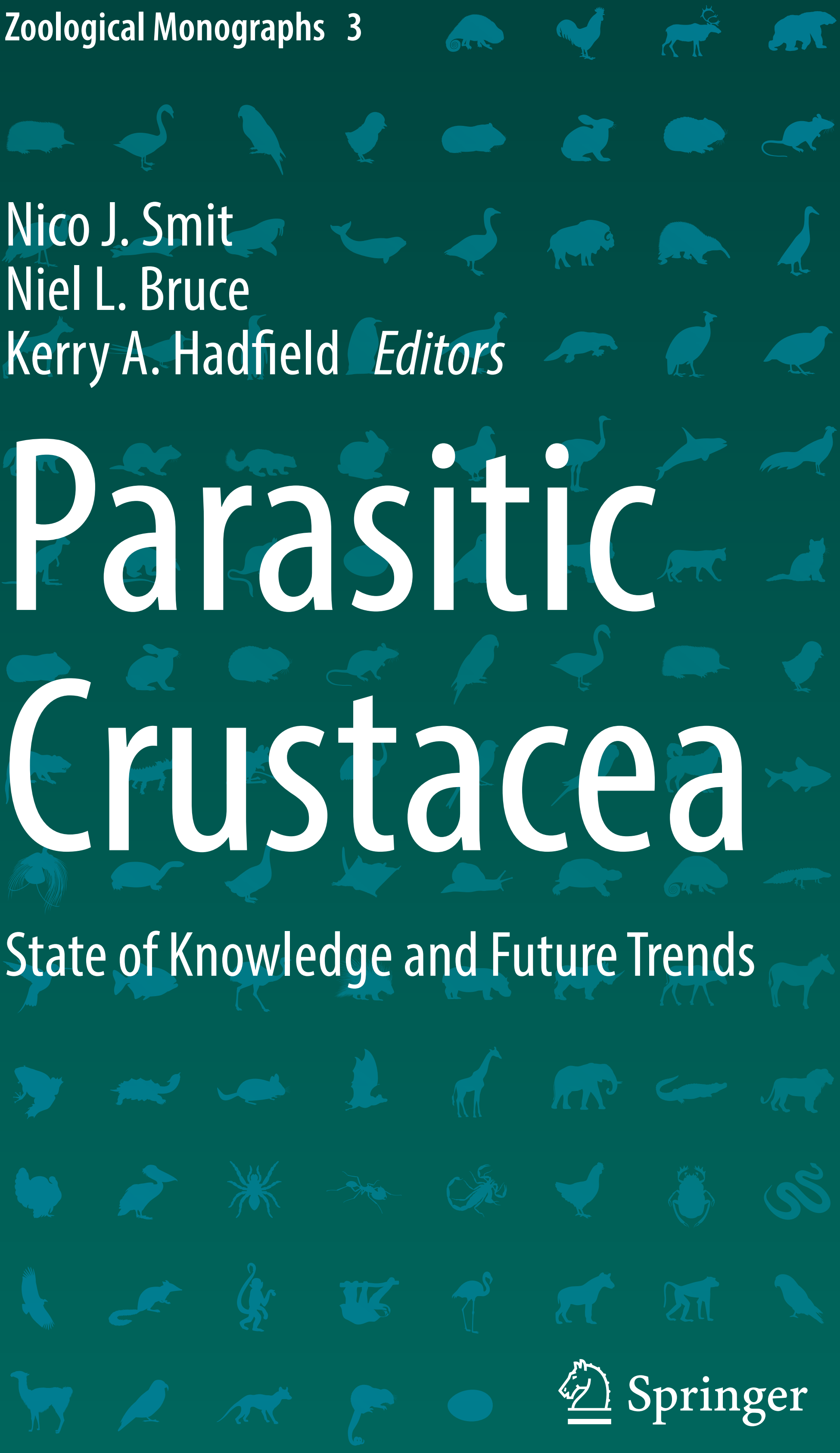
Zoological Monographs 3



Nico J. Smit
Niel L. Bruce
Kerry A. Hadfield *Editors*

Parasitic Crustacea

State of Knowledge and Future Trends

Springer

Zoological Monographs

Volume 3

Illustration of two stage 3 praniza larvae of the gnathiid isopod *Gnathia trimaculata* Coetzee, Smit, Grutter & Davies, 2009 parasitising blacktip reef sharks from the Great Barrier Reef, Australia (Illustration by Suanne Bosch)

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Editors

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Contents

About the Editors

Nico J. Smit is a Professor in Ecology and Director of Research of the Unit for Environmental Sciences and Management at North-West University, Potchefstroom Campus, South Africa. Nico's research focuses on the biodiversity, taxonomy and ecology of parasitic Crustacea and blood protozoa of marine and freshwater fishes and he has authored and co-authored more than 135 scientific papers and two edited books on these and other related topics. To date 15 PhD and 28 MSc students have graduated under his supervision. Nico has contributed to the management of national and international academic societies as president of the Parasitological Society of Southern Africa (PARSA), president of the South African Society of Aquatic Scientists (SASAqS) and committee member of the International Symposium on Fish Parasites (ISFP). Recently he has been the first South African aquatic parasitologist to be rated by the South African National Research Foundation (NRF) as an internationally acclaimed scientist.

Niel L. Bruce is an extraordinary Professor in Zoology at North-West University, Potchefstroom Campus, South Africa and a Research Associate of the Queensland Museum in Brisbane, Australia. He is a world expert on the taxonomy of marine isopod crustaceans, including the parasitic families. Niel has written more than 186 scientific papers, numerous reports, popular articles, five monographs and three edited books. He has worked at the Smithsonian Institution, Australian Museum, Zoological Museum in Copenhagen as Curator of Crustacea, National Institute of Water and Atmospheric Research in New Zealand as head of the Marine Invertebrate Biodiversity and Collections programs. Most recently Niel was Senior Curator at the Museum of Tropical Queensland. Niel's research continues to focus on the taxonomy, systematics, biogeography and biodiversity of tropical marine isopods, both free-living and parasitic forms. He has described or redescribed more than 500 species, 50 new genera and four new families of marine isopod. The other primary research focus, through graduate students, has been revisions of fish parasitic isopods of Southern Africa and Australia and Cirolanidae of Indonesia.

Kerry A. Hadfield is a Senior Lecturer in Zoology at North-West University, Potchefstroom Campus, South Africa and a committee member of the Parasitological Society of Southern Africa (PARSA). Dr. Hadfield received her doctoral degree from the University of Johannesburg where she revised several genera and species of cymothoid isopods from South Africa. Her focus has been predominantly on marine parasitic isopods of the families Cymothoidae and Gnathiidae but is now expanding to include most parasitic crustaceans. She is also one of the taxonomic editors for the World Register of Marine Species (WoRMS) and the World List of Marine Freshwater and Terrestrial Isopod Crustaceans. Kerry has published more than 20 papers describing one new genus of Isopoda and 15 new species (mostly from Africa).

Chapter 1

Introduction to Parasitic Crustacea: State of Knowledge and Future Trends

Nico J. Smit, Niel L. Bruce, and Kerry A. Hadfield

Abstract Parasitic crustaceans are globally considered to be some of the most successful and diverse parasites. They are ubiquitous in the aquatic environment and are known to occur on a wide range of vertebrate and invertebrate hosts. However, despite their common occurrence and large numbers, a book dedicated exclusively to these parasites has not been published. The book presented here provides detailed information on the major parasitic Crustacea groups, including those from Amphipoda, Ascothoracida, Branchiura, Cirripedia, Copepoda, Isopoda, Ostracoda, Pentastomida and Tantulocarida. Each chapter discusses the different aspects of the biology of these parasites, allowing for a better understanding of how the parasitic Crustacea function and for direct comparisons between different parasitic crustacean groups. In this book the authors review the history of discovery of the parasitic Crustacea; their biodiversity and taxonomy; their adaptations and types of crustacean symbiotic associations; their life cycle and life history strategies; their effects on their hosts; their role as vectors, hypersymbionts and hyperparasites and their molecular contribution (parasitic barnacles only), as well as their ecological significance. In addition to reviewing all of the relevant literature, new and unpublished data are included in all of the chapters. Altogether, this book highlights the morphological and ecological attributes that have made the parasitic Crustacea successful and aims to inspire and encourage current and future research into this ecological and economical important field of study.

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1.1 Introduction

The parasitic life strategy is so successful that currently there are more parasite species than free-living species worldwide. Parasitic species can be found in all the major groups of animals and plants ranging from unicellular organisms to arthropods and vertebrates. The different types of parasitism range from facultative, where the parasite usually is free living and may feed only occasionally on a host, to highly specialised obligate parasitism where the parasite undergoes total morphological transformation and is completely reliant on the host for survival. One group of parasites that highlights the full range of evolutionary adaptations to the parasitic lifestyle is the Crustacea.

Crustaceans are one of the most diverse metazoan phyla on Earth, demonstrating a remarkable variety of lifestyles, and a wide range of crustacean groups have entered into parasitic relationships with invertebrate and vertebrate hosts. Parasitism has evolved independently multiple times and across several groups in the Crustacea. Morphological adaptations to this lifestyle include reduction of setae, reduction or loss of appendages through fusion of body segments and, in many, development of a worm-like body. Approximate estimations of species numbers are impossible given the large number of potential hosts yet to be examined, but thousands are already known. Within the parasitic Crustacea, the Copepoda are the most diverse group in terms of morphology, species numbers and host utilisation, and their hosts include almost all other metazoan phyla. The Branchiura are exclusively parasitic, infecting marine and freshwater fish. The Ascothoracida are marine parasites of various echinoderms and cnidarians, occurring from the intertidal to the deep sea. Parasitic Cirripedia include all Rhizocephala, which parasitise other Crustacea, and some Thoracica, with *Rhizolepas* Day, 1939 species infecting polychaetes and one species of *Anelasma* Darwin, 1852 parasitising dogfish. The Tantulocarida is related to the Thecostraca; all are parasites of marine crustacean hosts. Pentastomids parasitise the respiratory passages of marine, freshwater and terrestrial vertebrates. One family of ostracods, Entocytheridae, is parasitic on the gills of freshwater decapod crustaceans. Among the Isopoda, the Cymothoida includes all the parasitic families; the Cymothooidea are predominantly parasites of fish, while the Bopyroidea and Cryptoniscoidea exclusively parasitise other crustaceans. The Cyamidae, ectoparasites of whales, are among only a few truly parasitic groups of Amphipoda.

Throughout the centuries, parasitic crustaceans have been studied on many levels, from the basic morphology and taxonomy to their complex biology and recently to cellular and molecular level. Thousands of research papers have been published on all aspects of their biology and as a group have featured in chapters within a wide range of books. These include basic parasitology textbooks such as Bush et al. (2001) and Goater et al. (2014), as well as more specialised text on marine parasitology (Rohde 2005) and fish parasitology (Woo 2006; Woo and Buchmann 2012). However, no single book exists that is completely devoted to this unique group of organisms. The aim of this book is to compile a single authoritative work by experts in the field, dealing with all the various aspects of the biology of parasitic Crustacea, so providing a concise summary of existing knowledge complemented with new information from the authors' own research. This will make it a one-stop knowledge hub for all researchers, lecturers, students and practitioners interested in parasitic Crustacea.

1.2 Chapter Synopsis

Following this introductory chapter, Chap. 2 presents the history of discovery for the different groups of parasitic Crustacea and their major historical influences. It introduces the different taxonomic groups and provides a synopsis of the discovery and growth of the knowledge for each taxon. The knowledge development in each group is reviewed, from the first parasite discovered to other key historical highlights in both the taxonomic and ecological areas that influenced the group up to the present. This serves as a preview to the host-parasite interactions that are covered in the subsequent chapters. Those specific researchers who added significant contributions to our knowledge of the parasitic Crustacea are also introduced (i.e. a "who's who" depicting leading parasitologists in this field). This review of the crustacean parasites provides a basic background to these abundant organisms, contributes to a better understanding of their unique niche in the aquatic environment and identifies the gaps of knowledge for these groups.

In Chap. 3, the authors reviewed the current understanding of the classification, systematics and global diversity (e.g. species richness patterns, patterns of host utilisation) of each of the parasitic Crustacea groups, highlighting areas of uncertainty or controversy that are in need of further research. Tabulated data on the taxa, species richness and hosts for the parasitic Crustacea groups were provided. Evidence of parasites from the fossil record, and the timing of origin of parasitic clades, were reviewed to provide insights into the history of coevolution between crustacean parasites and their hosts in order to set the scene for the following chapter.

The different life strategies and types of crustacean symbiotic associations, with examples, are discussed in Chap. 4. Most crustacean parasites are in some kind of association with other species: epibiosis, inquilinism, commensalism, mutualism, parasitism and eusociality. All six of these categories are discussed with examples. Regarding parasites, this can range from temporary to highly specialised permanent parasitism where the parasite undergoes total morphological adaptation, becoming metabolically completely reliant on the host for its survival. Parasitism is subdivided into ectoparasites, mesoparasites, endoparasites, parasitic castrators, parasitoidism and sponge hotels, the latter to accommodate the complex crustacean association with sponges. The chapter concludes with remarks on the global distribution of Branchiura, of which all the species are parasites of fish and amphibian tadpoles.

Parasites are said to only do two things: feed and reproduce. In Chap. 5, the authors focused on the way the parasitic Crustacea reproduce. These reproduction strategies can cause severe problems in aquaculture, aquariums and in our important food items around the world. Ironically, if their reproductive strategy is too successful, both the hosts and the parasites die. These life strategies have not received their warranted attention, and little is known about reproduction in many groups of crustaceans. In this chapter, the known reproductive strategies are distinguished, described and attributed to each crustacean group. Crustaceans have developed fascinating "tricks" in their strategies to take advantage of their hosts' behaviour, reproduction or vulnerabilities; environmental conditions; seasons; and a myriad of other factors to accomplish the impossible: find the right host in incredibly vast emptiness. Four new life cycles are suggested in the chapter: complex rebrooding, micro-male, mesoparasite and prey-predator transfer. Additionally, four new life cycle behaviours (nursery hiding, mid-moult stage, positive precursor, negative precursor) and four strategies (opossum attack, double parasitism, duplex arrangement, simple rebrooding) are named.

Chapter 6 discusses the effects parasitic Crustacea have on their respective hosts and aims at providing a holistic view of the direct impact of these parasites on ecological and economically important hosts. The pathological effects of a parasitic crustacean at the individual host level are relatively well understood; however, how they infect the physiological, immunological and reproductive status of hosts is much less studied. Quantifying these effects is difficult due to the poorly understood interactions between parasite, host and environmental determinants. Furthermore, the information of these parasitic Crustacea on the population and community levels is also scanty. The effects of sea lice on salmonids are probably the most understood and documented as these parasites cause a large economic impact on farmed salmon, resulting in a better understanding and control of this parasite. Unfortunately, this is not the case for other parasites where there is still much to be discovered if given the proper attention and funding.

Parasitic Crustacea also play an important role as definitive, intermediate and paratenic hosts, as well as vectors themselves. Chapter 7 presents this very interesting and seldom documented phenomenon. Several copepods are considered to be mechanical vectors or alternative hosts of a number of viral diseases between fishes. Ergasilids parasitic on the gill filaments of fishes can support the replication of shrimp viruses and likely act as viral vectors. Some branchiurans are thought to serve as mechanical vectors of several viruses to fishes, as well as acting as intermediate hosts for fish nematodes. Barnacles on the carapace and gill filaments of crabs can also support shrimp viruses. Several species of gnathiid isopods likely act as definitive hosts and vectors of fish blood parasites of the genus *Haemogregarina* Danilewsky, 1885; they may also transmit some fish viruses and may be paratenic or intermediate hosts for nematode larvae. Cymothoid isopods may transmit lymphocystis virus to fishes. It is likely that there are many more unpublished records of parasitic Crustacea vector associations, and areas of research are identified for future studies.

Parasitic crustaceans have also been reported to host their own symbionts. Chapter 8 deals with the reported records of hypersymbionts and hyperparasites on or in parasitic Crustacea. Microsporidians, peritrich ciliates, udonellids, tantulocarids and parasitic isopods have been found on parasitic copepods, isopods, branchiurans and barnacles. Information on peritrichs on Branchiura and Copepoda are noted, including unpublished data from the author. The monogenean group of udonellids are parasitic on copepods, and sometimes branchiurans, which occur on the skin of their host fish. Tantulocaridans have been reported from siphonostomatoid copepods. Parasitic isopods from the family Cabiropidae are hyperparasites of other parasitic isopods from the family Bopyridae, while other isopods from the family Cryptoniscidae are hyperparasitic on rhizocephalan barnacles. The effects of these hypersymbionts and hyperparasites on their respective hosts are also discussed, as well as biological control for sea lice and bopyrid isopods.

Molecular advances in the study of parasitic Crustacea are crucial for the understanding of their systematics, taxonomy and, even in some cases, life cycle elucidation. In Chap. 9, the authors present the phylogenetic position of Mycetomorpha within the Rhizocephala (parasitic barnacles) as a case study of how molecular-based phylogeny can serve to clarify morphological evolution and remove apparent homoplasies within the parasitic Crustacea. In Crustacea, phylogenetic analysis of parasitic forms has often been met with severe obstacles, both with respect to identifying their closest free-living relatives and with respect to intrinsic analysis of the parasitic species themselves. The reason for this is the paucity and sometimes almost total absence of characters that can be compared both between the parasites and their free-living forms and among the parasites themselves, as their very mode of life mostly entails various degrees of simplification in body morphology. With respect to the parasitic barnacles (Rhizocephala), the situation is much more critical because the parasites offer few, if any, traits that can reasonably be compared with other cirripedes and only few, very generalised traits for comparison between themselves. Until recently, rhizocephalan taxonomy relied exclusively on morphological larval characters, and only with DNA methods was it able to be confirmed that rhizocephalans are cirripedes and nested them within the taxon as the sister group to Thoracica. Additionally, recent hypotheses on family level relationships in Akentrogonida, based on larval structure and the sexual system, were largely confirmed, showing morphological characters can be powerful partners to molecular data in elucidating rhizocephalan phylogeny.

The book concludes with the ecological significance of the parasitic crustaceans discussed in Chap. 10. Crustaceans constitute the aquatic representatives of the most diverse animal phylum on the planet. The ecological “role” and significance of the free-living representatives have been well documented. For example, crustaceans comprise the majority of the zooplankton that function as primary consumers in aquatic food webs. Most work on the myriad parasitic crustaceans has focused on species that have become problematic for aquaculture. Much less is known about the ecological significance of the myriad parasitic forms. This stems largely from the fact that most parasitologists receive little if any training in ecology, and most aquatic ecologists receive little or no training in parasitology. Parasitic crustaceans can both transmit disease-causing organisms and create wounds that facilitate secondary infection, lower blood haematocrit levels and alter host immune function and metabolism, host movement patterns, feeding behaviour and interactions with other organisms. In high numbers, they can contribute directly to the death of the host and, in sublethal numbers, can be an indirect cause of death as well as reducing host growth and fecundity. Many crustacean parasites are themselves food for other organisms, sometimes including their own hosts. Any one of these can have consequences at the population level for the parasites and the hosts, as well as knock-on effects at the community level. This chapter reviews what is currently known about the ecology of parasitic crustaceans and highlights relevant literature in parasitology and aquatic ecology to chart the course of future study in this field.

1.3 Concluding Remarks

In conclusion, the authors and editors hope that on reading this book, the crustacean parasitologists will come away inspired by the contributions their work can make to the science of aquatic ecology, and aquatic ecologists should come away with an appreciation for the important role crustacean parasites play in the ecological systems.

Acknowledgements All the chapters of this book have been peer-reviewed by experts in the various fields of parasitic Crustacea, and the editors would hereby like to thank the nine anonymous reviewers for their time and constructive comments on each of the chapters. The editors would also like to thank Lars Koerner, Editor of Animal Sciences at Springer for initiating this project and his patience with us throughout the compilation of the book. Finally, we also like to thank Abinay Subramaniam, Project Coordinator (Books) for Springer Nature, for her assistance in preparing the final version of this book.

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Chapter 2
History of Discovery of Parasitic Crustacea

Kerry A. Hadfield

Abstract Parasitic Crustacea have been present in scientific literature since Linnaeus introduced the first classification system (binomial nomenclature). Crustaceans are considered to be the most morphologically diverse arthropods, with currently 19 parasitic orders known to science. This chapter reviews the history of discovery for each of the major parasitic Crustacea groups, highlighting some of the key developments that have influenced our current understanding of these parasites. Each taxonomic group is briefly introduced, followed by a synopsis on some of the outstanding contributions within that group. Knowledge development is followed, from the first parasites discovered to other historical highlights that influenced the groups up to this point. Other important discoveries (both taxonomic and ecological) are also noted, serving as a preview to the host-parasite interactions covered in the subsequent chapters. Additionally, several researchers who have added significant contributions to our knowledge of the parasitic Crustacea (specifically in taxonomy and discovery) are introduced, along with photographs of a select few. This historical review of the crustacean parasites provides a background to these diverse and abundant organisms and will contribute to a better understanding of their unique niche in the aquatic environment.

2.1 Introduction

Parasitic crustaceans were already represented at the introduction of binomial nomenclature by the Swedish taxonomist, Carl Linnaeus (Fig. 2.1a) (1758), including, amongst others, four species of fish parasitic isopods. In the more than two and a half centuries that followed, a great number of crustacean parasites were described, and while some parasitic crustacean groups, such as the copepods and isopods, are fairly well researched, limited information is available for the lesser known and less studied groups, such as the thoracicans and tantulocaridans.

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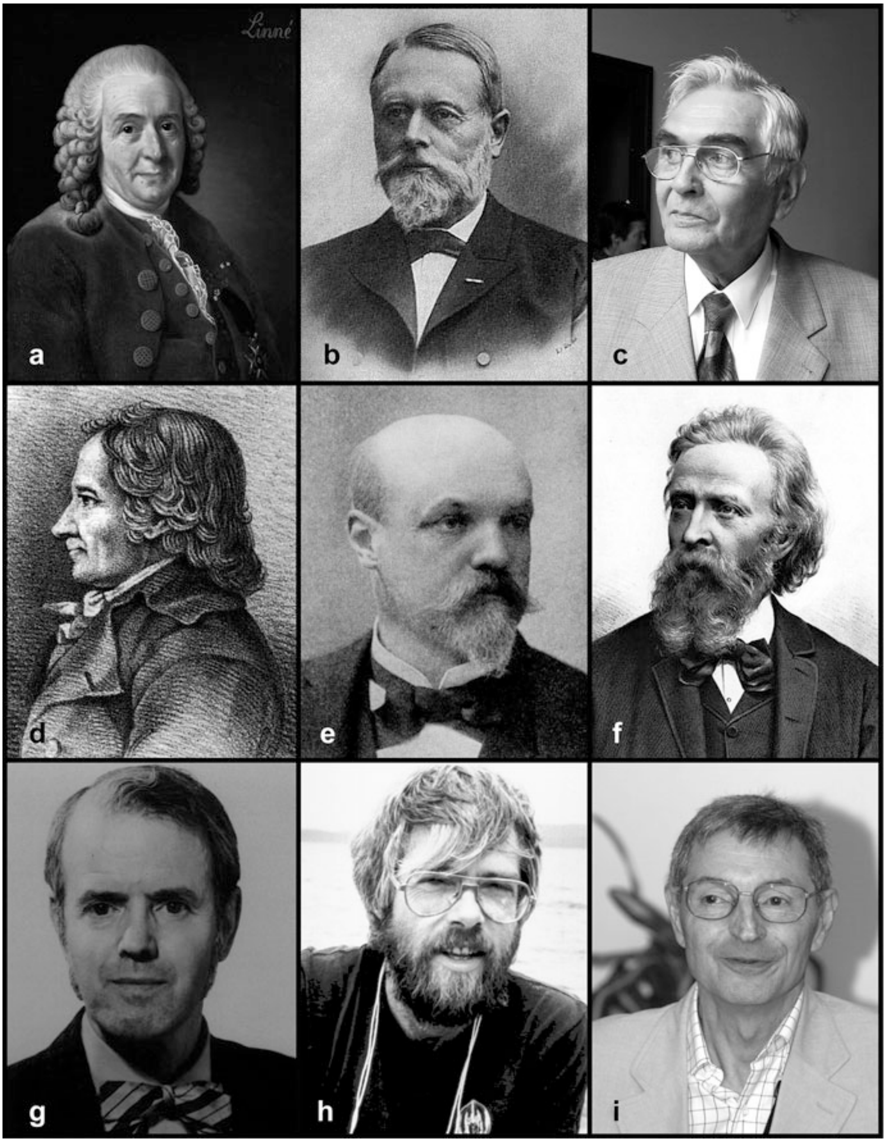

Fig. 2.1 (**a**) Carl Linnaeus, (**b**) Christian Frederik Lütken, (**c**) Hans-Eckhard Gruner, (**d**) Johan Christian Fabricius, (**e**) Carl Erik Alexander Bovallius, (**f**) Carl Friedrich Wilhelm Claus, (**g**) Thomas Elliot Bowman, (**h**) George "Richard" Harbison, (**i**) Philippe Laval. Image (**a**) oil on canvas by Alexander Roslin, © Wikipedia Commons public domain; image (**b**) © The Royal Library; image (**c**) from Coleman (2007); image (**d**) preface of Hope (1845); image (**e**) © Wikipedia Commons public domain; image (**f**) from Grobben (1899); image (**g**) from Ferrari (1996); image (**h**) courtesy of Woods Hole Oceanographic Institution Archives

Historically, crustacean collections were held in private collections or university museums. Collections from oceans were restricted to the intertidal regions or ship based, and for obvious reasons discovery lagged behind terrestrial discovery. The age of great ocean expeditions that fed into fish parasite knowledge included amongst others the US Exploring Expedition (several ships, 1838–1842), the *Galathea* Expedition (Danish, 1845–1847) and the *Siboga* Expedition (Dutch, 1899–1900). As scientific research developed, state (national) museums were founded as the major repositories for all natural history collections, such as the British Museum (founded in 1753 and the first national public museum in the world), the Muséum national d'histoire naturelle (1793) and in the New World, the US National Museum (1846), to name just three. As technology improved, scientists were able to use new techniques to not only collect parasites (such as SCUBA diving) but also to view them (such as scanning electron microscopy [SEM] and differential interference contrast [DIC] microscopy). Currently, the use of molecular biology techniques for parasites is on the rise. These techniques can assist with parasite identification and characterisation, as well as provide other useful information on the parasite origin and evolution (amongst other things).

The aim of this chapter is to reflect on the history of discovery for each of the major parasitic groups within Crustacea, showing that research on particular parasites increased with the presence of an individual or research group actively interested in that specific parasite group. It is envisaged that understanding the past research will indicate the gaps in our knowledge within these groups and contribute to identifying where research should focus in the future. The chapter focused primarily on the taxonomic and systematic discovery of parasitic crustaceans, along with notes on selected contributors to our knowledge of parasitic Crustacea. It should be noted that the chapter is not intended to be a checklist and does not refer to every researcher who has worked on the parasitic Crustacea.

2.2 Amphipoda

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Amphipoda Latreille, 1816

The status of any amphipod as a "true parasite" is often questioned, as there is no evidence that any have harmful effects upon their hosts. Amphipods associated with other animals are frequently referred to as commensals (i.e. members of Leucothoidae are typically found associated with sessile invertebrates such as sponges, utilising the current produced by the sponge to feed). Only a few groups of amphipods are recognised as parasitic: Cyamidae ("whale lice"), Hyperiidea and Trischizostomidae (see Table 2.1).

Table 2.1 Classification, up to family level, of the parasitic Crustacea according to the World Register of Marine Species (WoRMS) (2018)

Phylum Arthropoda Siebold & Stannius 1845
Subphylum Crustacea Brünnich, 1772
Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class Hexanauplia Oakley, Wolfe, Lindgren & Zaharof, 2013
Subclass Copepoda Milne-Edwards, 1840
Infraclass Neocopepoda Huys & Boxshall, 1991
Superorder Podoplea Giesbrecht, 1882
Order Cyclopoida Burmeister, 1834
Family Archinotodelphyidae Lang, 1949
Family Ascidicolidae Thorell, 1859
Family Botryllophilidae Sars G.O., 1921
Family Buproridae Thorell, 1859
Family Chitonophilidae Avdeev & Sirenko, 1991
Family Chordeumiidae Boxshall, 1988
Family Cucumaricolidae Bouligand & Delamare Deboutteville, 1959
Family Cyclopettidae Martínez Arbizu, 2000
Family Cyclopidae Rafinesque, 1815
Family Cyclopinidae Sars G.O., 1913
Family Cyclopoida incertae sedis
Family Enterognathidae Illg & Dudley, 1980
Family Enteropsidae Thorell, 1859
Family Fratiidae Ho, Conradi & López-González, 1998
Family Giselinidae Martínez Arbizu, 2000
Family Hemicyclopinidae Martínez Arbizu, 2001
Family Lernaeidae Cobbold, 1879
Family Mantridae Leigh-Sharpe, 1934
Family Micrallectidae Huys, 2001
Family Notodelphyidae Dana, 1853
Family Oithonidae Dana, 1853
Family Ozmanidae Ho & Thatcher, 1989
Family Psammocyclopinidae Martínez Arbizu, 2001
Family Pterinopsyllidae Sars G.O., 1913
Family Schminkepinellidae Martínez Arbizu, 2006
Family Smirnovipinidae Martínez Arbizu, 1997
Family Speleoithonidae Rocha & Iliffe, 1991
Family Thaumatopsyllidae Sars G.O., 1913
Order Harpacticoida Sars M., 1903
Family Balaenophilidae Sars G.O., 1910
Family Tisbidae Stebbing, 1910
Order Monstrilloida Sars G.O., 1901
Family Monstrillidae Dana, 1849
Order Poecilostomatoida Thorell, 1859

(continued)

Table 2.1 (continued)

	Family Abrsiidae Karanovic, 2008
	Family Anchimolgidae Humes & Boxshall, 1996
	Family Anomoclausiidae Gotto, 1964
	Family Antheacheridae Sars M., 1870
	Family Anthessiidae Humes, 1986
	Family Bomolochidae Claus, 1875
	Family Bradophilidae Marchenkov, 2002
	Family Catiniidae Bocquet & Stock, 1957
	Family Chondracanthidae Milne-Edwards, 1840
	Family Clausidiidae Embleton, 1901
	Family Clausiidae Giesbrecht, 1895
	Family Corallovexiidae Stock, 1975
	Family Corycaeidae Dana, 1852
	Family Echiurophilidae Delamare-Deboutteville & Nunes-Ruivo, 1955
	Family Entobiidae Ho, 1984
	Family Erebonasteridae Humes, 1987
	Family Ergasilidae Burmeister, 1835
	Family Eunicicolidae Sars G.O., 1918
	Family Gadilicolidae Boxshall & O'Reilly, 2015
	Family Gastrodelphyidae List, 1889
	Family Herpyllobiidae Hansen, 1892
	Family Intramolgidae Marchenkov & Boxshall, 1995
	Family Iveidae Tung, Cheng, Lin, Ho, Kuo, Yu & Su, 2014
	Family Jasmineiricolidae Boxshall, O'Reilly, Sikorski & Summerfield, 2015
	Family Kelleriidae Humes & Boxshall, 1996
	Family Lamippidae Joliet, 1882
	Family Leaniricolidae Huys, 2016
	Family Lichomolgidae Kossmann, 1877
	Family Lubbockiidae Huys & Böttger-Schnack, 1997
	Family Macrochironidae Humes & Boxshall, 1996
	Family Makrostrotidae Huys, Fatih, Ohtsuka & Llewellyn-Hughes, 2012
	Family Mesoglicolidae Zulueta, 1911
	Family Myicolidae Yamaguti, 1936
	Family Mytilicolidae Bocquet & Stock, 1957
	Family Nereicolidae Claus, 1875
	Family Octopicolidae Humes & Boxshall, 1996
	Family Oncaeidae Giesbrecht, 1893
	Family Paralubbockiidae Boxshall & Huys, 1989
	Family Philichthyidae Vogt, 1877
	Family Philoblennidae Izawa, 1976
	Family Phyllodicolidae Delamare Deboutteville & Laubier, 1961
	Family Pionodesmotidae Bonnier, 1898
	Family Poecilostomatoida incertae sedis

(continued)

Table 2.1 (continued)

Family Polyankyliidae Ho & Kim I.H., 1997
Family Praxillinicolidae Huys, 2016
Family Pseudanthessiidae Humes & Stock, 1972
Family Rhynchomolgidae Humes & Stock, 1972
Family Sabelliphilidae Gurney, 1927
Family Saccopsidae Lützen, 1964
Family Sapphirinidae Thorell, 1859
Family Serpulidicolidae Stock, 1979
Family Shiinoidae Cressey, 1975
Family Spiophanicolidae Ho, 1984
Family Splanchnotrophidae Norman & Scott T., 1906
Family Strepidae Cheng, Liu & Dai, 2016
Family Synapticolidae Humes & Boxshall, 1996
Family Synaptiphilidae Bocquet & Stock, 1957
Family Taeniacanthidae Wilson C.B., 1911
Family Telsidae Ho, 1967
Family Thamnomolgidae Humes & Boxshall, 1996
Family Urocopiidae Humes & Stock, 1972
Family Vahiniidae Humes, 1967
Family Ventriculinidae Leigh-Sharpe, 1934
Family Xarifiidae Humes, 1960
Family Xenocoelomatidae Bresciani & Lutzen, 1966
Order Siphonostomatoida Thorell, 1859
Family Archidactylinidae Izawa, 1996
Family Artotrogidae Brady, 1880
Family Asterocheridae Giesbrecht, 1899
Family Brychiopontiidae Humes, 1974
Family Caligidae Burmeister, 1835
Family Calverocheridae Stock, 1968
Family Cancerillidae Giesbrecht, 1897
Family Codobidae Boxshall & Ohtsuka, 2001
Family Coralliomyzontidae Humes & Stock, 1991
Family Dichelesthiidae Milne-Edwards, 1840
Family Dichelinidae Boxshall & Ohtsuka, 2001
Family Dinopontiidae Murnane, 1967
Family Dirivultidae Humes & Dojiri, 1980
Family Dissonidae Kurtz, 1924
Family Ecbathyriontidae Humes, 1987
Family Entomolepididae Brady, 1899
Family Eudactylinidae Wilson C.B., 1932
Family Hatschekiidae Kabata, 1979
Family Hyponeoidae Heegaard, 1962
Family Kroyeriidae Kabata, 1979

(continued)

Table 2.1 (continued)

Family Lernaeopodidae Milne-Edwards, 1840
Family Lernanthropidae Kabata, 1979
Family Megapontiidae Heptner, 1968
Family Micropontiidae Gooding, 1957
Family Nanaspididae Humes & Cressey, 1959
Family Nicothoidae Dana, 1852
Family Pandaridae Milne-Edwards, 1840
Family Pennellidae Burmeister, 1835
Family Pontoeciellidae Giesbrecht, 1895
Family Pseudocycnidae Wilson C.B., 1922
Family Pseudohatschekiidae Tang, Izawa, Uyeno & Nagasawa, 2010
Family Rataniidae Giesbrecht, 1897
Family Scottomyzontidae Ivanenko, Ferrari & Smurov, 2001
Family Siphonostomatoida incertae sedis
Family Sphyriidae Wilson C.B., 1919
Family Sponginticolidae Topsent, 1928
Family Spongiocnizontidae Stock & Kleeton, 1964
Family Stellicomitidae Humes & Cressey, 1958
Family Tanypleuridae Kabata, 1969
Family Trebiidae Wilson C.B., 1905
Subclass Tantulocarida Boxshall & Lincoln, 1983
Family Basipodellidae Boxshall & Lincoln, 1983
Family Deoterthridae Boxshall & Lincoln, 1987
Family Doryphallophoridae Huys, 1991
Family Microdajidae Boxshall & Lincoln, 1987
Family Onceroxenidae Huys, 1991
Subclass Thecostraca Gruvel, 1905
Infraclass Ascothoracida Lacaze-Duthiers, 1880
Order Dendrogastrida Grygier, 1987
Family Ascothoracidae Grygier, 1987
Family Ctenosculidae Thiele, 1925
Family Dendrogastridae Gruvel, 1905
Order Laurida Grygier, 1987
Family Lauridae Gruvel, 1905
Family Petrarcidae Gruvel, 1905
Family Synagogidae Gruvel, 1905
Infraclass Cirripedia Burmeister, 1834
Superorder Acrothoracica Gruvel, 1905
Order Lithoglyptida Kolbasov, Newman & Hoeg, 2009
Family Lithoglyptidae Aurivillius, 1892
Family Trypetesidae Stebbing, 1910
Superorder Rhizocephala Müller, 1862
Order Akentrogonida Häfele, 1911

(continued)

Table 2.1 (continued)

Family Akentrogonida incertae sedis
Family Chthamalophilidae Bocquet-Védrine, 1961
Family Clistosaccidae Boschma, 1928
Family Duplorbidae Høeg & Rybakov, 1992
Family Mycetomorphidae Høeg & Rybakov, 1992
Family Polysaccidae Lützen & Takahashi, 1996
Family Thompsoniidae Høeg & Rybakov, 1992
Order Kentrogonida Delage, 1884
Family Lernaeodiscidae Boschma, 1928
Family Parthenopeidae Rybakov & Høeg, 2013
Family Peltogastridae Lilljeborg, 1860
Family Sacculinidae Lilljeborg, 1860
Superorder Thoracica Darwin, 1854
Order Lepadiformes Buckeridge & Newman, 2006
Suborder Heteralepadomorpha Newman, 1987
Family Anelasmatidae Gruvel, 1905
Family Koleolepadidae Hiro, 1933
Family Rhizolepadidae Zevina, 1980
Suborder Lepadomorpha Pilsbry, 1916
Family Poecilasmatidae Annandale, 1909
Order Sessilia Lamarck, 1818
Suborder Balanomorpha Pilsbry, 1916
Family Pyrgomatidae Gray, 1825
Infraclass Facetotecta Grygier, 1985
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Amphipoda Latreille, 1816
Superfamily Lysianassoidea Dana, 1849
Family Trischizostomatidae Lilljeborg, 1865
Suborder Hyperiidea Milne-Edwards, 1830
Infraorder Physocephalata Bowman & Gruner, 1973
Superfamily Phronimoidea Rafinesque, 1815
Family Dairellidae Bovallius, 1887
Family Hyperiidae Dana, 1852
Family Lestrigonidae Zeidler, 2004
Family Phronimidae Rafinesque, 1815
Superfamily Platysceloidea Spence Bate, 1862
Family Brachyscelidae Stephensen, 1923
Family Lycaeidae Claus, 1879
Family Oxycephalidae Dana, 1852
Superfamily Vibilioidea Dana, 1852
Family Vibiliidae Dana, 1852

(continued)

Table 2.1 (continued)

Infraorder Physosomata
Suborder Senticaudata Lowry & Myers, 2013
Infraorder Corophiida Leach, 1814 (sensu Lowry & Myers, 2013)
Superfamily Caprelloidea Leach, 1814
Family Cyamidae Rafinesque, 1815
Order Isopoda Latreille, 1817
Suborder Cymothoida Wägele, 1989
Superfamily Bopyroidea Rafinesque, 1815
Family Bopyridae Rafinesque, 1815
Family Entoniscidae Kossmann, 1881
Superfamily Cryptoniscoidea Kosmann, 1880
Family Cabiropidae Giard & Bonnier, 1887
Family Cryptoniscidae Kossmann, 1880
Family Cyproniscidae Bonnier, 1900
Family Dajidae Giard & Bonnier, 1887
Family Podasconidae Giard & Bonnier, 1895
Superfamily Cymothooidea Leach, 1814
Family Anuropidae Stebbing, 1893
Family Aegidae White, 1850
Family Barybrotidae Hansen, 1890
Family Corallanidae Hansen, 1890
Family Cymothoidae Leach, 1814
Family Gnathiidae Leach, 1814
Family Tridentellidae Bruce, 1984
Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998
Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1998
Subclass Branchiura Thorell, 1864
Order Arguloida Yamaguti, 1963
Superfamily Arguloidea Yamaguti, 1963
Family Argulidae Leach, 1819
Subclass Pentastomida Diesing, 1836
Order Cephalobaenida Heymons, 1935
Family Cephalobaenidae Heymons, 1922
Order Porocephalida Heymons, 1935
Superfamily Linguatuloidea Haldeman, 1851
Family Linguatulidae Haldeman, 1851
Family Subtriquetridae Fain, 1961
Superfamily Porocephaloidea Sambon, 1922
Family Porocephalidae Sambon, 1922
Family Sebekidae Sambon, 1922
Order Raillietiellida Almeida & Christoffersen, 1999
Family Raillietiellidae Sambon, 1922
Order Reighardiida Almeida & Christoffersen, 1999

(continued)

Table 2.1 (continued)

Family Reighardiidae Heymons, 1926
Class Ostracoda Latreille, 1802
Subclass Myodocopa Sars, 1866
Order Myodocopida Sars, 1866
Suborder Myodocopina Sars, 1866
Superfamily Cypridinoidea Baird, 1850
Family Cypridinidae Baird, 1850

2.2.1 Cyamidae

The term "whale lice" is a misnomer as these are in fact crustaceans, with most cyamids being dorsoventrally flattened and unable to swim, relying on direct contact for transmission from one host to another. They have a rudimentary pleon with the posterior three pairs of legs enlarged and adapted to cling onto their host. Cyamids are known to attach to whales, dolphins and porpoises (Martínez et al. 2008), where they can be highly host specific, and more than one species can be found on one host at a time.

The first cyamid described was *Cyamus ceti* (Linnaeus, 1758) (originally as *Oniscus ceti* since the genus *Cyamus* was described by Latreille in 1796), and a number of new species were discovered in the 1800s. Christian Frederik Lütken (Fig. 2.1b) described seven new *Cyamus* species as well as the genus, *Platycyamus* Lütken, 1870, all of which were incorporated into the first cyamid monograph (Lütken 1873). Lütken, a Danish zoologist, worked on a number of aquatic groups including corals, jellyfish, crustaceans and annelids, but his passion lay with echinoderms and fishes, and thus only a few of his papers were dedicated to cyamids. Although cyamids were known in many parts of the world, between 1888 and 1931, no new cyamid species were described.

In 1967, Yuk-Maan Leung provided the first illustrated key for the cyamids along with a guide to the literature (Leung 1967). Leung also described the first life cycle of a cyamid (*Cyamus scammoni* Dall, 1872 on the grey whale) which provided valuable information on the reproductive behaviour of these parasites (Leung 1976). Around the same time, Hans-Eckhard Gruner (Fig. 2.1c) completed a comprehensive catalogue of the Cyamidae (Gruner 1975). Gruner contributed to the taxonomy of amphipods and isopods and was best known for his *Lehrbuch der Speziellen Zoologie* (Textbook on Special Zoology) published in 1980. A few years later, in 1999, Joel Martin and John Heyning provided an updated key and checklist for these parasites, which proved helpful in subsequent studies (Martin and Heyning 1999).

As cyamids are permanently attached to constantly moving cetaceans, in-depth studies on the parasites have been difficult; however, despite these challenges, many scientists have been able to report on their ecology. Juan Antonio Balbuena and Juan Antonio Raga published many papers on parasites of marine mammals and discussed the ecology and host relationships of whale lice on pilot whales (Balbuena and Raga 1991). Furthermore, Victoria Rowntree, an American whale researcher, has noted many behavioural aspects of these amphipods (on right whales in particular). Cyamids are known to aggregate in areas where there is the least amount of stress (out of the main water flow areas), such as the skin folds on the head, eyes, flippers, blowholes, lip margins, around barnacles and callosities (Leung 1970a, b; Rowntree 1996). The abundance of the cyamids on their host is inversely proportional to the host's swimming speed, with slower whales having several thousand on a single host and faster-swimming dolphins having fewer (Goater et al. 2014). The mouthparts of the cyamids are highly modified, with setae and short spines on the maxillae, maxillules and mandibles, for excavating and eating host skin. Rowntree (1996) confirmed that these ectoparasites eat whale skin containing pigments (seen in the intestines of the amphipods), and shortly thereafter Schell et al. (2000) confirmed this diet with the aid of stable carbon and nitrogen isotopes. More recently, Rowntree and colleagues have used genetic sequence variation in the whale lice of right whales in order to determine population histories (Kaliszewska et al. 2005).

Carl J. Pfeiffer, researcher of marine mammals, and his colleagues provided additional information on the anatomy of cyamids (marsupium, eggs, juveniles and cuticle) (Pfeiffer and Viers 1998), as well as on the ocular musculature (Levin and Pfeiffer 1999). Pfeiffer also completely revised the whale lice in a chapter dedicated to the crustaceans in the published book *Encyclopaedia of Marine Mammals* (Pfeiffer 2002).

Alan A. Myers and James K. Lowry, amphipod specialists from Ireland and Australia, respectively, also presented a new classification for the suborder Corophiidea (see Myers and Lowry 2003). However, most of the amphipod higher-level classification and phylogenetic relationships are still not agreed upon, with preliminary molecular work and the previously proposed relationships not being consistent (Väinölä et al. 2008). More recently, Myers and Lowry revised the amphipod classification, established a new suborder Senticaudata (including the Cyamidae), and introduced the level parvorder between infraorder and superfamily, a first for amphipod taxonomy (Lowry and Myers 2013). The family Cyamidae currently has 32 recorded species from six genera.

2.2.2 Hyperiidea

Parasitic amphipods, in the suborder Hyperiidea, have a large cephalothorax and eyes and are exclusively marine (mostly pelagic). These crustaceans live associated with other zooplankton where they may be parasitic or commensals on organisms such as jellyfish, ctenophores, molluscs and tunicates. The association of a hyperiid and gelatinous zooplankton is considered parasitic if the amphipod is within the tissue of the host for nutritional purposes (host tissue can be seen in the amphipod stomach contents after feeding) (de Lima and Valentin 2001).

The first three species of Hyperiidea were described in 1775. Johan Christian Fabricius (Fig. 2.1d) (a Danish zoologist) described two of these species, namely, *Cystisoma spinosum* (Fabricius, 1775) (*nomen dubium*) and *Scina crassicornis* (Fabricius, 1775). The third species, *Phronima sedentaria* (Forskål, 1775), was described by the Swedish researcher, Peter Forskål. Interestingly, both these men were students of Linnaeus at some point. Although these three species were the first named hyperiids, there was an earlier record in 1762 by H. Strøm of a hyperiid in association with a host, where *Hyperia medusarum* (Müller, 1776) was located inside a large jellyfish (Harbison et al. 1977).

Many of the early systematic monographs on these parasites were completed by the Swedish biologist Carl Erik Alexander Bovallius (1887a, b, c, 1889, 1890) (Fig. 2.1e) and the German zoologist Carl Friedrich Wilhelm Claus (1879a, b) (Fig. 2.1f). Thomas Elliot Bowman (an American carcinologist) (Fig. 2.1g) and Hans-Eckhard Gruner thoroughly reviewed the families and genera of Hyperiidea in 1973 (Bowman and Gruner 1973). This review became the foundation for all other systematic work on these amphipods. Not only did it focus on identifying the large collection of hyperiid Amphipoda sampled during the Dana Expedition (1928–1930), but it also included a detailed section on their morphology and ecology.

George "Richard" Harbison (Fig. 2.1h) noted that although other researchers had mentioned the parasitic mode of life, little research had been done on the life histories and host specificities of the parasitic amphipods. Using SCUBA to collect live material, Harbison and colleagues were able to observe a number of associations between the amphipods and their hosts that had never been noted before (Harbison et al. 1977; Madin and Harbison 1977). Many observations of living hyperiids were also made by Philippe Laval (from 1963 until he retired in 2004) (Fig. 2.1i). Laval was one of the first researchers to recognise that all hyperiids have a parasitic way of life (noted in his doctoral thesis in 1974), which was later confirmed by Harbison et al. (1977) and published (amongst others) an extensive paper on these parasites associated with gelatinous zooplankton (Laval 1980).

More recently, Wolfgang Zeidler (Fig. 2.2a), formerly working at the South Australian Museum, revised the taxonomy of the Hyperiidea (Zeidler 2003a, b, 2004a, b, 2006, 2009, 2012, 2015; Zeidler and De Broyer 2009). These extensive reviews included assessments of the systematic relationships between the genera as well as keys for the families, genera and species, drawings of the species and diagnoses for the different taxa. Hyperiidea has 283 accepted species and 76 genera of which Zeidler has described 12 families, 5 genera and 23 species.

2.2.3 Trischizostomidae

At present, there are 18 species of *Trischizostoma* Boeck, 1861, most of which are considered ectoparasites of fish species. These amphipods occur between 22 and 3655 m depth (Freire and Serejo 2004) and have specifically adapted styliform mouthparts and a modified gnathopod 1 for this parasitic way of life.

The first described *Trischizostoma* was *T. nicaeense* (Costa, 1853) (as *Guerina nicaeensis* Chevreux, 1905) from Nice, France. Elsie Wilkins Sexton (an English

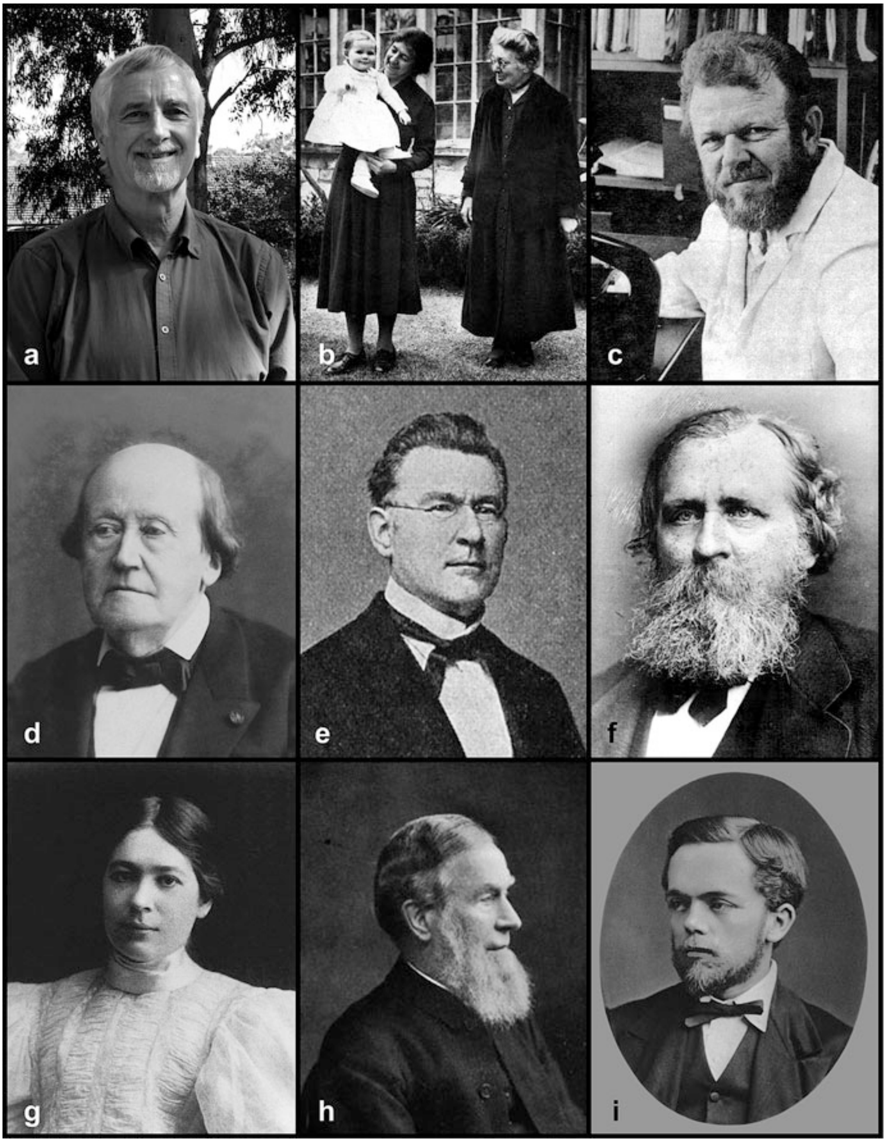

Fig. 2.2 (**a**) Wolfgang Zeidler, (**b**) Elsie Wilkins Sexton (on the right), (**c**) Jerry Laurens Barnard, (**d**) Henri Milne Edwards, (**e**) Jörgen Matthias Christian Schioedte, (**f**) Frederik Vilhelm August Meinert, (**g**) Harriet Richardson, (**h**) Thomas Roscoe Rede Stebbing, (**i**) Edward John Miers. Image (**b**) from Spooner (1960); image (**c**) from Thomas (1992); images (**d**), (**e**) and (**h**) © Wikipedia Commons public domain; image (**f**) from Truesdale (1993); image (**g**) from Damkaer (2000); image (**i**) from Gordon (1971)

zoologist) (Fig. 2.2b) published a review of the genus in 1908, highlighting the historical moments as well as including species descriptions and drawings of the species known at that time (Sexton 1908). Sexton's research into these amphipods helped to clarify the taxonomy of the genus. She had accurate and superior illustrations by the standard of the day and continued to work even after her 80th birthday.

In 1961, Jerry Laurens Barnard (Fig. 2.2c) described a new species of *Trischizostoma* and in doing so divided the genus into two groups: those with a large conspicuous rostrum, strongly styliform mouthparts and an entire telson and those with a smaller deflexed rostrum, much less styliform mouthparts and a telson cleft to the middle (Barnard 1961). Barnard was an outstanding amphipod taxonomist, primarily working on the Gammaridea. Years later, Vinogradov (1991) published a key for the genus in Russian. In 2004, Freire and Serejo (2004) provided a key to the Brazilian species and recorded the first *Trischizostoma* from the Southwest Atlantic Ocean. A recent publication by Winfield et al. (2017) added the first record from the north-east Pacific. The distribution of these two groups now is as follows: the "entire telson" group are known from the north-east and south-west Atlantic Ocean, the north-west and north-east Pacific Ocean and the Indo-Pacific, while the "notched telson" group are from the south-east Atlantic and south-west Indian Ocean (Winfield et al. 2017).

2.3 Isopoda

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Class Malacostraca Latreille, 1802
Subclass Eumalacostraca Grobben, 1892
Superorder Peracarida Calman, 1904
Order Isopoda Latreille, 1817

Isopods were named in reference to the legs being of similar size and shape (see Bunkley-Williams and Williams 1994). There are 95 families of Isopoda, with approximately 10,300 isopod species worldwide (Ahyong et al. 2011), including the terrestrial taxa. Only seven families are known to be parasitic, and these all belong within the suborder Cymothoida (see Brandt and Poore 2003), and all parasitise either fish or crustaceans.

There are a few instances of isopods living symbiotically with other groups, but the trophic nature of the association remains unknown. Some examples include the cirolanid species *Cartetolana integra* (Miers, 1884) (an obligate associate of crinoids; see Bruce 1986a); the cirolanid *Neocirolana hermitensis* (Boone, 1918) (possibly a brood predator of hermit crabs; see Bruce 1994a); the sphaeromatids from *Xynosphaera* Bruce, 1994b (burrows into soft corals; see Bruce 1994b); and the relatively large sphaeromatid genus *Oxinasphaera* Bruce, 1997 (exclusively associated with marine sponges; see Lörz and Bruce 2008).

The oldest parasitic isopod has recently been determined by Nagler et al. (2017). A fossilised isopod reported to be 168 million years old appears to be "deeply nested" within the suborder Cymothoida, and most closely related to Gnathiidae. This is based on morphological characteristics such as the sucking-piercing mouthparts (seen in ectoparasitic isopods) and strongly curved dactyli (used to attach to their hosts).

However, the first isopods named were in 1758 by Carl Linnaeus (Fig. 2.1a) (also known as Carl von Linné after his ennoblement). The tenth edition of his publication *Systema Naturae* (1758) was designated as the starting point for binomial and zoological nomenclature by the International Congress of Zoology. That work included the description of seven isopod species, namely, *Aega psora* (Linnaeus, 1758), *Anilocra physodes* (Linnaeus, 1758), *Asellus aquaticus* (Linnaeus, 1758), *Cymothoa oestrum* (Linnaeus, 1758), *Cymothoa scopulorum* (Linnaeus, 1758), *Oniscus asellus* Linnaeus, 1758 and *Saduria entomon* (Linnaeus, 1758). Four of these species are parasitic: *Aega psora* and *Anilocra physodes* are external attaching parasites, while *Cymothoa oestrum* and *C. scopulorum* are found in the buccal cavity of various fish species. *Cymothoa* Fabricius, 1793, is recognised as the first unequivocally fish parasitic isopod genus.

The first significant contributor after Linnaeus was the English naturalist, William Elford Leach. Leach, who was one of the world's leading crustacean experts at that time and friend to both Cuvier and Lamarck (great naturalists of the time), established the parasitic families Cymothoidae and Gnathiidae. Furthermore, Leach also described 25 genera, eight of which are fish parasitic (six still valid), and 36 species between 1775 and 1818. Sadly, there is reportedly no known portrait of Leach (Harrison and Smith 2008). However, what is arguably the most memorable fact about Leach is his interesting play on the name Caroline/Carolina in nine acronymic isopod genera in 1818: *Anilocra* Leach, 1818; *Canolira* Leach, 1818; *Cirolana* Leach, 1818; *Conilera* Leach, 1818; *Livoneca* Leach, 1818, *Nelocira* Leach, 1818; *Nerocila* Leach, 1818; *Olencira* Leach, 1818; and *Rocinela* Leach, 1818. It is believed that this was in reference to Queen Caroline of Britain (estranged wife of the Prince of Wales) and was a repetitive insult to the woman who was described as an "unlovable adulteress" (see Bruce 1995). Around the same time these cymothoids were being discovered, Constantine Samuel Rafinesque (a French polymath) founded the family Bopyridae.

In 1840, Henri Milne Edwards (Fig. 2.2d) completed the first review of Crustacea from all over the world, including the description of 30 new cymothoid species. Some years later, Danish authors, Jörgen Matthias Christian Schioedte (Fig. 2.2e) and Frederik Vilhelm August Meinert (Fig. 2.2f), produced a series of outstanding monographs from 1879 to 1884 comprehensively revising (on a global scale) the families Aegidae and Cymothoidae (Schioedte and Meinert 1879, 1881, 1883, 1884). These detailed monographs became the foundation for future studies of these parasitic isopods and described an impressive 63 new species (49 of which are still valid).

The "first lady of isopods", Harriet Richardson (Searle) (Fig. 2.2g), was an American carcinologist. In her 22 years of publishing on isopods, she described 58 new genera and 268 new species of isopods, with her best-known work being *A monograph on the isopods of North America* (Richardson 1905). A number of these isopods were from the parasitic families Bopyridae (23 species) and Cymothoidae (22 species). At 40 years old (1914), Richardson gave birth to a handicapped son and spent much of her time thereafter caring for him and only occasionally publishing papers, with her last paper being published in 1926 (Damkaer 2002).

Around the same time, other isopod taxonomists were describing species from the Indo-West Pacific region. Reverend Thomas Roscoe Rede Stebbing (Fig. 2.2h) was a British zoologist, who focused on Crustacea (specifically isopods and amphipods) and described 77 new species of isopods in his 1873–1912 publications. His work included many new genera and reports of these crustaceans from little studied areas, particularly in the Indian Ocean, such as India and South Africa (Stebbing 1910a, b). Edward John Miers (Fig. 2.2i), also a British zoologist and the crustacean curator at the Natural History Museum in London, described 40 new isopod species from 1875 to 1905 mainly from the Indo-Pacific region including Malaysia, Australia, New Zealand and South America (Miers 1876, 1877, 1880).

Another noteworthy contributor was the French naturalist, Théodore André Monod (Fig. 2.3a), a genuine polymath with many different interests. He was also a leading expert on the Sahara and published more than 1200 publications in his 98 years. Of those publications, more than 50 were on isopods. Taking every opportunity to explore and conduct research around the world, he described 5 new genera and 60 new species of isopods and documented isopods from around the world including Australia, France and frequently from various parts of Africa. Monod made major contributions to some families, notably his monumental monograph of the Gnathiidae (Monod 1926) and his influential review of the Cirolanidae (Monod 1930), as well as the first reports on fish parasitic Isopoda from areas such as Vietnam (Monod 1934) and western Africa (Monod 1924, 1931).

The US carcinologist, Thomas Elliot Bowman (Fig. 2.1g), published 163 scientific papers and described 65 new isopod species. His primary interest lay with the isopods, but he also published several papers on copepods. He had a lively personality and a passion for his work that did not stop even after his retirement. Most of Bowman's publications were taxonomic, but he also worked on the ecology and biology of these crustaceans.

Perhaps the greatest contributor to isopod taxonomy in recent decades is the Australian taxonomist, Niel Lucien Bruce (Fig. 2.3b). Bruce has described or redescribed more than 600 species of isopod (381 new species, 56 new genera), covering many different environments and families, in particular the Aegidae, Cirolanidae, Corallanidae, Cymothoidae and Sphaeromatidae. He has more than 180 scientific papers, 6 monographs and 4 edited books and is one of the leading isopod experts on both the free-living and parasitic species. Although most of Bruce's work has focused on Australian species, many of his publications have revised generic concepts and nomenclature and have resolved some of the many problematic taxonomic issues within these families (Bruce 1986b, 1987a, b, c, 1990).

Within the suborder Cymothoida there are two distinct parasitic groups—those parasitising fishes and those parasitising crustaceans. The group parasitising crustaceans (infraorder Epicaridea) include the Bopyroidea and Cryptoniscoidea (see

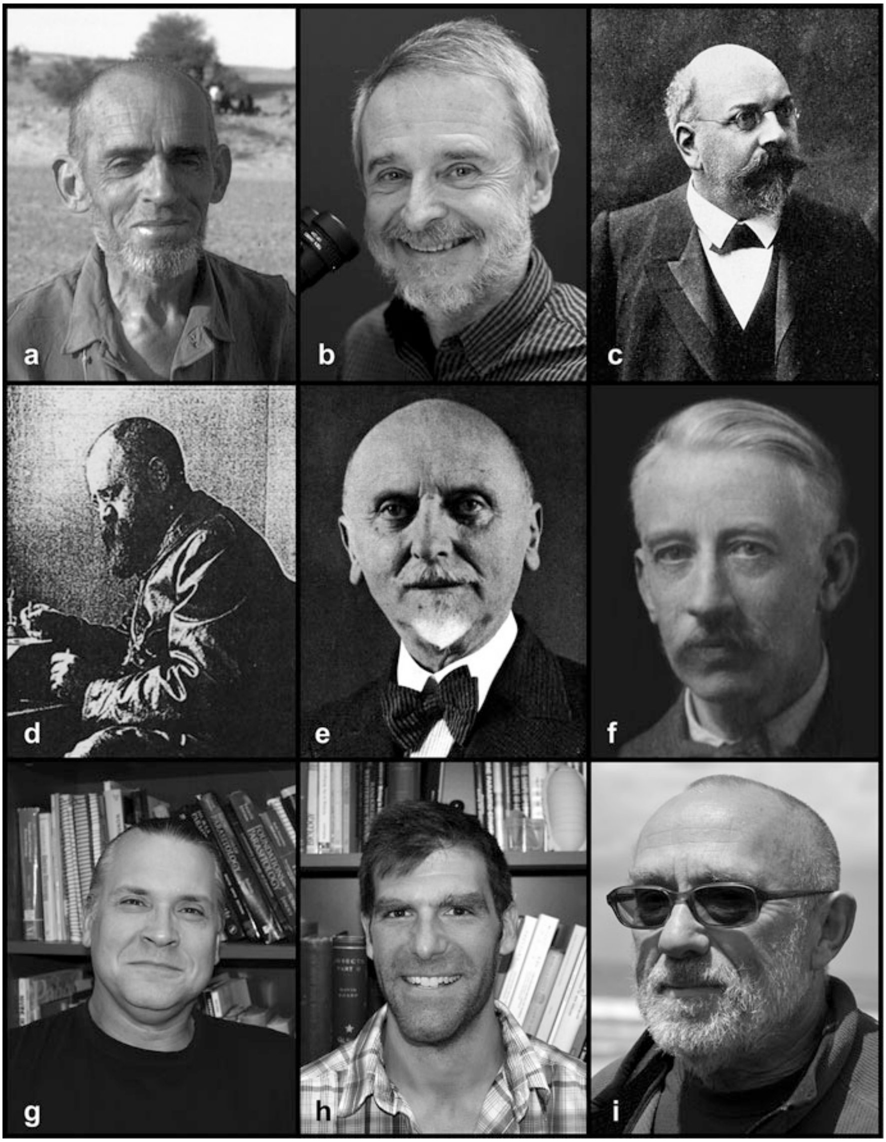

Fig. 2.3 (**a**) Théodore André Monod, (**b**) Niel Lucien Bruce, (**c**) Alfred Mathieu Giard, (**d**) Jules Bonnier, (**e**) Hugo Frederik Nierstrasz, (**f**) Geraldo Abraham Brender à Brandis, (**g**) Christopher B. Boyko, (**h**) Jason D. Williams, (**i**) John C. Markham. Images (**a**) and (**c**) © Wikipedia Commons public domain; image (**d**) from sm-wimereux.univ-lille1.fr/accueil/historique/index.php; image (**e**) from Jordan (1938); image (**f**) © Streekarchief Gooi en Vechtstreek/gooienvechthistorisch.nl

Table 2.1). The Bopyroidea has three families: Bopyridae, Entoniscidae and Ionidae. The Cryptoniscoidea has nine accepted families: Asconiscidae, Cabiropidae, Crinoniscidae, Cryptoniscidae, Cyproniscidae, Dajidae, Entophilidae, Hemioniscidae and Podasconidae. *Proteolepas bivincta* Darwin, 1854 (from the family Crinoniscidae), was originally thought to be a parasitic barnacle; however, in 1993 William Anderson Newman noted how Darwin had misidentified the isopod's broken attachment limbs as first antennae of the barnacle cyprid.

The second group are the isopods that are temporarily or permanently parasitic on fish. These isopods belong to the superfamily Cymothooidea and include six partly or wholly parasitic families (as well as "micropredators"). They are the families Anuropidae, Aegidae, Barybrotidae, Corallanidae, Cymothoidae, Gnathiidae and Tridentellidae (see Table 2.1).

Dajidae parasitise other crustaceans, usually decapods (Bush et al. 2001; Rohde 2005), and the Entoniscidae are internal parasites that live in the haemocoel of their crab hosts. Some members of the superfamily Cryptoniscoidea are cryptic parasites and hyperparasites of other crustaceans. Cyproniscids and cabiropsids are parasitic on free-living isopods and Podasconidae are parasites of amphipods. In the Cryptoniscidae, genera such as *Danalia* Giard, 1887, and *Liriopsis* Schultze in Müller, 1859, are hyperparasitic on rhizocephalan cirripedes, which parasitise crustaceans such as the false king crab (Peresan and Roccatagliata 2005). Limited information is available on the monogeneric family Tridentellidae, but the mouthparts appear to be well adapted for rasping and piercing into fish host tissues (Bruce 1984). Barybrotidae is a monotypic genus, with the only known species *Barybrotes indus* Schioedte & Meinert, 1879 recorded from the gills of the devil ray *Mobula mobular* (Bonnaterre, 1788) (previously *Mobula diabolus*) (see Moreira and Sadowsky 1978). The Aegidae and Corallanidae are temporary parasites as they often leave the host after their blood meal, but more frequently, these isopods have been classed as free-living micropredators (Brusca 1983; Bruce 1993, 2004, 2009). The three more well-known groups are discussed below in more detail.

2.3.1 Bopyridae

Members of this family are parasitic on other crustaceans, especially crabs and shrimps. To date, there are 10 subfamilies, 167 genera, 607 species and 12 subspecies. These parasitic isopods are usually found within the branchial chamber of their hosts causing a noticeable protuberance, but there are several species that attach to the host's abdomen. The first described bopyrid was *Bopyrus squillarum* Latreille, 1802 from the Baltic prawn. This species inhabits the gill chamber of *Palaemon adspersus* Rathke, 1837.

French zoologists, Alfred Mathieu Giard (Fig. 2.3c) and Jules Bonnier (Fig. 2.3d), described 70 epicaridean isopod species together (38 of which were bopyrids). Bonnier proceeded to describe another 31 bopyrid species thereafter, although only six remain valid today. Bonnier started his zoological career after meeting Giard and was his student for nearly 30 years. In his 1900 review of the bopyrids, Bonnier named a species after Giard, *Bopyrina giardi* Bonnier, 1900, but it has since been synonymised with *Bopyrina ocellata* (Czerniavsky, 1868).

Furthermore, the infectious protozoan parasite genus *Giardia* Künstler, 1882, was named in honour of Giard for providing the first description of *Giardia lamblia* (Lambl, 1859) Kofoid & Christiansen, 1915. Sadly, both men passed away in 1908, Giard on his 62nd birthday and Bonnier at 49 years of age from a brain disease he contracted while on a trip in 1904.

Another duo that published 36 genera and 146 nominal isopod species together are Hugo Frederik Nierstrasz (Fig. 2.3e) and Geraldo Abraham Brender à Brandis (90 still valid) (Fig. 2.3f). Of these, 23 genera and 80 species are still valid bopyrid taxa. Nierstrasz was a Dutch zoologist who summarised the isopod knowledge at that time in his contributions to the *Siboga* Expedition (1923–1941), which took place from March 1899 to February 1900 in the Indonesian Archipelago (Nierstrasz and Brender à Brandis 1923; Nierstrasz 1931). Brender à Brandis was a Dutch artist, and it can reasonably be inferred that he was the illustrator for the bopyrid drawings in these joint publications.

Christopher B. Boyko (Fig. 2.3g) (with more than 100 publications) is one of the world leading bopyrid specialists publishing in the present era. Boyko and Jason D. Williams (Fig. 2.3h) (both American researchers) have made valuable contributions on these isopods including a review of the global diversity of the epicarideans (Williams and Boyko 2012). This publication provided a thorough overview of the bopyrids and cryptoniscoids including phylogeny and historic patterns, human-related issues, feeding biology and impacts on the hosts as well as biogeography and biodiversity of these isopods. Furthermore, these authors have detailed the methods for detection, collection and preservation of epicaridean parasitic isopods (Boyko and Williams 2016) and presented a new classification based on a molecular phylogenetic analysis (Boyko et al. 2013).

John C. Markham (Fig. 2.3i) has made substantial contributions to bopyrid knowledge describing 29 genera and 95 species of bopyrids. Other noteworthy publications include the evolution and zoogeography of the bopyrids (Markham 1986), revision of bopyrids from the north-western Atlantic Ocean (Markham 1988), Thailand (Markham 1985) as well as from Hong Kong and southern China (Markham 1982). Jianmei An (Fig. 2.4a) has also provided many valuable contributions on bopyrids. Many of these papers include reviews of the different genera, especially from China, as well as the description of new species (36 species) (An et al. 2009, 2015a, b).

2.3.2 Cymothoidae

Cymothoid isopods are obligate parasites of both marine and freshwater fishes that show high variability and consequently have often been misidentified (Smit et al. 2014). These isopods are ectoparasites, found in all oceans but with the greatest diversity in tropical and subtropical waters, feeding on fish host blood or haemolymph and possibly muscle tissue and mucus. There are 369 known cymothoid species in 43 genera. As previously mentioned, the first described parasitic isopods were *Aega psora*, *Anilocra physodes*, *Cymothoa oestrum* and *C. scopulorum*, of which the last three species are valid

Fig. 2.4 (**a**) Jianmei An, (**b**) Vernon Everett Thatcher (on the right), (**c**) Jean-Paul Trilles, (**d**) Richard C. Brusca, (**e**) Ernest H. Williams Jr, (**f**) Lucy Bunkley-Williams, (**g**) Nico J. Smit, (**h**) Kerry A. Hadfield, (**i**) Gary Poore. Image (**b**) from Boeger (2011)

cymothoid isopods. The first illustrations of a cymothoid, however, appeared many years later (Desmarest 1825).

Cymothoid research has often been confined to a particular geographical region where a practicing taxonomist was based or where research vessels were sampled.

An example is Vernon Everett Thatcher (Fig. 2.4b), who published on cymothoids from a previously neglected area, South America freshwaters (Thatcher 1991, 2000). Thatcher described 15 new species from the region and produced papers on the mouthpart and pleopod morphology, comparing the morphology of the marine and freshwater cymothoids in some instances (Thatcher 1995, 1997).

Jean-Paul Trilles (Fig. 2.4c), a French parasitologist, has made notable contributions to the Cymothoidae, including many redescriptions and comprehensive taxonomic synonymies. One of the most significant publications on cymothoids is his *Prodromus*, an extensive catalogue of the cymothoids that provided an invaluable resource for subsequent workers on this family (Trilles 1994). Several other publications were on museum holdings as well as the description of new cymothoid species (see Trilles 1972, 1977, 2008).

The invertebrate zoologist, Richard C. Brusca (Fig. 2.4d), published the first modern review and influential monograph of the Cymothoidae of the Eastern Pacific (Brusca 1981). This monograph included information on cymothoid morphology, taxonomy, history, zoogeography, phylogeny and the first hypothesis of the evolution of these parasites. It was published in the cladistic phylogeny era of Crustacea, and provided the foundation for all future work in this field, where it is still the point of comparison for all modern phylogenies. Brusca has published over 160 articles and 13 books including the largest-selling text on invertebrate zoology *Invertebrates*, co-authored with his brother Gary Brusca. Some of his other noteworthy works include field guides of isopods from Costa Rica (Brusca and Iverson 1985) and the phylogenetic analysis and classification of isopods (Brusca and Wilson 1991).

Ernest (Bert) H. Williams Jr (Fig. 2.4e) and Lucy Bunkley-Williams (Fig. 2.4f) (a husband and wife team from Puerto Rico) have made significant contributions to knowledge of the Cymothoidae from the Caribbean, Japan and Thailand. This couple described 27 new species, corrected many errors in literature, and provided several noteworthy ecological notes for these isopods (Williams et al. 1982; Williams and Bunkley Williams 1986, 2000; Bunkley-Williams and Williams 1998). Other contributors to the biodiversity and taxonomy of cymothoids include V. V. Avdeev (a Russian researcher) who described 15 cymothoid species, Pieter Bleeker (a Dutch medical doctor, ichthyologist and herpetologist) who described 13 species, and N. Krishna Pillai (an Indian carcinologist) who described nine cymothoid species.

Recently, Nico J. Smit (Fig. 2.4g), Niel L. Bruce (Fig. 2.3b) and Kerry A. Hadfield (Fig. 2.4h) reviewed the global diversity of the cymothoids (Smit et al. 2014). Within this review, they included historic, biogeographic, systematic, taxonomic, reproductive and ecological information for these isopods. These three authors have also completed a number of taxonomic revisions of several genera from southern Africa (Hadfield et al. 2010, 2013, 2014, 2015; Hadfield and Smit 2017), including the description of several new species. Trilles (1994) mentioned there was a lack of information from the Southern Hemisphere, and specifically South Africa and South America, and these papers aimed at addressing this knowledge gap. Furthermore, these authors produced a publication on revising poorly known type material to minimise potential future misidentifications within one of the more complicated genera, *Ceratothoa* Dana, 1852 (Hadfield et al. 2016).

2.3.3 Gnathiidae

Gnathiids differ from the other isopods in having only five functional pairs of legs, and only their larval stages are parasitic. The first recognisable drawing of a gnathiid was made by a Dutch zoologist, Slabber (1769), who drew a larval form and was uncertain as to which family the strange isopod belonged. The first adult male, *Gnathia maxillaris* (Montagu, 1804) (described as *Cancer maxillaris*), was described a few decades later by Montagu, who then went on to describe the first gnathiid larva found feeding on a fish host (Montagu 1804, 1813). Due to the unique appearance of this isopod, Leach (1814) established a new genus, *Gnathia* Leach, 1814. However, there was plenty of confusion regarding the appearance of three very different life forms (the adults, the swollen praniza larvae and the smaller zuphea larvae), which led researchers to believe that they were separate species (Risso 1816; Bate 1858). It was by accident that Hesse (1864) established the link between the different forms while keeping a praniza in water to sketch when it moulted into an adult. Forty years later, the first life cycle of a gnathiid, *Gnathia maxillaris*, was described by Smith (1904). This was the first account of the different life stages and development of these isopods, and Smith was able to observe that the adult stages do not feed.

There are currently 226 gnathiid species, in 12 different genera. Australian researchers, Brian Cohen and Gary Poore (Fig. 2.4i), described 30 of these species as part of a thorough review of gnathiid phylogeny and biogeography (Cohen and Poore 1994). Ten years later, Nico Smit (Fig. 2.4g) and Angela Davies-Russell (Fig. 2.5a) assembled a complete review of these gnathiid isopods summarising all of the morphology, life stages, behaviour and pathology up to this point (Smit and Davies 2004). These two authors also confirmed that gnathiids can act as vectors of fish blood parasites such as *Haemogregarina bigemina* Laveran & Mesnil, 1901 (see Chap. 7; Davies and Smit 2001).

Brian Kensley (Fig. 2.5b, g), posthumously, along with Marilyn Schotte (Fig. 2.5g) and Gary Poore (Figs. 2.4i and 2.5g), published descriptions of 12 new gnathiid species from the Indian Ocean (Kensley et al. 2009). Kensley (a zoologist born in South Africa) was a researcher at the Smithsonian National Museum of Natural History, specialising in systematics of isopods (and decapods), and has at least 20 species named after him. He published more than 150 crustacean-related articles in his lifetime as well as several field guides, including a guide to the Caribbean (Kensley and Schotte 1989) and South African (Kensley 1978) marine isopods and had many collaborations with other isopodologists (Fig. 2.5g).

Recent research on gnathiids from Japan has been published by Yuzo Ota and Katsuhiko Tanaka (from Japan), and Jörundur Svavarsson (from Iceland) worked on gnathiid ecology and taxonomy as well as deep-sea isopods. Several other ecological studies have also been completed on these small parasitic isopods. Their role in cleaning symbiosis has been studied by Lexa Grutter (Australia) (see Grutter 1996, 2003) as well as molecular studies to link juveniles to their adult counterparts and so identify the species (Grutter et al. 2000). Most of the current publications on gnathiid

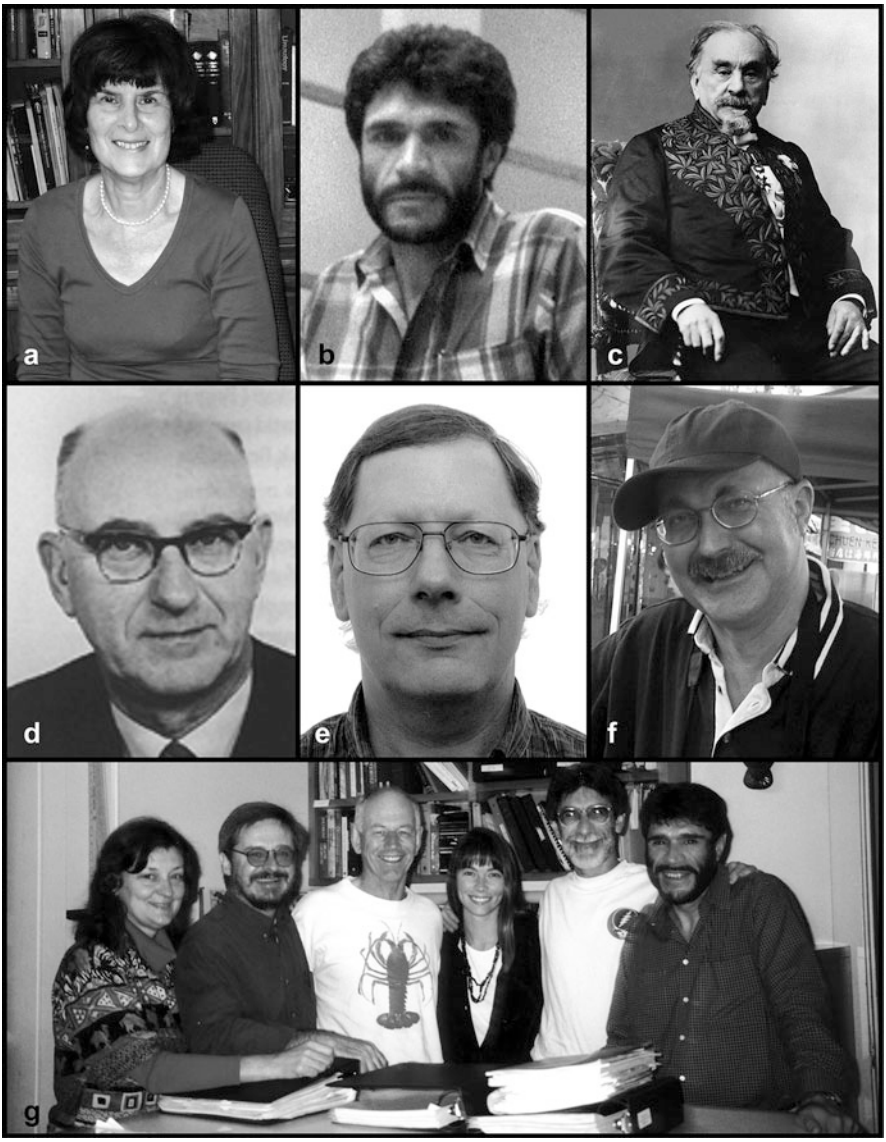

Fig. 2.5 (**a**) Angela Davies-Russell, (**b**) Brian Kensley, (**c**) Henry de Lacaze-Duthiers, (**d**) Hans Olof Brattström, (**e**) Mark Joseph Grygier, (**f**) Jens Thorvald Høeg, (**g**) isopod experts: Marilyn Schotte, Niel Bruce, Gary Poore, Wendy Moore (Brusca), Richard (Rick) Brusca and Brian Kensley (taken in 1997). Image (**b**) from Schotte (2005); image (**c**) © Wikipedia Commons public domain; image (**d**) obtained from Hans G. Hansson at www.bemon.loven.gu.se/petymol.b.html; image (**g**) © Richard Brusca

ecology and behaviour (especially on coral reefs) are being investigated by Paul Sikkel (from Arkansas State University, USA) and colleagues (see Chap. 10). This research team is focusing on the role of these parasites in the marine food webs, their habitat associations, and their effect on the host fishes.

2.4 Ascothoracida

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Subclass Thecostraca Gruvel, 1905
Infraclass Ascothoracida Lacaze-Duthiers, 1880

Ascothoracids are marine ecto- and meso-parasites, occurring in shallow intertidal habitats as well as the deep sea. They are diverse in morphology, biology and host range, and both the juvenile and adults are parasitic on echinoderms (excluding regular urchins and sea cucumbers) and cnidarians (e.g. corals, gorgonians, zoanthids) (Grygier and Høeg 2005). Ascothoracida is one of the three infraclasses of Thecostraca and Kentrogonida (see Table 2.1) and has approximately 107 known species in 6 families and 23 genera (Ahyong et al. 2011).

The French biologist, Henry de Lacaze-Duthiers (Fig. 2.5c) (who was an assistant to Henri Milne Edwards), described the first ascothoracid species as *Laura gerardiae* Lacaze-Duthiers, 1865. This species parasitises the gold coral, *Savalia savaglia* (Bertoloni, 1819), from Tunisia and Algeria (Lacaze-Duthiers 1865, 1883).

Although the first described, *Laura gerardiae* is not the most studied ascothoracid species. *Ulophysema oeresundense* Brattström, 1936, described by the Swedish zoologist Hans Olof Brattström (Fig. 2.5d), is one of the best researched ascothoracids. Brattström, who founded the journal *Sarsia* (named after the Norwegian natural scientists M. Sars and G.O. Sars), became an expert in ascothoracids following his PhD thesis research on echinoderms. He described the genus *Ulophysema* Brattström, 1936, and named five ascothoracid species. Furthermore, Brattström provided detailed reviews of the ecology, life cycle, morphology and larval development of *U. oeresundense* (Brattström 1936, 1947, 1948a, b). Shortly thereafter, Melander (1950) completed studies on the chromosomes of *U. oeresundense*, and the species was used in numerous reviews and comparisons with other species. As this parasite is found enclosed in different organs of irregular sea urchins (most often in the genital glands or perivisceral cavity), the ultrastructure of its integument was also studied by Bresciani and Jespersen (1985).

In 1976, Vladimir Lvovich Wagin produced a valuable monograph on the Ascothoracida (in Russian), including documentation of all the information known on these parasites up to that point (Wagin 1976). Most of the information gathered was from Russian articles that were largely inaccessible to the western world at that time. Only nine genera were listed in the infraclass in the 1970s; thereafter, research on the group was focused on taxonomy, with majority of the new genera and species being described in the 1980s. However, since 2000, only one new ascothoracid species has been recorded, *Gorgonolaureus helenae* Kolbasov, 2004.

Most of the earlier studies on ascothoracids were primarily taxonomic and morphologically based; however, information regarding their ecology and life stages was also available in several publications. The adult stages of these parasites are striking and have distinguishing characteristics for easier species identification; however, the larval forms often need to be reared into adults in a laboratory before they can be identified. Studies on the larval stages became important, especially with the use of a scanning electron microscope (SEM) as utilised by Itô and Grygier (1990) on *Baccalaureus falsiramu*s (Itô and Grygier 1990). Later Grygier (1992) reported on rearing larvae and their development, and most recently, Kolbasov et al. (2008a) thoroughly studied the external morphology of the first and second a-cyprid larvae.

In the last few years, research on these ascothoracid parasites has slowed down; however, there are still key players continuing in this field. Mark Joseph Grygier (Fig. 2.5e), an American based in Japan, is currently one of the world's leading experts on Ascothoracida and one of the most prolific authors on this group. Grygier has described 10 new ascothoracid genera as well as 51 new species (almost half of the known species in the infraclass). Grygier (1981) reviewed the sperm of *Dendrogaster* Knipovich, 1890, and determined that it was the most primitive sperm discovered in Crustacea (Grygier 1981). Two years later, he separated the crinoid-infecting *Waginella* Grygier, 1983, from *Synagoga* Norman, 1888, which disrupted the subordinal classification suggested by Wagin, which was based on the phylum of the host (Grygier 1983). The classification of the Ascothoracida was then updated by Grygier (1987), who divided the group into two orders and six families. A few years later Grygier (1996) completed a rare demographic study on a deep-sea parasite *Parascothorax synagogoides* Wagin, 1964, parasitising the brittlestar *Ophiophthalmus normani* (Lyman, 1879) (see Grygier 1991), and in 1996, he published a comprehensive account of the Ascothoracida (Grygier 1996).

Current research on the Ascothoracida focuses on the phylogenetic relationships within the group and in relation to the other Thecostraca taxa. Jens Thorvald Høeg (Fig. 2.5f), a professor at the University of Copenhagen, and colleagues recently studied the evolution of parasitic Thecostraca and supported Ascothoracida as a monophyletic taxon with high confidence. The taxon sampling in this infraclass is still limited according to Pérez-Losada et al. (2009) and the classification could once again change after more research. Other studies have included the evolution of morphology and ecology of the Thecostraca (Høeg et al. 2009) and support that Ascothoracida and Cirripedia are the sister groups to Facetotecta (Pérez-Losada et al. 2009).

2.5 Cirripedia

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Subclass Thecostraca Gruvel, 1905
Infraclass Cirripedia Burmeister, 1834

Barnacles are amongst the most economically important marine crustaceans, renowned for fouling ship hulls and marine structures. They are sessile as adults, with motile larval stages, and in intertidal rocky shores form the recognisable "barnacle zone". Barnacles are known to be both parasites and commensals (occurring in sponges as well as on corals, whales, etc.) and can act as castrating parasites of crabs (family Sacculinidae).

2.5.1 Acrothoracica

This superorder of barnacles is only partially parasitic. These tiny barnacles, called burrowing barnacles, burrow into calcareous substrates such as mollusc and thoracican barnacle shells. Within the family Trypetesidae, there are two genera, *Tomlinsonia* Turquier, 1985 (with two known species), and *Trypetesa* Norman, 1903 (five known species), which are found exclusively inhabiting the shells of hermit crabs (Williams et al. 2011).

Trypetesa lampas (Hancock, 1849) was the first burrowing barnacle described, with Hancock discovering it in the shells of gastropods that were inhabited by hermit crabs (Hancock 1849). Charles Darwin (Fig. 2.6a) noticed it was very similar to *Cryptophialus* Darwin, 1854 but placed into *Alcippe* Hancock, 1849 (now *Trypetesa* Norman, 1903) (see Darwin 1854). In 1872, Noll placed both *Alcippe* and *Cryptophialus* into Darwin's order Abdominalia. In 1905, Gruvel realised that the cirri on the terminal body segments thought to be abdominal appendages (hence the order's name) was in fact from the thorax, so the order was changed to Acrothoracica. Around the same time, Norman (1903) changed the genus name from *Alcippe* to *Trypetesa*, as the former name was preoccupied (homonym) by birds in the family Pellorneidae.

Jack Tomlinson (Fig. 2.6b), who was recognised as one of the world authorities of this group, revised the burrowing barnacles known at that time, including information on all of the different systems, taxonomy and ecology (Tomlinson 1969, 1987). More recently there have been many studies on the larvae as well as phylogeny and systematics of this group by Gregory Kolbasov (Fig. 2.6c) and colleagues (Kolbasov 2002, 2009; Kolbasov et al. 2014), as well as the phylogenetic relationships of the different barnacle orders (Lin et al. 2016). However, the data on the ecology of these barnacles, especially on the Trypetesidae, are scanty.

In 2011, the first publication of egg predation by a burrowing barnacle was recorded (Williams et al. 2011). *Trypetesa lampas*, removed from ovigerous female hosts, were found to contain hermit crab eggs, chorions, as well as yolk in their gut. There is still uncertainty surrounding how these barnacles feed, but this research documented how they can have significant negative effects on hermit crab reproduction. Other studies have showed blue-green algae-like particles in the gut of *Trypetesa lampas* (see Kamens 1981), and it may be that barnacles in male hermit crabs filter feed on particles from the water, whereas barnacles in females feed on the hermit crab eggs (Williams et al. 2011). Murphy and Williams (2013) verified this

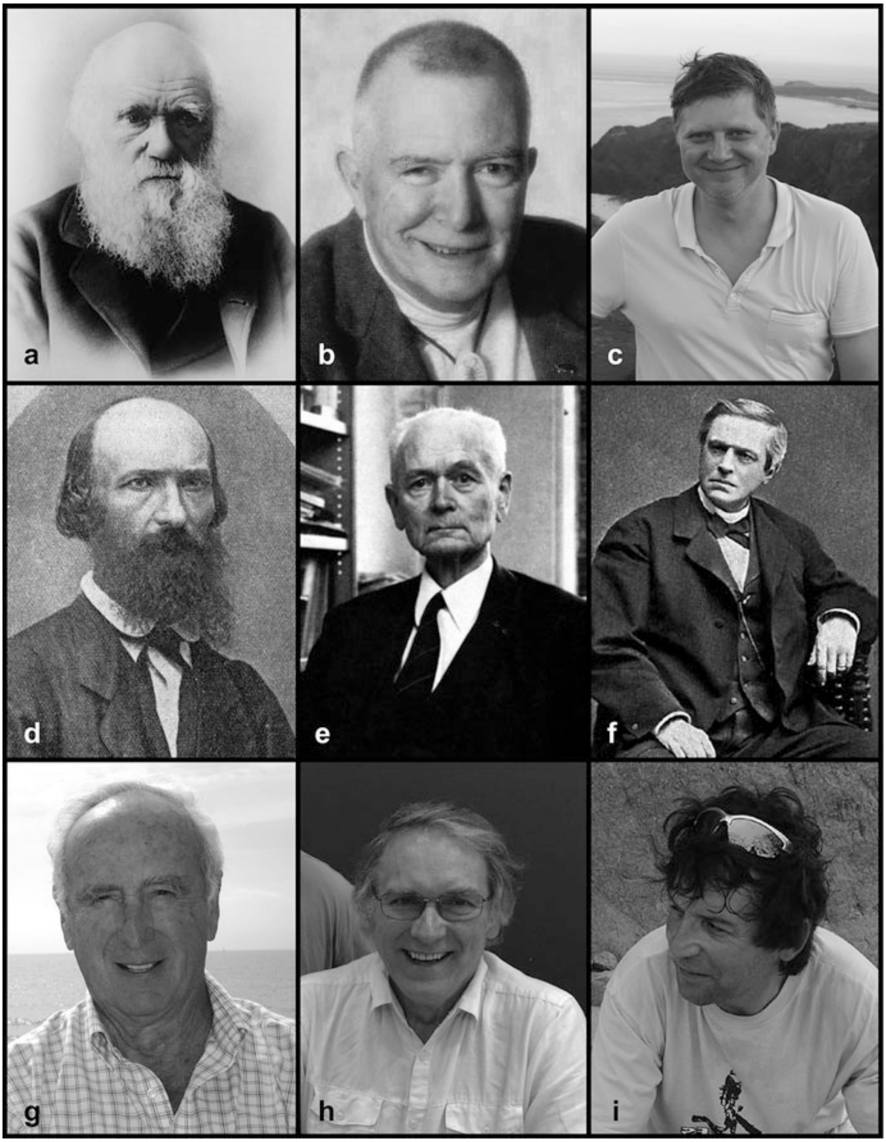

Fig. 2.6 (**a**) Charles Darwin, (**b**) Jack T. Tomlinson, (**c**) Gregory Kolbasov, (**d**) Johann Friedrich Theodor (Fritz) Müller, (**e**) Hilbrand Boschma, (**f**) Sven Ludvig Lovén, (**g**) William Anderson Newman, (**h**) Geoffrey Allan Boxshall, (**i**) Rony Huys. Images (**a**), (**d**), (**e**) and (**f**) © Wikipedia Commons public domain; image (**b**) from public obituary at www.oakdaleleader.com/obituaries/jack-tomlinson

study and suggested that the more accurate term for these barnacles may be "transient parasites" as they can be harmful in some cases but cause no harmful impact in other cases. Larsen et al. (2016) added that the barnacles do not rely on the egg predation to any substantial degree and found much of the data they collected on prevalence, load, reproductive cycles, and host relationships differed from previous studies. This highlighted the fact that there is still a lot of work to be done on these barnacles before we fully understand their ecology.

2.5.2 *Rhizocephala*

This order contains the obligate parasites and was first discovered by Cavolini (1787) but only grouped together as Rhizocephala by the German zoologist, Johann Friedrich Theodor (Fritz) Müller (Fig. 2.6d) in 1862 (Müller 1862). They are endoparasites of other crustaceans, especially decapods. Currently there are 2 orders, 11 families, 41 genera and 288 species known. The adult females have lost most of the traits usually associated with Crustacea and are also known to influence the morphology and biology of their hosts which sets them apart from other groups. These adult female parasitic barnacles consist of an "externa" (an external sac-like body for reproduction) and an "interna" (a root-like body inside the host for nutrient uptake), with the male inside the female externa, joined by a small stalk (Høeg 1995; Høeg and Lützen 1995). Many rhizocephalans are known to cause parasitic sterilisation or castration of their crustacean hosts. Depending on the species, these parasites can lower reproductive outputs, cause eggs to die within a few days or completely inhibit gonad processes required for reproduction (Høeg 1995). Along with the degeneration of the gonads, rhizocephalans can also cause feminisation of male hosts. This may include testes converting to ovaries, changes in the overall shape and size of the hosts and possibly even changing the behaviour of the host (Høeg 1995).

Rhizocephalans are divided into two orders: Akentrogonida and Kentrogonida (see Table 2.1). Whereas all kentrogonids exhibit similar characteristics (including the presence of the specialised female post-settlement stage, the kentrogon, as well as the equivalent male stage, the trichogon), all of the akentrogonids do not have similar characteristics other than the absence of the kentrogon (Walker 2001). Within the Kentrogonida is the family Sacculinidae, which is one of the more renowned groups of parasites due to their ability to cause parasitic sterilisation in crabs. The genus *Sacculina* Thompson, 1836, holds the majority of the rhizocephalan species with approximately 129 known species. The first described species was *Sacculina carcini* Thompson, 1836, making it one of the most studied barnacle parasites.

Hilbrand Boschma (Fig. 2.6e), a former director of the Rijksmuseum van Natuurlijke Historie (Naturalis), Leiden, Netherlands, had a particular interest in rhizocephalans. Boschma (and colleagues) described half of the currently recognised rhizocephalan species (2 families, 8 genera and 144 species). Most of these species are in the genus *Sacculina*, with 98 of the 128 known species named by Boschma. Some of his more substantial publications were on rhizocephalans from the North

Atlantic (Boschma 1928), from the British Museum collections (Boschma 1933), as well as notes and new species from Sacculinidae (Boschma 1937, 1950, 1955).

Jens Thorvald Høeg (Fig. 2.5f) has also added numerous contributions on the ecology of these parasites. In 1991, Høeg reviewed the sexual system of the rhizocephalans and a year later added ultrastructure information regarding their morphology (Høeg 1992). He also completed taxonomic and phylogenetic studies with colleagues round the same time (Høeg and Rybakov 1992; Høeg and Lützen 1993), as well as revised the biology and life cycle of these barnacles (Høeg 1995).

Other contributors to this group include Olga Korn and colleagues, from the Russian Academy of Sciences, Moscow, who have published several papers on the larval development and ecology of the rhizocephalans (Kas'yanov et al. 1997; Korn et al. 2000; Kashenko et al. 2002) as well as reproductive studies on several species (Korn 1985, 1989; Korn et al. 2004). Bo Øksnebjerg, in his review of the Mediterranean and Black Sea rhizocephalans, provided a thorough summary of available information on the biology, ecology, biogeography and taxonomy of these parasites, including information for each of the 25 species known from the region at that time (Øksnebjerg 2000). Henrik Glenner, from the University of Bergen, has published many papers on barnacles and related crustacean groups too, most relating to the evolution and phylogenetic relationships of the parasitic barnacles (Glenner and Hebsgaard 2006; Glenner et al. 2010).

As rhizocephalans affect the reproductive systems of their hosts, it was proposed that these parasites could possibly aid in biological control of invasive host species. Murphy and Goggin (2000) analysed the genetic discrimination of sacculinid parasites to determine if they could control invasive European green crabs that have had a negative effect on the softshell clam fisheries in North America. Unfortunately, the parasite is not host specific, and it could spread if it were introduced as a control agent (Murphy and Goggin 2000). This was put to the test by Goddard et al. (2005). Four native North American crab species were infected with the European green crab's natural parasite, *Sacculina carcini* Thompson, 1836. Although the parasite preferred the green crab, there were still a significant number of native crabs infected (all without producing a reproductive sac) which would result in the loss of many indigenous species.

Using both molecular and morphological techniques in classifying these parasitic barnacles has recently resulted in some interesting findings. A new genus, *Polyascus* Glenner, Lützen & Takahashi, 2003, was described after analyses on ten *Sacculina* species showed three asexually reproducing species formed a monophyletic clade and failed to support a monophyletic *Sacculina* clade (Glenner et al. 2003). Furthermore, in a different study using both techniques again, three species of *Sacculina* were found on a single host in a single locality for the first time (Tsuchida et al. 2006). Recent information on the phylogeny (using morphological characters and molecular data), from Høeg and Glenner and colleagues, can be seen in Chap. 9.

2.5.3 Thoracica

Thoracican barnacles are what most people would recognise as a barnacle. They are acorn or stalked (goose-neck) barnacles, and almost 1000 species are known worldwide. Many are symbionts on corals and sponges, with others associated with molluscs, sea snakes, turtles, whales and crustaceans (Ross and Newman 1967). Whale and turtle barnacles, which live on the skin of several whale and turtle species, appear to be parasitic but do not absorb nutrients from the hosts themselves and are considered commensals (Frick et al. 2011). Only two genera were originally thought to be parasitic, namely, the monotypic genus *Anelasma* Darwin, 1851, comprising *Anelasma squalicola* (Lovén, 1844), and *Rhizolepas* Day, 1939 (with two species, *R. annelidicola* Day, 1939, and *R. gurjanovae* Zevina, 1968). However, after recent publications, more genera have been recognised as parasitic.

Anelasma squalicola parasitises deep-water lantern sharks of the family Etmopteridae (Long and Waggoner 1993). Although this species was described many decades ago, it has rarely been studied. It was first noted by Gunnerus (1763) on the velvet belly lantern shark, *Etmopterus spinax* (Linnaeus, 1758), but he did not name or adequately describe it. This paper was largely overlooked by researchers, and only a decade later did the Swedish marine zoologist Sven Ludvig Lovén (Fig. 2.6f) (1844) formally describe it as "*Alepas squalicola*". Shortly thereafter, Charles Darwin (Fig. 2.6a) realised in his monographic review of barnacles (Darwin 1851) that the species was in the wrong genus and assigned it to his new genus, *Anelasma*. Recently, the feeding strategy of this species was analysed to determine if the barnacle is purely parasitic or is still capable of using suspension feeding to obtain nutrition (Ommundsen et al. 2016). The authors concluded that the barnacle uses the host exclusively as a food source using a *de novo* evolved feeding mechanism. Other noteworthy publications on *A. squalicola* include the phylogenetic analysis of these barnacles (Rees et al. 2014), as well as studies that it causes retarded growth in the shark reproductive organs (Yano and Musick 2000).

The other thoracican barnacle genus, *Rhizolepas*, parasitises polychaetes. The first species of the genus was *R. annelidicola* originally described from South Africa by John Hemsworth Day on the scale-worm, *Laetmonice producta* Grube, 1876. It does not have an open mouth or anus, oral appendages or digestive diverticula and undoubtedly obtains its food from the host via its extensive root system (Day 1939).

In 1969, Arnold Ross and William Anderson Newman (Fig. 2.6g) detailed information on a coral-eating barnacle, *Hoekia monticulariae* (Gray, 1831) from a then monotypic genus (with updated information in Ross and Newman 1995). This species was found to feed on coral tissue and differs from *Anelasma* and *Rhizolepas* in having modified the basic feeding mechanism rather than using a separate absorptive process (root system), making it the only sessile barnacle to be wholly parasitic (Ross and Newman 1969, 1995; Frick et al. 2011). There seems to be host specificity in this group of parasites as only *Hydnophora* Fischer von Waldheim, 1807, corals are infected (Ross and Newman 2000).

Another barnacle recently recognised as parasitic is *Koleolepas avis* (Hiro, 1931). This species, from the monotypic family Koleolepadidae, feeds actively on the sea anemone's tentacles (Yusa and Yamato 1999). It lives with these anemones (usually from the genus *Calliactis* Verrill, 1869) that are attached to the gastropod shells inhabited by hermit crabs (usually from the genus *Dardanus* Paulson, 1875) (Yusa et al. 2001; Hosie 2014).

The Microlepadidae are also known to live on diadematid echinoids (sea urchins). First described in 1907, *Microlepas diademae* Hoek, 1907, was studied after Paulus Peronius Cato Hoek observed a specimen on the end of a club-shaped spine on the hat-pin sea urchin in Indonesia (Hoek 1907). No other species were described until 1991 when Mark Grygier (Fig. 2.5e) and William Anderson Newman (Fig. 2.6g) added another genus and two new species to this group of parasites (Grygier and Newman 1991). Although their method of feeding has not been thoroughly studied, these barnacles cause detrimental effects to their host. Grignard and Jangoux (1994) concluded that the barnacles inhibited the growth of the urchin spine upon which it attaches. The thoracopods are not used for filter-feeding, and it is unlikely that they scavenge, so it is possible that much of their food is obtained from host tissue (Grygier and Newman 1991).

Lastly, the symbiotic genus *Octolasmis* Gray, 1825 is reported to cause damage to its decapod hosts (such as the blue crab *Callinectes sapidus* Rathbun, 1896). The first species, *Octolasmis warwicki* Gray, 1825, was described in 1825 by John Edward Gray. These parasites are found in large numbers and infect the gill chambers where they are attached to the lamellae of their host (Voris et al. 2000). Due to the high number of parasites, the gas exchange of the hosts can also be affected, with heavily infested hosts dying in extreme cases (Gannon and Wheatly 1992).

2.6 Tantulocarida

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Subclass Tantulocarida Boxshall & Lincoln, 1983

Tantulocaridans are micro-crustaceans that infest several marine crustacean hosts including amphipods, copepods, cumaceans, isopods, ostracods and tanaids as ectoparasitic larvae (Boxshall and Vader 1993). They are often found attached to the external surfaces of these hosts and can occur in all depths and temperatures in the marine waters. These minute parasites are the smallest of the parasitic Crustacea with size ranges between 80 and 400 μm (Kolbasov et al. 2008b).

Although originally discovered by Jules Bonnier (Fig. 2.3d) in 1903, these parasites were misidentified for many years (as copepods and isopods). In 1975, Becker described a new parasitic crustacean genus infesting copepods off the coast of Peru. This parasite, *Basipodella harpacticola* Becker, 1975, was incorrectly placed into the subclass Copepoda. In 1980, *Deoterthron* Bradford & Hewitt, 1980, was discovered parasitising ostracods in New Zealand (Bradford and Hewitt 1980). Bradford and Hewitt (1980) noticed that the two genera were closely related but considered them to belong with the Cirripedia rather than the Copepoda. Grygier (1983) noted that although he agreed these species belonged in the then "Maxillopoda" (now Oligostraca and Multicrustacea), they did not fit in either the Copepoda or Cirripedia. In resolving this uncertainty, Geoffrey Allan Boxshall (Fig. 2.6h) and Roger J. Lincoln (1983) proposed a new class, Tantulocarida, with the two genera *Basipodella* Becker, 1975 and *Deoterthron*, distinct but of similar rank to the Cirripedia and Copepoda.

Although this group of tiny parasites gained attention from 1975, Boxshall and Lincoln (1987) studied the description of a parasite named *Cumoniscus kruppi* Bonnier, 1903 (originally classified as an epicaridean isopod) which they then added to the Tantulocarida making it the first described tantulocaridan species. This species was unable to be classified to family level due to the lack of information on other life stages; however, Huys et al. (1993) rectified this after discovering a tantalus larva on a small male cumacean (the only species to be found on a cumacean up to that point).

Following the formation of this new class, many new tantulocaridan genera and species have been described. Many genera are monotypic, and this subclass has 5 families (see Table 2.1), 23 genera and 36 known species (Ahyong et al. 2011) although, due to their tiny size, many more are thought to occur but have not been discovered yet. Geoffrey Allan Boxshall (Fig. 2.6h) has made a noteworthy contribution to this tantulocaridan taxonomy, being involved in the description of three families, three genera and ten species.

Boxshall and Rony Huys (Fig. 2.6i) have published on various aspects of the dual life cycle (Boxshall and Lincoln 1987; Huys 1991; Huys et al. 1993), with Gregory Kolbasov (Fig. 2.6c) and colleagues adding information on the external morphology of the different life stages (Kolbasov et al. 2008b). Recent studies focus more on the phylogeny of the group and suggest that the Deoterthridae and Basipodellidae are possibly paraphyletic or polyphyletic which could change the number of families in the future (Kolbasov et al. 2008b; Savchenko and Kolbasov 2009; Petrunina et al. 2013). However, more studies are still required in all aspects of this group as there are still many unknowns (most likely due to their small size).

2.7 Copepoda

Superclass Multicrustacea Regier, Shultz, Zwick, Hussey, Ball, Wetzer, Martin & Cunningham, 2010
Subclass Copepoda Milne-Edwards, 1840

Copepods ("oar-footed") are one of the most abundant crustacean taxa, so named after the pair of swimming legs that move together like the oars on a sculling ship. They are known to be free-living, symbiotic (or "associates") and parasitic. Those that are parasitic are known to infect a large range of hosts (almost every phylum), from sponges and echinoderms to fish and mammals. Parasitic copepods are usually found on the external surfaces of their hosts, often sheltered in microhabitats such as the gills, nostrils, mantle cavities and genital folds, but there are some that are endoparasites, occurring in the muscles, digestive tracts and body cavities of their hosts (Huys and Boxshall 1991).

The Greek philosopher Aristotle (Fig. 2.7a) is considered to be the first person to take note of a copepod. In his book, *History of Animals* (350 BC), he mentions how the tuna and swordfish are infected with a parasite which was nicknamed the “gadfly”. It looked like a “grub” and was found next to the fins, resembling a scorpion in shape, and the size of a spider. Over the years, various researchers have pondered on what parasite is referred to in this text, possibly isopods or branchiurans; however, based on the descriptive traits given, it is believed to be a copepod (Damkaer 2002). Aristotle also mentioned “sea lice” found on the red mullet, devoid of blood and with a flat tail, and that most likely refers to branchiurans.

It was centuries later when the first drawing of a copepod appeared. Guillaume Rondelet (Fig. 2.7b) (a medical physician and zoologist) illustrated a fish parasite along with its tuna host, with the parasite attached near the pectoral fin (Rondelet 1554). The information confirmed Aristotle’s observations on the tuna, and two names were proposed: *Oestrus* (the marine “horsefly”) and *Asilus* (the marine “gadfly”). This particular species is believed to be the large and easily noticeable species, *Brachiella thynni* Cuvier, 1830 (see Kabata 1979).

In 1671, Paolo Silvio Boccone (Fig. 2.7c) noticed a copepod (which he referred to as a leech “sangsue”) from a swordfish that was “tormented by a flea”. It was apparently the size of a pea and attached firmly to the host (Boccone 1671). This most probably referred to the symbiotic barnacle known to occur on these hosts. Over the years, several other pedunculate barnacles have been recorded associated with copepods, but the copepods seem unaffected by the barnacles (Williams 1978; Benz 1984).

Although the free-living copepods were ranked with other crustaceans from an early stage, the parasitic forms appeared to be a lot more problematic. Many early scientists placed these parasites with molluscs or worms, and it was only in 1819 when Jacques Simon Amand Suriray recognised them as “caligids and neighbouring genera” and noticed the early development of young hatching from the egg “filaments” (Suriray 1819).

In what is undoubtedly the most extensive review of the early contributions to copepodology, *The Copepodologist’s Cabinet*, by David M. Damkaer (Fig. 2.7d), is a compilation of early copepod history and the 90 researchers whose work contributed to the advancement of copepod knowledge from 350 BC to 1832 (Damkaer 2002). It includes detailed information on the copepodologists, with historic portraits and illustrations, and a thorough history of discovery for the copepods. This was the first of a projected three volumes in the series, with the second detailing the research up to the nineteenth century (currently in production), with an overlap of the third publication which will include the Golden Age of Copepodology and conclude with research completed up to approximately 1950 (Damkaer 2002).

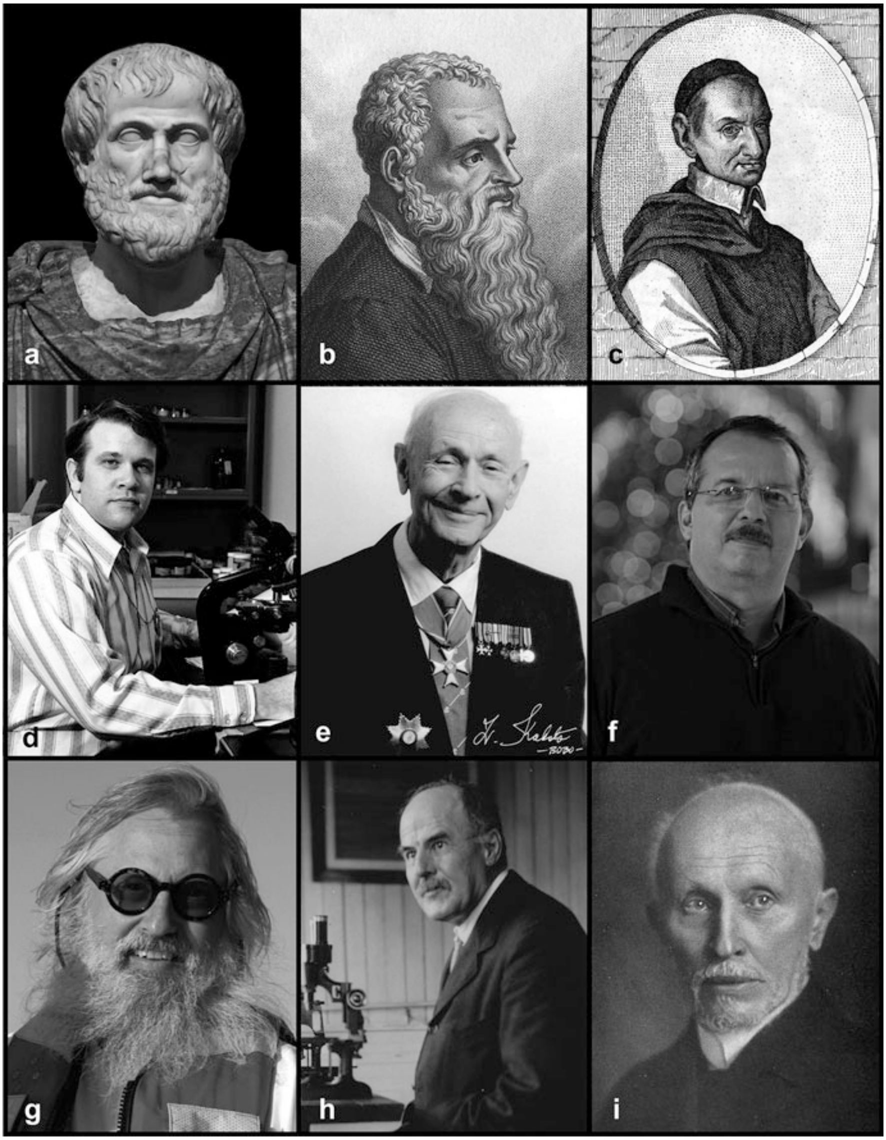

Fig. 2.7 (**a**) Aristotle [marble portrait bust, Roman copy (second century BC) of a Greek original (c. 330 BC), (**b**) Guillaume Rondelet, (**c**) Paolo Silvio Boccone, (**d**) David M Damkaer, (**e**) Zbigniew 'Bob' Kabata, (**f**) Eduardo Suárez-Morales, (**g**) George William Benz, (**h**) Charles Branch Wilson, (**i**) Johannes Thiele. Images (**a**), (**c**) and (**i**) © Wikipedia Commons public domain; image (**b**) from Mian et al. (2014); image (**e**) from Benz and Goater (2015); image (**g**) from Bullard (2016); image (**h**) from History of the Marine Biological Laboratory at https://history.archives.mbl.edu/archives/topics/people/gallery

Another significant contributor to copepod taxonomy was Zbigniew "Bob" Kabata (Fig. 2.7e). Kabata was a world-renowned fish parasitologist and one of the pioneers of research into fish parasitology and diseases. He was born in Poland, and his fascination with marine science began while working as a deckhand on a North Sea trawler out of Aberdeen. Kabata became internationally recognised as the world's copepod expert with 159 publications (including his books *Parasitic Copepoda of British Fishes* and *Parasites and Diseases of Fish Cultured in the Tropics*) (Kabata 1979, 1985) describing 20 new genera and more than 100 new species. His work on this group has been acknowledged by other researchers in this field through patronymy of 22 taxa, the most memorable of which must be the copepod genus and species *Bobkabata kabatabobbus* Hogans & Benz, 1990.

Currently, two of the most recognised names in copepodology are Geoffrey Allan Boxshall (Fig. 2.6h) and Rony Huys (Fig. 2.6i) (British and Belgian zoologists respectively) from the Natural History Museum, London. Both researchers have made noteworthy contributions to other parasitic crustacean groups, but their copepod publications have formed the foundation for many of the subsequent studies in this group and have established themselves as world leading authorities on copepods (Huys and Boxshall 1991; Boxshall and Halsey 2004; Huys 2009). Boxshall has been involved in the naming of 338 taxa (of which 317 are still valid). Those copepod taxa that are in use include a new infraclass, a new order, 16 families, a subfamily, 67 genera and 231 species. Likewise, Huys has named 334 taxa of which 308 are still valid, including a new infraclass, a new order, 16 families and 2 subfamilies, 128 genera, 2 subgenera, 157 species and a subspecies. In fact, both of these copepodologists have named genera after each other in honour of their extraordinary work in this group of crustaceans, namely, *Boxshallia* Huys, 1988, and *Huysia* Jaume, Boxshall & Iliffe, 1998.

2.7.1 Cyclopoida

Cyclopoids have an abdomen that is narrower than the thorax, and the first antenna is of intermediate length (only half the length of the body). The first two cyclopoids were described by Carl Linnaeus (Fig. 2.1a), namely, *Cyclops quadricornis quadricornis* (Linnaeus, 1758) and *Lernaea cyprinacea* Linnaeus, 1758. *Cyclops* Müller, 1785, is one of the most common freshwater copepod genera with approximately 200 valid species. It belongs to the family Cyclopidae, which is the largest cyclopoid family with over 1100 valid species. Members of this family are predominantly free-living; however, several species are intermediate hosts for numerous pathogenic human and fish parasites such as Guinea worm (*Dracunculus medinensis* (Linnaeus, 1758)), as well as cestodes (tapeworms) and nematodes (round worms) (Piasecki et al. 2004). Recently, *Eucyclops bathanalicola* Boxshall & Strong, 2006 was described from Lake Tanganyika in a rare occurrence of a freshwater copepod parasitic on an invertebrate host (mantle cavity of *Bathanalia straeleni* Leloup, 1953). This association is also noteworthy as it also represents a unique account of a parasite in what is primarily a free-living family (Boxshall and Strong 2006).

The second cyclopoid species discovered by Linnaeus belongs to the genus *Lernaea* Linnaeus, 1758, a widely known genus of freshwater fish parasites, commonly referred to as anchor worms. *Lernaea cyprinacea* was originally described from Europe in 1745 under a trinomial name but was then redescribed by Linnaeus in 1758 (see Kabata 1979). Anchor worms burrow into the skin of its host fish and can cause a disease called lernaeosis where haemorrhagic ulcers occur at the attachment site. Death of the host can occur due to secondary infections and severe bleeding (Khalifa and Post 1976; Kabata 1985). This species has been recorded worldwide and is thought to have been spread through the movement of aquarium species (Innal and Oldewage 2012). The family Lernaeidae is probably one of the most studied cyclopoid groups due to its importance in aquaculture. *Lernaea* spp. have been reported to cause mass mortalities as early as 1880. According to Kocyłowski and Miączyński (1960), lernaeosis almost demolished an entire population of crucian carp in the Masurian Lake District (Poland) in 1880. An interesting case of catfish mortality due to gill damage (including epithelial hyperplasia, telangiectasis and haemorrhage) caused by *Lernaea cyprinacea* was also noted in Arkansas by Goodwin (1999). Bighead carp in the same tanks, with approximately the same number of copepods externally, did not die. Fish mortalities due to gill damage from *Lernaea* copepodids had never been reported before. This was most likely due to the polyculturing of the catfish with the bighead carp (an excellent host for *Lernaea*) and the filter-feeding apparatus of the carp preventing large infestations on their gill filaments.

2.7.2 Harpacticoida

This order includes mainly free-living copepods, although there are some symbiotic and parasitic species. One genus, *Balaenophilus* Aurivillius, 1879 (with three species), known to occur on the external surfaces of turtles, whales and manatees, appears to be both epibionts and parasites. Kazunari Ogawa and colleagues recorded the first copepod on a sea turtle and noticed the turtle's skin inside the gut, which led the authors to the conclusion that the copepods feed on the turtle and not algae or diatoms (Ogawa et al. 1997). According to Badillo et al. (2007), there was definite evidence of *Balaenophilus* ingesting whale and sea turtle host tissue; however, the extent of this on the host is unknown. Mild signs of a tissue reaction was also observed in turtles with large numbers of copepods present at one time (>500). However, when Suárez-Morales et al. (2010) confirmed the presence of these copepods on manatees, they could not see any effect on the hosts. Healthy skin was observed at the site of attachment when *Balaenophilus manatorum* (Ortíz, Lalana & Torres, 1992) was removed, and no difference was seen in their reproduction or behaviour. Thus, their status as parasites remains unclear at this point.

The family Tisbidae contains free-living and symbiotic copepods as well as parasitic copepods. The parasitic species (many from the subfamily Cholidyinae) are usually found in the gills or on the external surfaces of octopuses (Humes and Voight 1997; Avdeev 2010). Juvenile *Genesis vulcanoctopusi* López-González, Bresciani & Huys, 2000, however, were located within the connective tissue of the octopod integument, indicating the possibility that these parasites may have both endo- and ectoparasitic phases (López-González et al. 2000). The first species described from this family was *Tisbe furcata* (Baird, 1837). Arthur Grover Humes listed specimens labelled as *T. furcata* from the mantle of *Ocnus planci* (Brandt, 1835), a sea cucumber (see Humes 1980); however, the identification was by Monticelli in 1892 and is doubtful. Massy (1909) first reported a copepod on a deep-sea octopus that was later described by Farran (1914) as *Cholidya polypi* Farran, 1914 (see Humes and Voight 1997).

2.7.3 Monstrilloida

Monstrilloids are only parasitic in the postnaupliar and preadult stages, with adults being free-swimming and non-feeding zooplankters. The endoparasitic forms are known to occur in polychaetes, molluscs and other invertebrates (Davis 1984; Huys et al. 2007). According to Mexican marine biologist and researcher, Eduardo Suárez-Morales (Fig. 2.7f) (2011), the first reported monstrilloid was from a Norwegian fjord in 1842 (Krøyer 1842). A single preadult specimen of *Monstrilla typica* (Krøyer, 1849) (originally named *Thaumatoessa typica* in the 1842 publication) was illustrated by Krøyer but without any description. This description was only provided in 1849 (with a slight alteration to the original name), along with the diagnosis of a new genus (Krøyer 1849). The monstrilloid naupliar stage was first described by Giesbrecht (1893), shortly followed by the drawings and descriptions of the nauplius and development of the endoparasites of *Haemocera* by Malaquin (1901). In 1994, Grygier re-examined the "*Thaumatoessa* (*Thaumaleus*) *typica*" type specimen in order to determine its identity and moved it into the genus *Monstrilla* Dana, 1849. Shortly thereafter, Grygier (1995) published an annotated chronological bibliography of the Monstrilloida.

Within this order, only one family, Monstrillidae, is recognised. Until recently, eight genera were considered valid, but Mark Joseph Grygier (Fig. 2.5e) and Susumu Ohtsuka (2008) briefly revised the status of each genus and determined only three should retain their validity, with the other five all being synonymised into the genus *Monstrilla*. They then proceeded to add an additional genus, *Maemonstrilla* Grygier & Ohtsuka, 2008. Six years later, Suárez-Morales and Mckinnon (2014) added another genus *Australomonstrillopsis* Suárez-Morales & McKinnon, 2014, giving a current total of five accepted genera.

Most of the species within Monstrilloida have been described by Eduardo Suárez-Morales (Fig. 2.7f) and colleagues (75 valid taxa), including a single genus, 73 species and 1 subspecies. The systematic position of this order however is still unclear. According to Huys et al. (2007), Monstrilloida fall within a fish parasitic clade of the Siphonostomatoida, sharing a common ancestor with caligiform families. However, this is considered unconfirmed by some researchers, and more information is required before any definitive changes in classification can be made (Suárez-Morales 2011). The original status of the Monstrilloida therefore remains as is at this stage (Suárez-Morales and McKinnon 2014).

2.7.4 Poecilostomatoida

Most poecilostomatoid copepods are ectoparasites, attaching to the external surfaces or the gills of their hosts (fish or other invertebrates); however, there are several endoparasitic species that live within the body of their hosts too. The first described species for this order was the ectoparasite *Lernentoma asellina* (Linnaeus, 1758), an uncommon parasite found in the gills of gurnards from the family Triglidae. This copepod is from the family Chondracanthidae that was revised by Ju-shey Ho, from California State University, Long Beach. Ho's work on symbiotic copepods has exceeded 257 publications on these crustaceans from around the world. In 1970 and 1971, Ho revised the Chondracanthidae (when it still was in the order Cyclopoida) in order to clarify the confusion surrounding these crustacean's identification, re-examining and redescribing every specimen and verifying its identity. At the time, only 30 genera were known; however, there are now 51 known genera in this family containing 193 species and 4 subspecies. Recently, Østergaard et al. (2003) used phylogenetic analyses to determine the phylogeny within the family, which clarified some of the questions regarding past and present subfamilies of Chondracanthidae.

The Splanchnotrophidae is a small but interesting family of copeopods which parasitise opisthobranch gastropods (including nudibranchs and pteropods) (Huys 2001). They are usually deeply embedded inside their host with only the distal urosome and egg sacs visible (Uyeno and Nagasawa 2012). Currently, there are 6 genera and 31 species within the family. The first two described species were *Lomanoticola brevipes* (Hancock & Norman, 1863) and *Splanchnotrophus gracilis* Hancock & Norman, 1863.

Another family, Ergasilidae, comprises fish parasitic copepods, where only the females are parasitic. Most species are found in freshwater and most attach to the host gills. There are 29 genera, 261 species and 2 subspecies presently regarded as valid species in this family. The first genus to be described was *Ergasilus* von Nordmann, 1832, with two species, *Ergasilus gibbus* Nordmann, 1832, and *Ergasilus sieboldi* Nordmann, 1832. *Ergasilus sieboldi* attaches to the gill filaments using its second antennae and can cause tissue damage or secondary infections at the site of attachment. The nutrition of *E. sieboldi* was noted by Einszporn (1965a, b), and it is known to cause severe fish losses in aquaculture (see Piasecki et al. 2004). Over the years, several researchers mentioned different life stages of *E. sieboldi*, but there were many discrepancies between the different reports as they were often not complete studies on the life cycle. In 1991, Abdelhalim et al. (1991) were able to provide complete information on all of the different life stages for this species.

The family Taeniacanthidae has 21 genera with 121 species. These copepods are parasitic on marine fishes and sea urchins. The first species of taeniacanthid described was *Tucca impressus* Krøyer, 1837, an ectoparasite on porcupinefish and pufferfish. Morphologically Taeniacanthidae are closely related to Bomolochida and were previously placed within that family until 1911 when Wilson separated the taeniacanthids and the bomolochids (Wilson 1911). However, it was only in 1932 when Wilson elevated both of these groups to family level, removing them from Ergasilidae. Dojiri and Cressey (1987) revised the family and, including new species descriptions, keys to all genera, host-parasite lists, distribution, morphology, ecology as well as notes on the relationships between the closely related Bomolochidae, Taeniacanthidae and Tuccidae.

2.7.5 Siphonostomatoida

This order of copepods contains approximately 75% of the fish parasitic copepods. Most are found in marine waters and are recognised by the siphon-like mouth tube containing stylet-like mandibles to attach and feed from their hosts. The first three species described from this order were *Pennella filosa* (Linnaeus, 1758), *P. sagitta* (Linnaeus, 1758) and *Salmincola salmoneus* (Linnaeus, 1758).

Some of the more noticeable siphonostomatoids are commonly referred to as sea lice. These copepods are from the family Caligidae. The first recognised species in this family was *Lepeophtheirus pectoralis* (Müller, 1776), followed shortly thereafter by *Caligus curtus* Müller, 1785. Currently there are approximately 508 known species in this family in 30 genera. These parasites are of particular concern due to their impact on certain commercially important fish species, such as farmed and wild Atlantic salmon. In fact, *Caligus rogercresseyi* Boxshall & Bravo, 2000, has been recognised as the most pathogenic ectoparasite of farmed salmon in Chile and is also a potential vector for the transmission of the infectious salmon anaemia (ISA) virus (Oelckers et al. 2014; also see Chap. 7).

The family Lernaeopodidae is another ecological and economically important group of fish parasites. Most females have large, fleshy bodies that attach to the host via a small chitinous plug called a bulla. The bulla is inserted into the epidermis of the host and held by the maxillary arms (Boxshall 2005). To date there are 48 genera, 334 species and 12 subspecies in the family. *Salmincola salmoneus* (Linnaeus, 1758) was the first lernaeopodid species described and is commonly referred to as a gill maggot. Gill maggots from the genus *Salmincola* Wilson, 1915, can occur in large numbers and cause significant mortalities in aquaculture facilities (Sutherland and Wittrock 1985), but they are less abundant in wild populations and have a smaller impact (Amundsen et al. 1997).

Members of the family Eudactylinidae are mostly parasitic on the gills of elasmobranchs (although some genera are found on teleost fishes such as *Heterocladius* Deets & Ho, 1988, and *Jusheyus* Deets & Benz, 1987). There are 12 genera and 57 species known in this family. The earliest record of a species from this family is the subspecies *Nemesis lamna lamna* Risso, 1826. Damage caused by *Nemesis* species include tissue erosion due to the rasping feeding of the copepod, swollen and pale areas at the site of attachment, thickening of respiratory epithelium, as well as the prevention of water flow between secondary lamellae (Benz 1980; Benz and Adamson 1990).

George William Benz (Fig. 2.7g), in his doctoral thesis, discussed the evolutionary biology of siphonostomatoids that are parasitic on vertebrates based on the 18 families fitting this criterion (Benz 1993). Benz went on to publish numerous articles on these copepods, including the description of a new family, 5 new genera and 17 species. Benz was both a student and close colleague of Kabata, and it seems fitting that his final publication before he passed away in 2015 was a memorial tribute paying homage to his mentor and friend (Benz and Goater 2015).

2.8 Branchiura

Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998
Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1998
Subclass Branchiura Thorell, 1864

These parasitic Crustacea, often referred to as “fish lice”, are small flattened ectoparasites of fish. Occasionally these parasites can occur on other hosts such as alligators (Ringuelet 1943), salamanders (Poly 2003) and tadpoles (Stuhlmann 1891; Wolfe et al. 2001). They all belong to the order Arguloida and family Argulidae with four recognised genera, *Argulus* Müller, 1785; *Chonopeltis* Thiele, 1900; *Dipteropeltis* Calman, 1912; and *Dolops* Audouin, 1837 (see Table 2.1). Approximately 168 species are known worldwide (Ahyong et al. 2011), and only *Argulus* occurs in marine environments, the other genera being exclusively freshwater parasites. William J. Poly summarised the global diversity of all branchiurans in freshwater and highlighted the current distribution of each of the different genera in the different biogeographic regions of the world (Poly 2008). A year later, Ole Sten Møller reviewed the history and taxonomy of this group, giving a chronological account of each group’s history from previously inaccessible literature (Møller 2009). This publication provides valuable information on the Branchiura systematics and morphology and is a helpful aid for any researcher working on these parasites. Recently, Neethling and Avenant-Oldewage (2016) compiled an extensive review of the Branchiura. This compendium features a full overview of the four genera, stating the characteristics and taxonomic changes for each genus, as well as the geographical distributions and host records for each species, and is a comprehensive synopsis of literature on these parasites up to this point.

The phylogenetic position of the branchiurans has been complicated with many different theories and misinterpretations of certain characters that were used to define this unique group (especially with the second maxilla). These parasites were first termed Branchiura (or gill-tails) by Thorell (1864), based on the importance of the "tail" morphology, but had been previously placed within the siphonostome Copepoda by Heller (1857) and Krøyer (1863). The idea that the Branchiura were more closely linked to the Branchiopoda ("Phyllopoda" in Thorell, 1864) was not widely accepted, and in 1875, Claus reaffirmed that the Branchiura were more closely related to the copepods. Claus (1875) suggested placing the group as a suborder within the Copepoda and Leydig (1889) concurred. In 1902, when Charles Branch Wilson (Fig. 2.7h) revised the parasitic copepods of the family Argulidae, these branchiurans were still viewed as copepods. This extensive review covered 29 species of *Argulus*, 9 species of *Dolops* and 1 species of *Chonopeltis* (Wilson 1902). Finally, Johannes Thiele (Fig. 2.7i) studied the cephalic appendages of the Branchiura and concluded these parasites were not in fact copepods as commonly thought (with no first maxilla in the mouth cone) and should rather be on a level equal to the copepods and phyllopods (Thiele 1904). However, even after this breakthrough, the classification remained unchanged. Almost 30 years later, Martin (1932) completed an in-depth study on the mouth cone and once again suggested Branchiura as a subclass, but it took another 10 years before this new classification was eventually acknowledged in another publication (Ringuelet 1943). Since then (with a few exceptions), the Branchiura and Copepoda have been considered separate groups.

2.8.1 Argulus

The first branchiuran species described was *Argulus foliaceus* (Linnaeus, 1758) (originally named *Monoculus foliaceus*), although Branchiura are thought to be mentioned as early as tenth century China. According to Piasecki and Avenant-Oldewage (2008), a monk named (Kao) Tsan-ning mentioned how goldfish that eat bark from poplar trees will not breed "lice", and this was most likely referring to an *Argulus* species (Møller 2009). Wilson (1902) had originally stated that fish lice were first mentioned by a fisherman from Strasbourg, Léonard Baldner, in 1666. Baldner apparently described and pictured the birds, fishes and aquatic animals of the neighbourhood and specifically mentioned "Pou des poissons" (fish louse).

Argulus is the most specious genus of the family Argulidae, with approximately 127 species, and is widely distributed around the world. The genus was named in recognition of the numerous ommatidia in the compound eyes (diminutive of the mythical Greek beast, *Argus*, which had a hundred eyes) (Wilson 1902). The majority of the earlier studies focused on the first *Argulus* species, *A. foliaceus.* The nervous and genital systems as well as other microscopic anatomy of *A. foliaceus* were described by Leydig (1850, 1889), with studies on the larval development initiated by Claus (1875). Wilson (1902, 1904a, b) continued the larval and hatching research, with additional data added on the genital system and the circulatory system. Wilson also covered the taxonomic studies of North American *Argulus* (Wilson 1916, 1920a, b, 1921, 1923, 1924), some of which were revised by Meehan (1940). Wilson (1944) admired some of the new data provided by Meehan, especially the key to the genus, but disagreed with the taxonomic species revisions calling it a "serious encroachment upon the genus". The taxonomy and identification keys of African *Argulus* species were completed by Cunnington (1913), Monod (1928), Fryer (1956, 1959, 1961a, b, 1965a, b, 1968) and Rushton-Mellor (1994a, b, c), while the South American species were covered by Brian (1947) and Ringuelet (1943, 1948).

More recently, research has focused on histology and ultrastructure analysis of various *Argulus* structures and how they relate to the ecology of these parasites. Tam and Avenant-Oldewage (2006) used gut ultrastructure to determine that the first larval stage uses yolk, and not blood, as the primary source of nutrition. Three years later, Tam and Avenant-Oldewage (2009) also used the digestive cell ultrastructure to determine that the elaborate enteral diverticula are part of the anterior midgut, and not similar to the midgut glands seen in other Crustacea.

2.8.2 Chonopeltis

This genus is endemic to sub-Saharan Africa and currently has 13 valid species. The first species described was *Chonopeltis inermis* Thiele, 1900 from Lake Rukwa. The genus is named in reference to the "cone- or funnel-shaped shield" (Møller 2009). Other than three publications (Wilson 1902; Thiele 1904; Monod 1928), almost 40 years passed from when the genus was established to new data being published on it (Brian 1940).

Probably one of the main contributors to our knowledge on this genus is Geoffrey Fryer (Fig. 2.8a). Fryer recognised three different species from the single variant species, *C. inermis* var. *schoutedeni* described by Brian (1940). One species was established as *C. schoutedeni* Brian, 1940, while the other two species were described by Fryer as new to science (*C. congicus* Fryer, 1959, and *C. flaccifrons* Fryer, 1960a). This discovery made him the authority of more than half of the *Chonopeltis* species known at the time (Fryer 1959, 1960a). Furthermore, Fryer completed noteworthy ecological studies on this genus, noting for the first time that the adults are sedentary (Fryer 1956), and there is a lack of cephalic lobe rods in *C. flaccifrons* (see Fryer 1960a). Fryer went on to describe several more species, produce a key for the genus and show the difference between *Chonopeltis* and the already known *Argulus* and *Dolops* larvae with the lack of metanauplius or juvenile-like morphology in the first descriptions of the *Chonopeltis* larval stages (Fryer 1964, 1974, 1977).

The majority of the more recent species descriptions and distributions have been by South African researchers, Jo and Liesl van As (another husband and wife team) (Fig. 2.8b, c) (van As 1986, 1992; van As and van As 1993, 1996, 1999a, b) as well as Annemariè Avenant-Oldewage (Fig. 2.8d) (Avenant-Oldewage 1991; Avenant-Oldewage and Knight 1994, 2008). Additionally, van As and van As (1996) provided the first SEM image of the *Chonopeltis* larva; and Avenant-Oldewage and colleagues used histology to elucidate the morphology of the digestive system

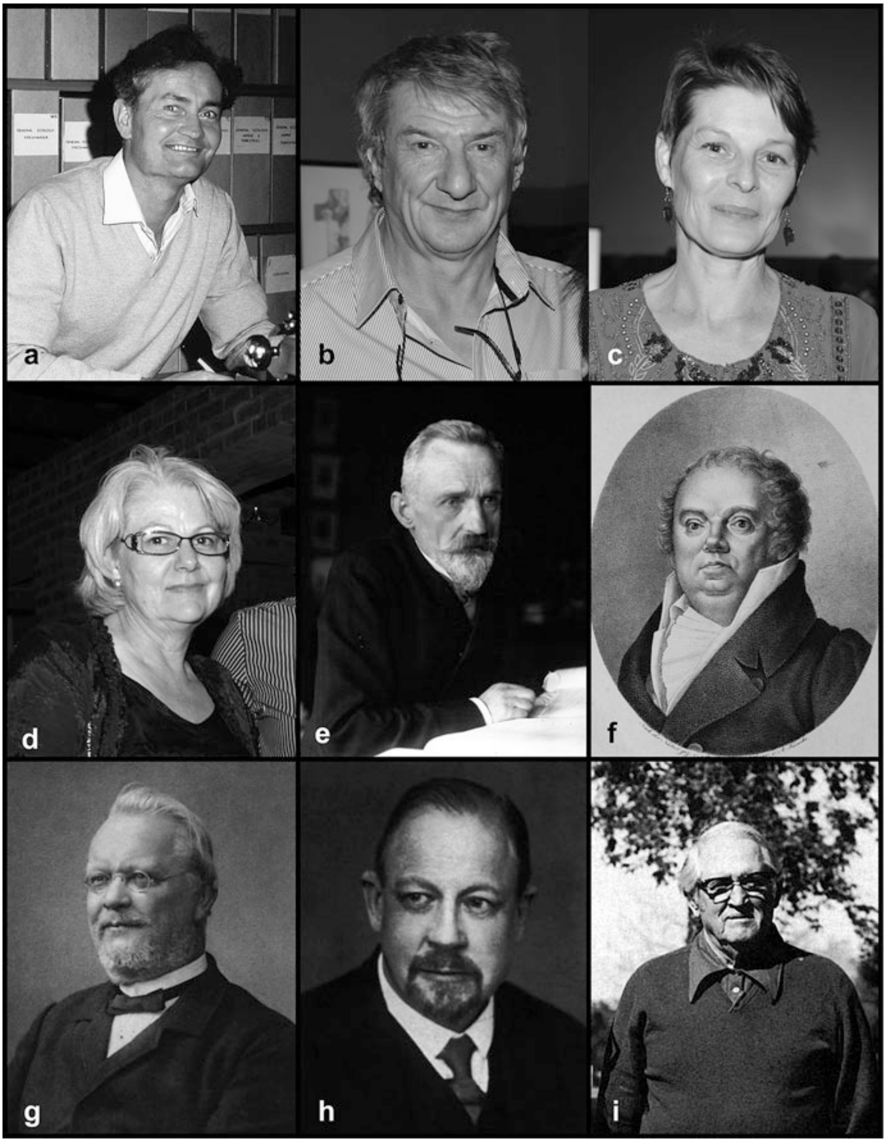

Fig. 2.8 (**a**) Geoffrey Fryer, (**b**) Jo van As, (**c**) Liesl van As, (**d**) Annemariè Avenant-Oldewage, (**e**) Eugène Louis Bouvier, (**f**) Karl Asmund Rudolphi, (**g**) Karl Georg Friedrich Rudolf Leuckart, (**h**) Richard Heymons, (**i**) John Teague Self. Images (**a**), (**e**), (**f**) and (**g**) © Wikipedia Commons public domain; image (**h**) from Röhlig et al. (2010); image (**i**) from Janovy (1996)

(Swanepoel and Avenant-Oldewage 1993; Avenant-Oldewage et al. 1994). In 2017, Van As et al. revised the southern African species of *Chonopeltis* and found that contrary to earlier theories, each river system does not have its own species of *Chonopeltis.* After careful examination of all *C. meridionalis* Fryer, 1964; *C. victori* Avenant-Oldewage, 1991; and *C. koki* Van As, 1992, material, it was concluded that all are indeed the same species, *C. meridionalis*, and occur in multiple river systems but only on cyprinid hosts (Van As et al. 2017).

2.8.3 *Dipteropeltis*

Until recently, *Dipteropeltis* was a monotypic genus, with the sole species being *Dipteropeltis hirundo* Calman, 1912, described by William Thomas Calman (a Scottish zoologist). However, recently Neethling et al. (2014) described a second species, *Dipteropeltis campanaformis* Neethling, Malta & Avenant-Oldewage, 2014, from Brazil. This genus is only known from South America and is the only branchiuran genus endemic to that region. These parasites infect piranhas (Carvalho et al. 2003) and can sometimes occur in certain areas with a prevalence as high as 73% (Mamani et al. 2004). As *Dipteropeltis* species have not been collected very often, and studies on members of this genus are very limited, information on other life stages, development and ecology is scanty.

2.8.4 *Dolops*

All but 2 of the 13 known *Dolops* species are known from South America. *Dolops ranarum* (Stuhlmann, 1891) and *D. tasmanianus* Fryer, 1969 are known from sub-Saharan Africa and Tasmania (Australia), respectively, making this genus widespread but confined to the southern hemisphere. The first *Dolops* was noticed by the French entomologist Jean Victoire Audouin (1837) who thought the specimens looked like *Argulus* but without the suction discs. The meaning of the generic name is uncertain but has a Greek mythology origin. Unaware of the naming of *Dolops*, Heller described *Gyropeltis* Heller, 1857, which was based on the South American species. Although it was described after Audouin, Heller's description contained detailed drawings and notes not seen in the publication by Audouin. Due to this, some authors used *Gyropeltis* rather than *Dolops* (see Krøyer 1863; Thorell 1864). Only 33 years later (and 60 years after describing *Dolops*) did Bouvier (1897) use the correct genus name and explain how, even if it seems less informative, *Dolops* was sufficiently described by Audouin and is the accepted authority for the genus.

Most of the information on the South American *Dolops* stems from the work of the French carcinologist Eugène Louis Bouvier (1897, 1898, 1899a, b) (Fig. 2.8e). New species and keys have been published over the years, but there is much that is still unknown about these parasites. Ringulet (1943, 1948) provided a key to the South American *Dolops* species. Weibezahn and Cobo (1964) described species from Venezuela, while José Celso de Oliveira Malta and colleagues (Malta 1982; Malta and Varella 1983) described species from the Brazilian Amazon. Recent publications from this area focus on the development of young as well as combined host-parasite interactions (Gomes and Malta 2002; Carvalho et al. 2003; Mamani et al. 2004).

Fryer also studied the sperm transfer of several *Dolops* species (Fryer 1958, 1960b, 1969), described a new species from Tasmania (Fryer 1969) and made observations on the distribution of the species in this genus (Fryer 1969). Interestingly, most of the information known about *Dolops* has been completed on a single species from South Africa, *Dolops ranarum*. The major contributors to this knowledge are Annemariè Avenant-Oldewage (Fig. 2.8d) and colleagues. These contributions include a complete redescription of the species (Avenant et al. 1989a), second published drawing of a *Dolops* larva (Avenant et al. 1989b), digestive system morphology (Avenant-Oldewage and Van As 1990), as well as the feeding behaviour and effect on its host fish (Avenant-Oldewage 1994).

2.9 Pentastomatida

Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998
Class Ichthyostraca Zrzavý, Hypša & Vlášková, 1998
Subclass Pentastomida Diesing, 1836

Pentastomes are obligate vermiform parasites and are commonly referred to as "tongue worms" due to the resemblance of some species to a vertebrate tongue. The adult parasites have two pairs of retractile hooks on either side of the mouth, creating a grouping of five anterior appendages from which the group's name is derived ("five mouths", although only one is an actual mouth). They are often found in the upper and lower respiratory tracts of vertebrates (birds, reptiles, amphibians, mammals and even humans) where they lay eggs (Paré 2008). These eggs are excreted out via the digestive system of the definitive host and then ingested by an intermediate host (most often a fish or small herbivorous mammal).

The French veterinarian Philibert Chabert (1787) noticed the first tongue worm inside the nasal cavities of horses and dogs. However, the first species, *Linguatula serrata* Frölich, 1789, was only named 2 years later, from the lung of a hare. This species is one of the most synonymised pentastomes with 13 junior synonyms. The Swedish-born "father of helminthology", Karl Asmund Rudolphi (Fig. 2.8f), recognised that these worms were different to others and placed them into a single group, the genus *Pentastomum* Rudolphi, 1812. However, he was still unable to place them (like many others after him), and they have been grouped with various taxa including annelids, mites, myriapods, onychophorans and tardigrades (see Abele et al. 1989). Dujardin (1845) believed these parasites were different from all the other worms and most closely resembled arthropods based on their striated muscles. Using molecular techniques, Abele et al. (1989) concluded that pentastomids belong in the Crustacea as they are more closely related to fish lice (*Argulus*) rather than any of the other possible taxa mentioned above. Almeida and Christoffersen (1999) also used cladistics on the pentastomids and challenged some of the older ideas. With the recent discovery of fossil data, there is even more discussion on the phylogenetics and status of this group (see Castellani et al. 2011).

In 1851, the first family, Linguatulidae, was established. Nine years later, the German zoologist, Karl Georg Friedrich Rudolf Leuckart (Fig. 2.8g), determined the first comprehensive study on the life cycle of a linguatulid and divided *Pentastomum* into two subgenera, namely, *Linguatula* Frölich, 1789 and *Pentastomum* (Leuckart 1860). Sambon (1922a, b) revised Linguatulidae and identified differences between the different linguatulid groups as well as added new subfamilies and genera. Another German zoologist, Richard Heymons (Fig. 2.8h), published several papers and described ten pentastomid species. Other substantial publications include the monograph on the pentastomids from Africa (Fain 1961), the review of the pentastomid history by Nicoli (1963) and several publications by Haffner on the biology of these parasites (Haffner 1971, 1973).

One of the world authorities on pentastomes was John Teague Self (Fig. 2.8i). From publishing new species to host-parasite interactions and biological relationships, he explored all aspects of these parasites where possible. John Riley, another important contributor to Pentastomida, described 2 genera and 43 species, some with Self. Riley (with over 45 publications on pentastomids) published noteworthy work on the biology of pentastomids (Riley 1986), revisions of several genera (Riley et al. 1990; Riley 1994), and has a genus named in honour of his large contribution to the taxonomy of Pentastomida, *Rileyella* Spratt, 2003. This name has since changed to *Yelirella* Spratt, 2010 (which is an anagram of *Rileyella*) as *Rileyella* was a junior homonym for a tachinid fly from North America (Spratt 2010).

To date there are 4 orders, 2 superfamilies, 7 families, 26 genera, 130 species and 2 subspecies in this subclass (see Table 2.1). Recently, Gary Poore (Fig. 2.4i) has revised the nomenclature of the pentastomids giving a list of all of the valid species (Poore 2012). Brazilian researchers, Martin Lindsey Christoffersen and José Eriberto de Assis, have published a substantial review of Pentastomida. This thorough monograph includes a detailed history on the subclass with information on all the known species (including updated synonymies, host and distribution lists), as well as notes on their phylogeny and effects on their hosts.

2.10 Ostracoda

Superclass Oligostraca Zrzavý, Hypša & Vlášková, 1998
Class Ostracoda Latreille, 1802

Ostracods are small crustaceans found in both marine and freshwaters. The body resembles a clam and is encased by two valves, which forms a carapace. Very little was known about these crustaceans eating preferences for many years. The first mention was by Baird (1850) where he stated that most are essentially carnivorous; nothing specific about their feeding mode was noted. Most ostracods these days are considered to be free-living, predators or scavengers, but there are a few instances of symbiotic (and possibly parasitic) relationships.

One of the first records of a parasitic relationship was by Marshall (1903) when he described the first entocytherid ostracode. William S. Marshall, an Assistant Professor of Zoology at the University of Wisconsin, named this species *Entocythere cambaria* Marshall, 1903, and believed it fed on the blood of its crayfish host. Other members of the podocopan family Endocytheridae have also been listed as parasites but were corrected to commensals when the entocytherids were able to survive for long periods without a host (Young 1971). These ostracods are now considered to be obligate ectosymbionts of other crustaceans (Williams and Weaver 2018).

Other ostracods thought to be parasitic are those from the order Myodocopida. Research by Wilson (1913), Monod (1923) and Harding (1966) reported on myodocopidan ostracod parasitism based on the attachment of these crustaceans on their various hosts. Charles Branch Wilson (Fig. 2.7h) was the first to categorically state that these *Cypridina* Milne-Edwards, 1840, ostracods were parasitic (upon the gills of several fish), that the occurrence was not accidental and that it was not temporary (formation of a pocket to keep the crustacean in place). However, it was debated that these crustaceans are not truly parasitic and only attach to injured or unhealthy fish that are trapped (Cohen 1983). According to Stepien and Brusca (1985), adult fishes in large, nearshore cages were attacked at night by zooplankton swarms, primarily consisting of the luminescent ostracod, *Vargula tsujii* Kornicker & Baker, 1977, and the cirolanid isopod, *Cirolana diminuta* Menzies, 1962. Although the ostracods attached and fed on mucus and skin of the fish, they did not appear to inflict serious harm on the host. They were only found inside fish damaged by the cirolanid isopods and thus could not be considered parasites in this instance.

The attachment and actual effects of these myodocopidan ostracods on the hosts needed to be studied, and so Bennett et al. (1997) compared the histopathology and feeding appendages of ostracods with different feeding strategies. The "parasitic" ostracod investigated, *Sheina orri* Harding, 1966, was found in the gills of the epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre, 1788) in Australia. The authors noted that this crustacean used their mandibular and maxillular claws to attach to the gills, which caused damage to the gills. The claws seemed to be adapted for this purpose, and the damage to the gills suggested they had been attached for a considerable amount of time. Thus, it is a parasite for at least part of its life cycle. This study also found that Wilson's (1913) description of *Photeros parasitica* (Wilson, 1913) (originally as *Cypridina parasitica*) was so similar to *Sheina orri* that it is most likely parasitic too. More individual studies on the different symbiotic ostracods need to be completed in order to determine if true parasitism is found in other ostracod species.

2.11 Concluding Remarks

This chapter reviews many of the historical highlights from the different parasitic Crustacea groups and provides a succinct background to these diverse organisms. Reviewing the literature has revealed how many of the earlier discoveries were dependant on research vessels and expeditions which covered only specific areas. With time, these discoveries became more linked to the area where the respective taxonomist was based and what material they had at their disposal. This led to a biased account on species diversity, influenced by the researcher rather than the presence of the parasite. Furthermore, most of the early biologists were involved in many different fields and described new species from diverse taxa. Over the years, this pattern has altered, and there are now more taxa-specific parasitologists working on species from around the world. It is important to note that many of the currently known crustacean parasitologists are however near retirement; thus, young researchers need to be trained to continue their outstanding work. With a better understanding of what has been done, we can now focus on what needs to be done in order to gain further insight into this unique group of parasites and their niche in the aquatic environment.

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Chapter 3
Biodiversity and Taxonomy of the Parasitic Crustacea

Geoffrey Boxshall and Polly Hayes

Abstract Crustaceans have independently adopted a parasitic mode of life on numerous occasions, and this chapter reviews the classification and species richness of each of the parasitic clades, which lie within two major pancrustacean lineages, the Multicrustacea and the Oligostraca. Tabulated data are presented on the genera, species richness and host usage of the whale lice (Cyamidae); the generic and species richness of the families of hyperiidean amphipods; the generic and species richness and the host usage of the families and subfamilies of epicaridean isopods; the species richness, salinity regime and host taxon of cymothoid isopods; the generic and species richness and the host usage of the families of Ascothoracida and Rhizocephala; the species of Tantulocarida and their hosts; the generic and species richness and the host usage of the families and family-level groupings of cyclopoid and siphonostomatoid copepods; the species richness and salinity regimes of the genera of Branchiura; and the species richness and host usage of the genera of tongue worms (Pentastomida). Parasitic crustaceans use a total of 15 different phyla as hosts.

3.1 Introduction

Over 7000 species of Crustacea are parasitic, exploiting an enormous range of invertebrate and vertebrate hosts in marine and fresh waters, and many more crustaceans exhibit other kinds of interspecific associations (symbioses) including commensalism, inquilinism, mutualism and phoresis, with a similarly wide range of hosts. It is often difficult to determine the precise nature of a close symbiotic association between two species, mainly because we lack sufficient data on the biology of the symbionts. Here we define parasitism as the symbiotic relationship

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between two organisms where one (the parasite) is nutritionally dependent upon the other (the host) to complete its life cycle, and has a negative impact on the fitness of the host (see Combes 2001). This definition excludes intraspecific relationships between so-called parasitic males and the conspecific females that serve as their hosts and provide them with nutrients, such as the dwarf males of chondracanthid copepods which attach to and derive nutrients from the nuptial organs of the adult female (Østergaard and Boxshall 2004).

Although many crustaceans involved in interspecific relationships have been categorised simply as symbionts or associates because of the lack of available biological data, there are clear examples of commensalism, inquilinism, mutualism, and phoresis. The relationship between a suspension feeding turtle or whale barnacle and its host, for example, is best described as a phoresis in which the barnacle is transported by, but is not nutritionally dependent on, the host as these epibiontic barnacles are still suspension feeders. Similarly, numerous crustaceans are inquilines, inhabiting the burrows or domiciles of their hosts. For example, most *Hemicyclops* Boeck, 1872, species (Copepoda, Clausidiidae) are loose associates living in the burrows of their marine invertebrate hosts, while species of *Sunaristes* Hesse, 1867 and *Intersunaristes* Huys, 1995 (Copepoda, Canuellidae) reside within the gastropod shells being used for protection by hermit crabs (Ho 1988). A good example of a mutualistic association involving crustaceans is the cleaner shrimp. Numerous species from several families of decapod shrimps have adopted cleaning: they typically exhibit stereotypic behaviour patterns as a signal to client fish that come to be cleaned (Becker et al. 2005). Both species benefit: the cleaner derives food by removing parasites and other debris from the client fish, and the fish is cleaned. Most cleaner shrimp species are able to forage for other kinds of food, so the relationship is not obligatory. Commensalism is a relationship in which one organism derives benefit from exploiting a common food source with another (the host), which is not adversely affected. Many inquilines are also commensals, so the clausidiid copepods and the entocytherid ostracods that inhabit the burrows of their invertebrate hosts probably feed on particles of food released during the feeding activity of their hosts. The use of a common food source allows such relationships to also be classified as commensalism. These different kinds of symbioses form a continuum, and definite boundaries between parasitism and other close symbiotic relationships are not always apparent. Categorising relationships is therefore something of an inexact science!

The classification of the Arthropoda as a whole and of the Crustacea in particular is in a state of flux, and it is now widely accepted that the Hexapoda emerged from within the Crustacea, although there remains some uncertainty as to the precise sister-group relationship within the Crustacea (cf. von Reumont et al. 2009; Regier et al. 2010). As a consequence, it is recognised that the Crustacea is not a monophyletic taxon (e.g. Edgecombe 2010; Giribet and Edgecombe 2013); it is a paraphyletic assemblage which, together with the Hexapoda, forms the monophyletic Pancrustacea (also referred to as Tetraconata). The phylogenetic study of the Arthropoda by Regier et al. (2010), based on phylogenomic analysis of nuclear-coding sequences, recognised four main lineages, Oligostraca, Vericrustacea, Xenocarida and Hexapoda, within the

Pancrustacea. The first three of these constitute the traditional Crustacea (see Martin and Davis 2001 for recent classification scheme). In contrast, the phylotranscriptomics-based analysis of Oakley et al. (2013) recovered a different arrangement of major lineages within the Pancrustacea: the Oligostraca and Hexapoda were supported but the Xenocarida and Vericrustacea were not. The Xenocarida of Regier et al. (2010) comprised the Remipedia and Cephalocarida and was the sister group of the Hexapoda. In the Oakley et al. (2013) scheme, the Remipedia alone is the sister group of the hexapods, while the cephalocarids are placed as sister group to the Branchiopoda. These differences do not impact the present chapter as neither the cephalocarids nor the remipedes include any parasitic representatives. The Vericrustacea of Regier et al. (2010) comprised the Branchiopoda and a clade comprising Malacostraca, Copepoda and Thecostraca. In the Oakley et al. (2013) scheme these two clades are separate: the Branchiopoda is recovered together with the Cephalocarida, while the Malacostraca, Copepoda and Thecostraca together form a major lineage, the Multicrustacea. Within the traditional Crustacea only two lineages contain parasites: the Oligostraca, recovered by both Regier et al. (2010) and Oakley et al. (2013), and the Multicrustacea of Oakley et al. (2013) which was also recovered as a monophyletic sub-clade of the Vericrustacea by Regier et al. (2010). Both the Oligostraca and Multicrustacea were also recovered in the phylogenomic analysis of Schwentner et al. (2017). The focus of this chapter is these two parasite-containing lineages, the Oligostraca and the Multicrustacea.

The Oligostraca comprises the Branchiura, Mystacocarida, Ostracoda and Pentastomida (e.g. Regier et al. 2010; Giribet and Edgecombe 2013; Oakley et al. 2013). Molecular and spermatological evidence places the Pentastomida (tongue worms) and Branchiura (fish lice) as sister taxa, and these two wholly parasitic taxa together are referred to as the Ichthyostraca (Zrzavý et al. 1998). There has been controversy concerning this relationship since data from Cambrian fossils (see Waloszek et al. 2006) have been interpreted as evidence that pentastomids are stem-lineage derivatives of the Euarthropoda and should therefore be placed outside the Pancrustacea (e.g. Castellani et al. 2011). Divergence times are central to this debate: Sanders and Lee (2010), using data from five genes, estimated a divergence time of 519 Ma (but with confidence limits of 292 to 616 Ma), which could support an estimate of a Cambrian split between the Pentastomida and Branchiura. However, using a much larger dataset, Oakley et al. (2013) derived a maximum estimate of 424 Ma for this split which conflicts with the suggested presence of pentastomids in the Cambrian. Here we follow the molecular evidence, derived from ever expanding data sets, which consistently groups the Pentastomida and Branchiura together (Abele et al. 1989; Regier et al. 2010; Oakley et al. 2013). The recent description of a putative fossil pentastomid, *Invavita piratica* Siveter, Briggs, Siveter & Sutton, 2015, ectoparasitic on a fossil myodocopan ostracod from the Silurian (Siveter et al. 2015) will be considered in detail in Sect. 3.2.6 below.

The Multicrustacea lineage comprises the Thecostraca, Copepoda and Malacostraca (Regier et al. 2010; Oakley et al. 2013), to which can now be added the Tantulocarida. On the basis of morphological evidence, the Tantulocarida were already treated as the sister group of the Thecostraca (Huys et al. 1993), but Petrunina et al. (2014) have now provided sequence data for tantulocaridans which confirm their placement as “very close relatives” of the Thecostraca. The classification of Tantulocarida within the Thecostraca was supported, but with lower confidence, so Petrunina et al. (2014) concluded that further data would be needed to resolve this uncertainty. The Tantulocarida is wholly parasitic, the Thecostraca and Copepoda contain several wholly parasitic lineages and the Malacostraca contains some large parasitic clades nested within major taxa exhibiting a wide range of life styles, such as the Amphipoda and Isopoda.

These changes in our understanding of the higher-level systematics of crustaceans have had relatively little impact on the integrity of the main constituent taxa of each lineage, so, for example, the Amphipoda, Branchiura, Copepoda, Isopoda, Pentastomida and Thecostraca, which provide the main taxonomic focus for this volume, are all still recognised as monophyletic taxa, as they were in the overview of crustacean classification by Martin and Davis (2001). Indeed, the flow of molecular sequence data has shown these taxa to be robust and in addition has helped to resolve some existing uncertainties, such as the questionable monophyly of the Ostracoda. Evidence supporting the classification of the Myodocopa and Podocopa together as a monophyletic Ostracoda has been regarded as weak (e.g. Spears and Abele 1998; Oakley and Cunningham 2002), and Wakayama (2007) even hypothesised that calcified carapaces evolved separately in the Myodocopa and Podocopa. However, the bulk of the recent phylotranscriptomics-based analyses by Oakley et al. (2013) recovered the Ostracoda as a monophyletic clade.

3.2 Taxonomic Account

3.2.1 Malacostraca

The Malacostraca is a well-defined taxon within the Multicrustacea characterised by its distinctive tagmosis, namely, the division of the postcephalic trunk into an eight-segmented pereon-bearing pereopods and a primitively seven-segmented pleon-bearing pleopods, and by numerous features of the limbs, such as the biflagellate antennules. The phylogenetic relationships of the major taxa within the Malacostraca have been the topic of much debate. Following the Richter and Scholtz (2001) scheme, the most basal offshoot within the Malacostraca is the Leptostraca, and the main lineage is the Eumalacostraca (sensu Calman 1909). The mantis shrimps (Hoplocarida) then separate off from the remaining eumalacostracans which form a clade referred to as the Caridoida by Richter and Scholtz (2001). Within the Caridoida, only the two taxa which contain parasites, the Decapoda and the three relevant orders of Peracarida, are considered here.

3.2.1.1 Decapoda

Numerous decapods live in symbiotic associations, but few have been categorised as parasites. In the Brachyura, for example, some pinnotherid crabs live in association with bivalve molluscs, cryptochirid crabs inhabit galls in scleractinian corals, eumedonine crabs are symbiotic in echinoderms, and portunids of the genus *Lissocarcinus* Adams & White, 1849 are associated with holothurians and sea anemones. In the Caridea, the symbiotic palaemonid shrimps, formerly placed in a separate subfamily Pontoniinae that is no longer regarded as valid (De Grave et al. 2015), comprise 124 genera and 652 species, about 70% of which are obligate symbionts of coral, echinoderm, mollusc and sponge hosts. The nature of the symbiosis is often uncertain but evidence is emerging that a parasitic mode of life is widely distributed among these shrimps (Ďuriš et al. 2011).

Cryptochirid crabs have been treated as commensals, parasites and, more neutrally, as obligate symbionts (Van der Meij and Schubart 2014), but Kropp (1986) clearly demonstrated that cryptochirid species such as *Hapalocarcinus marsupialis* Stimpson, 1859, *Utinomiella dimorpha* (Henderson, 1906) and *Cryptochirus coralliodytes* Heller, 1861, feed on coral mucus and coral pieces, rather than feeding on suspended food particles. Simon-Blecher and Achituv (1997) concluded that *C. coralliodytes* is parasitic on faviid corals because settlement on a coral polyp resulted in death of the polyp; the crabs also inhibited coral growth rate and created depressions in the coral skeleton around the pits. There is uncertainty as to whether cryptochirids are commensal or parasitic on their coral hosts, but the evidence for parasitism is stronger in *C. coralliodytes*.

Pea crabs (Brachyura: Pinnotheridae) have been shown to cause damage to the gills of their bivalve hosts, and infected mussels have been shown to have lower tissue weights and slightly greater shell weights than equivalent uninfected mussels (Seed 1969). Most pinnotherids are associated with bivalve mollusc hosts, but the range of hosts utilised is very wide, including gastropod molluscs, holothurians, tunicates and polychaetes.

The Eumedoninae is a subfamily of pilumnid crabs which currently comprises 33 species in 13 genera, and all are obligate symbionts of echinoderm hosts (Ng 2014). Little is known about the biology of the crabs and their impact on the host. Caulier et al. (2014) reported the presence of host tissue in the stomach of the portunid *Lissocarcinus orbicularis* Dana, 1852, but considered it likely that it fed primarily on detritus from the sediment and organic material ingested by its holothurian host or deposited on the dorsal and cloacal integument of the host.

3.2.1.2 Amphipoda

The classification of the Amphipoda has undergone profound change since Martin and Davis (2001), whose updated classification of Crustacea accepted four suborders of amphipods: Caprellidea, Gammaridea, Hyperiidea and Ingolfiellidea. The composition and status of the first two of these have been extensively revised (Myers and Lowry 2003; Lowry and Myers 2013), while the Hyperiidea and Ingolfiellidea are still treated as valid and their composition has not changed markedly. The two main groups of amphipods that have been considered as parasites are the whale lice (Family Cyamidae) and the Hyperiidea. The monophyly of the Hyperiidea remains to be tested, but it is currently retained as a valid suborder of highly specialised pelagic amphipods which are often referred to as parasitoids rather than parasites (e.g. Lützen 2005). Cyamids were traditionally treated as a wholly parasitic infraorder (the Cyamida) of the amphipod suborder Caprellidea (cf. Martin and Davis 2001), but their status has changed. They are now treated only as a family of parasites contained within a much larger clade, the suborder Senticaudata, which contains 99 families formerly included within the Gammaridea (Lowry and Myers 2013) in addition to the families previously placed in the Corophiidea by Myers and Lowry (2003). So the Cyamidae is now classified as a family within the parvorder Caprellidira, in the infraorder Corophiida, and members of this latter taxon are mostly free-living and are predominantly detritivores.

In addition to these two main groups, obligate symbiotic and a few parasitic species have been reported from families, such as Lepidepecreellidae and Lafystiidae, known from marine invertebrate hosts, such as echinoids (Schiaparelli et al. 2015) and fish hosts (Bousfield and Kabata 1988), respectively.

Cyamidae

There are 32 extant species of whale lice found on various cetacean hosts (Table 3.1), and one species was known to parasitise the now extinct Steller's sea cow (Sirenia). Whale lice are dorsoventrally flattened amphipods (Fig. 3.1a–d) with short bodies ranging in length from about 8 up to 27 mm. The cephalothorax is small and is usually coalescent with the first pereonite, the free pereonites are broad and the pleon is reduced to a minute process. The mouthparts are well armed and are used to excavate and detach pieces of tissue from the surface of the host, but the maxillipeds are typically reduced to a small plate. Pereopods 1 and 2 and 5 to 7 are prehensile and provided with claws that are used for attaching to the host, but pereopods 3 and 4 are rudimentary and are represented by pairs of typically clavate gills. The arrangement of the gills and accessory gills, if present, provides informative taxonomic characters (e.g. Leung 1967). In adult females, these same pereonites also carry the two pairs of oostegites which form the ventral brood pouch (Fig. 3.1b) containing the eggs and developing juveniles. Males lack a ventral brood pouch but have paired penes (Fig. 3.1d).

Cyamids cannot swim and lack any planktonic dispersal phase in their life cycle; it has therefore been presumed that infestation spreads only during intraspecific bodily contact between host individuals.

Table 3.1 Species richness of genera of Cyamidae (Amphipoda), with known hosts ($n = 32$)

Genus	No. species	Recorded hosts (family: species)
Balaenocyamus Iwasa-Arai & Serejo, 2018	1	Balaenoptridae: *Balaenoptera acutorostrata* Lacépède, 1804; *B. musculus* (Linnaeus, 1758); *B. physalus* (Linnaeus, 1758)
Cyamus Latreille, 1796	17	Balaenidae: *Balaena mysticetus* Linnaeus, 1758; *Eubalaena australis* (Desmoulins, 1822); *E. glacialis* (Müller, 1776) Balaenoptridae: *Megaptera novaeangliae* (Borowski, 1781) Delphinidae: *Orcinus orca* (Linnaeus, 1758) Eschrichtiidae: *Eschrichtius robustus* (Lilljeborg, 1861) Monodontidae: *Delphinapterus leucas* (Pallas, 1776), *Monodon monoceros* Linnaeus, 1758 Physeteridae: *Physeter macrocephalus* (Linnaeus, 1758) Ziphidae: *Berardius bairdii* Stejneger, 1883
Isocyamus Gervais & van Beneden, 1859	5	Delphinidae: *Delphinus delphis* Linnaeus, 1758; *Globicephala melas* (Traill, 1809); *G. macrorhynchus* Gray, 1846; *Grampus griseus* (Cuvier, 1812); *Lagenorhyncus albirostris* (Gray, 1846); *Orcinus orca*; *Peponocephala electra* (Gray, 1846); *Pseudorca crassidens* (Owen, 1846); *Steno bredanensis* (Cuvier in Lesson, 1828); *Tursiops truncatus* (Montagu, 1821) Phocoenidae: *Phocoena phocoena* (Linnaeus, 1758) Ziphidae: *Mesoplodon europaeus* (Gervais, 1855)
Neocyamus Margolis, 1955	1	Physeteridae: *Physeter macrocephalus* Phocoenidae: *Phocoenoides dalli* (True, 1885)
Platycyamus Lütken, 1870	2	Ziphidae: *Berardius bairdii*, *Hyperoodon planifrons* Flower, 1882, *H. ampullatus* (Forster, 1770), *Mesoplodon grayi* von Haast, 1876
Scutocyamus Lincoln & Hurley, 1974	2	Delphinidae: *Cephalorhynchus hectori* (van Beneden, 1881), *Lagenorhynchus albirostris*
Syncyamus Bowman, 1955	4	Delphinidae: *Delphinus delphis*, *Globicephala macrorhynchus*, *Pseudorca crassidens*, *Stenella coeruleoalba* (Meyen, 1833), *S. longirostris/clymene* (Gray, 1850), *S. attenuata/frontalis* (Cuvier, 1829), *Tursiops truncatus*

Hyperiidea

There are currently 283 accepted species of hyperiideans grouped in 2 infraorders (Table 3.2), the Physocephalata (180 species) and the Physosomata (103 species) which are distinguished by a combination of characters including the length of the head, form of the eyes and features of the antennae and mouthparts (Bowman and Gruner 1973). Hyperiideans typically have bilaterally compressed bodies which may be slender or nearly spherical according to genus, but the pereon is typically enlarged and the coxal plates are reduced and weakly developed. Hyperiideans typically have large and conspicuous compound eyes which often cover most of the head, but a few

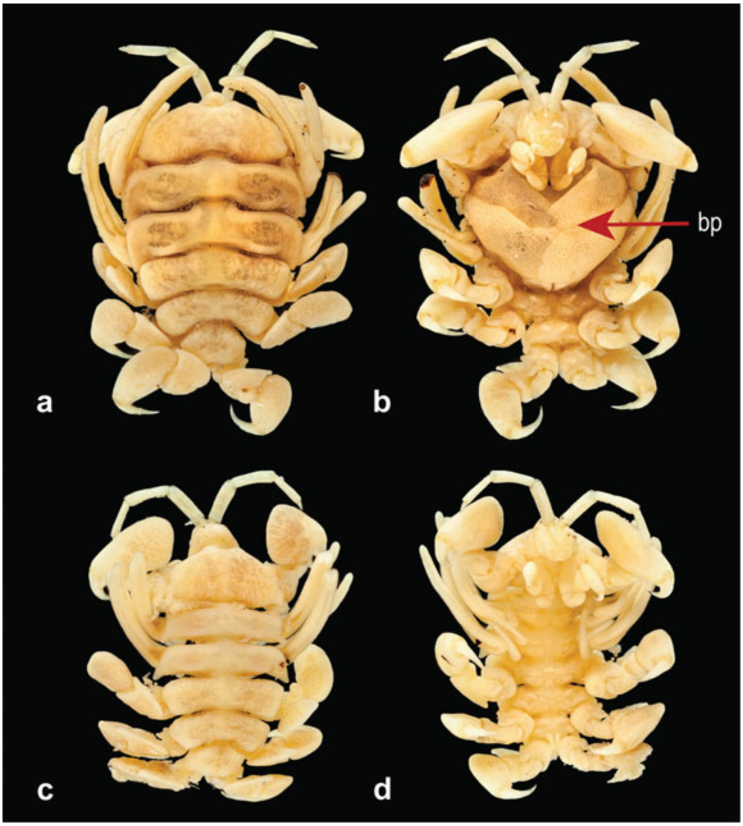

Fig. 3.1 Amphipoda: Cyamidae: *Cyamus ovalis* Roussel de Vauzème, 1834. (**a**) dorsal female, (**b**) ventral female showing brood pouch (bp), (**c**) dorsal male, (**d**) male ventral showing paired penes. Images © Natural History Museum, London

genera have small eyes or lack eyes altogether. The mouthparts are small: the mandibles often lack a dental process (in Physosomata) and the maxillules often lack an inner lobe (in Physocephalata).

Hyperiideans inhabit the open oceanic water column and live in association with gelatinous zooplankton including jellyfish, siphonophores, ctenophores, salps and radiolarians (Harbison et al. 1977; Madin and Harbison 1977). Hyperiideans are found in all oceanic temperature regimes, from polar to tropical, and are vertically distributed from epipelagic to abyssal depths. These symbiotic associations may be obligatory at certain phases of the life cycle, and some species exhibit a degree of host specificity. However, for most species information is lacking on the precise nature of the symbiotic association. If the hyperiidean feeds primarily on material filtered by the host, then the relationship may be best classified as commensalism. However, remains of host gonads and other host tissues have been found in the stomach contents of these amphipods, and in such cases they could be treated as parasites (Madin and Harbison 1977; de Lima and Valentin 2001).

Table 3.2 Species richness of families of Hyperiidea (Amphipoda)

Infraorder	Family	No. genera	No. species
Physocephalata	Amphithryridae	3	9
	Anapronoidae	1	2
	Bougisidae	1	1
	Brachyscelidae	1	5
	Cyllopodidae	1	2
	Cystisomatidae	1	6
	Dairellidae	1	1
	Eupronoidae	2	9
	Hyperiidae	7	29
	Iulopididae	1	2
	Lestrigonidae	6	17
	Lycaeidae	2	11
	Lycaeopsidae	1	2
	Oxycephalidae	8	18
	Paraphronimidae	1	2
	Parascelidae	5	7
	Phronimidae	2	11
	Phrosinidae	3	8
	Platyscelidae	4	11
	Pronoidae	1	1
	Thamneidae	1	1
	Tryphanidae	1	1
	Vibiliidae	2	24
Physosomata	Archaeoscinidae	2	6
	Chuneolidae	1	3
	Lanceolidae	2	17
	Megalanceolidae	2	3
	Metalanceoloidae	1	1
	Microphasmidae	2	2
	Microscinidae	1	1
	Mimonecteolidae	1	7
	Mimonectidae	3	13
	Mimoscinidae	1	3
	Prolanceolidae	1	1
	Scinidae	4	46

Data from World Amphipoda database (Horton et al. 2018)

3.2.1.3 Isopoda

Our understanding of systematic relationships within the Isopoda is in a state of flux, with different classification schemes evident in Dreyer and Wägele (2002), Brandt and Poore (2003), Wilson (2009) and Boyko et al. (2013). No consensus has yet emerged in the treatment of the Epicaridea—ranked as a suborder in the traditional scheme (Martin and Davis 2001). The fate of the Epicaridea is central to this chapter as it is a species rich and wholly parasitic group. Dreyer and Wägele (2002) suggested that the Epicaridea should be treated as a family, the Bopyridae, placed within the Cymothoida, whereas Brandt and Poore (2003) concluded that the elimination of the epicaridean families might not be necessary. Using combined molecular and morphological data, the analysis by Wilson (2009) placed the Cymothoidae, Gnathiidae and Bopyroidea, together with the Sphaeromatidae, on a basal lineage that was recovered as sister group to all remaining isopods. None of these analyses was able to explore large molecular data sets and it is only recently that taxon sampling within the Isopoda has expanded to include broad representation of epicaridean taxa. Boyko et al. (2013) generated a new phylogeny for the epicarideans and also shed light on their relationships with the cymothooideans: classifying the epicarideans in two superfamilies, the Bopyroidea and Cryptoniscoidea, all of which are obligate parasites of marine crustacean hosts. The Epicaridea was found to be monophyletic with respect to the Cymothooidea, which was the sister group in Boyko et al.'s (2013) analysis. Wilson (2009) included many fewer epicarideans in his broader analysis of peracaridans but also recovered the cymothooideans (plus the Gnathiidae) as sister taxon to the Bopyroidea.

Isopods are typically dorsoventrally flattened peracaridans characterised by a relatively short head fused to the first pereon segment which bears the maxillipeds, a pereon of seven segments each bearing a pair of similar pereopods and the ventral brood pouch in mature females, and a pleon which usually exhibits some fusion between the posterior pleon segments and telson. The pleopods are typically biramous and flattened, serving as gills for gaseous exchange. The head lacks a carapace, has sessile compound eyes and typically reduced uniramous antennules. Isopods are morphologically diverse and parasitic forms often show extreme modification both in body form and in structure of the paired appendages. Here we focus on the Bopyroidea, Cryptoniscoidea and Cymothooidea including the Gnathiidae. The first two contain parasites of crustaceans, the third contains parasites of fishes, while gnathiids are free-living as adults but have blood-feeding juveniles. The gnathiids are usually included within the Cymothooidea (e.g. Williams and Boyko 2012) but Wilson et al. (2011) expressed doubt over the relationship between the gnathiids and the cymothooideans. The gnathiids are considered separately here, for convenience, because the biology of these protelean parasites is so different.

Epicarideans have complex life cycles involving two hosts, both crustaceans. Life cycles have been elucidated for relatively few species but where known (e.g. Williams and An 2009) the first (intermediate) host is a pelagic copepod (Calanoida). The infective epicaridium larva locates a calanoid host and moults into the microniscus stage (Fig. 3.2a) which feeds on the body fluids of the copepod before detaching from the host and moulting into the cryptoniscus larva. This is the infective stage for the definitive crustacean host on which reproduction takes place. The life cycle appears similar in both Bopyroidea and Cryptoniscoidea (Williams and Boyko 2012).

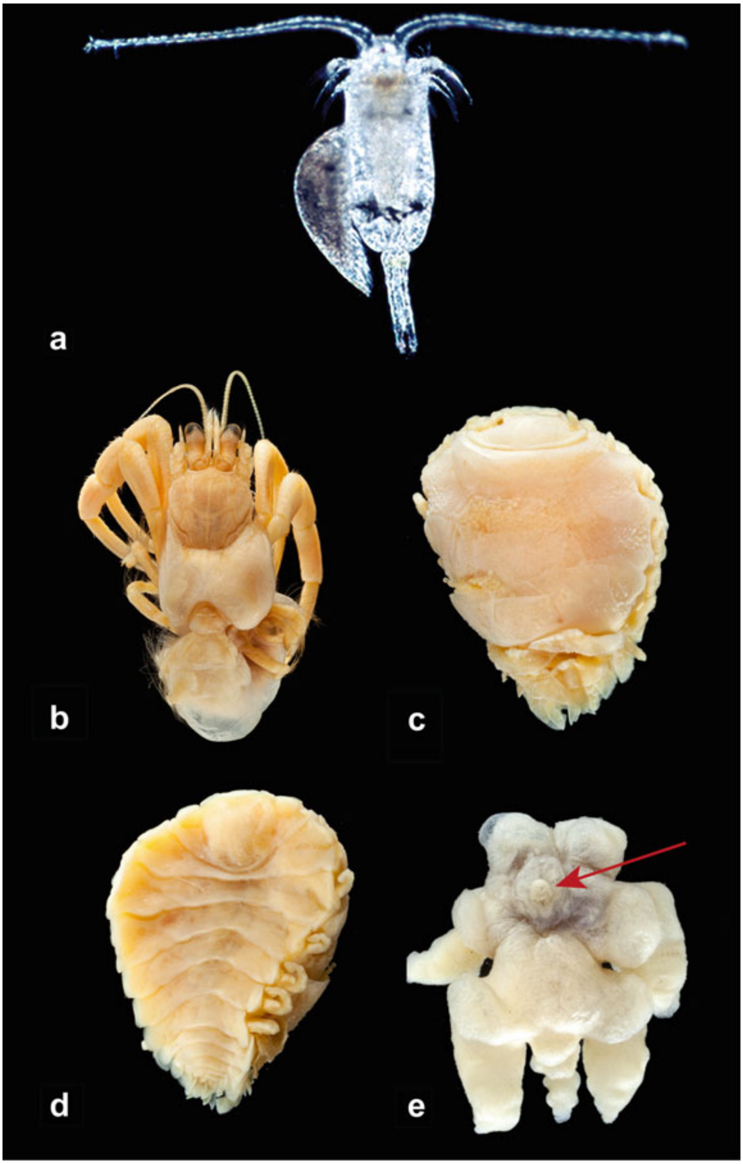

Fig. 3.2 Isopoda: Bopyroidea and Cryptoniscoidea. (**a**) microniscus larva attached to planktonic calanoid copepod, (**b**) bopyridised hermit crab, *Pagurus bernhardus* (Linnaeus, 1758), showing swelling on right side induced by presence of *Pseudione hyndmanni* (Bate & Westwood, 1867), (**c**) adult female *Pseudione hyndmanni*, ventral view showing expanded marsupium formed by oostegites, (**d**) adult female *P. hyndmanni*, dorsal view, (**e**) *Hemioniscus balani* Buchholz, 1866, ventral view showing defined head region (*arrow*). Images © Natural History Museum, London

Bopyroidea

Boyko et al. (2013) redefined the Bopyroidea as a monophyletic taxon consisting of three families, Bopyridae, Entoniscidae and Ionidae. This is a rapidly changing situation since Williams and Boyko (2012) included the Dajidae within the Bopyroidea (rather than the Cryptoniscoidea) and only accorded the Ionidae subfamily status as the Ioninae, within the Bopyridae. The Bopyroidea currently comprises 651 species, all of which are parasitic on decapod crustaceans (Table 3.3), and they can induce conspicuous swellings in the branchial chambers of their hosts (Fig. 3.2b).

The morphology of more basal bopyroideans is relatively little modified from free-living isopods but more derived forms can have highly transformed bodies, especially in the adult females, lacking externally expressed segmentation and with reduced limbs (Williams and Boyko 2012). The mature females are usually larger and more profoundly modified than adult males which retain a generalised, isopod-like body form. Females are often asymmetrical (Fig. 3.2c, d), and the oostegites forming the ventral brood pouch can be enlarged or even form attachment suckers, as in some Hemiarthrinae. The body segments carry large lateral plates in some species and their margins as well as the margins of the pleopods can show extensive digitations. Endoparasitic forms, such as the Entoniscidae, show the most extreme modifications, with females lacking expressed segmentation and with reduced or absent pereopods.

The preferred microhabitat of the parasite on its host largely follows taxon boundaries: members of the subfamilies Argeiinae, Bopyrinae, Keponinae (except *Rhopalione* Pérez, 1920), Orbioninae and Pseudioninae are typically found in the branchial chamber of their host, while members of the Athelginae, Phyllodurinae and most Hemiarthrinae are ectoparasitic on the abdomen of the host. Members of the Ionidae are also branchial parasites, while the Entoniscidae are endoparasites (Williams and Boyko 2012; Boyko et al. 2013).

Cryptoniscoidea

The revision by Boyko et al. (2013) included relatively few representatives of this superfamily, so relationships between the nine cryptoniscoidean families remain poorly understood. Boyko et al. (2013) transferred the Dajidae and Entophilinae from the Bopyroidea into the Cryptoniscoidea, raising the status of the latter from subfamily to family at the same time. There are 146 valid species of cryptoniscoideans, and they utilise a broad range of crustacean hosts including ostracods, barnacles, peracaridans, euphausiaceans and decapods (Table 3.3).

Dajid females are typically ovate and can be highly modified: some genera have chelate antennae to grip round the eyestalks of their euphausiacean hosts. The remaining eight families contain endoparasites or partially embedded mesoparasites of other crustaceans. These females can exhibit extreme modification with unsegmented sac-like bodies lacking limbs, including pereopods. In some families, such as the Hemioniscidae, females retain segmentation in the anterior part of the body only

Table 3.3 Species richness and host taxa of families and subfamilies of Epicaridea (Isopoda)

Family: subfamily	No. genera	No. species	Host group
Superfamily Bopyroidea[a]			
Bopyridae:			
Argeiinae	9	13	Decapoda: Caridea, Stenopodidea
Athelginae	9	44	Decapoda: Anomura
Bathygyginae	1	1	Decapoda: Caridea
Bopyrinae	27	123	Decapoda: Caridea
Hemiarthrinae	28	60	Decapoda: Caridea
Keponinae	31	94	Decapoda: Achelata, Axiidea, Brachyura, Gebiidea
Orbioninae	8	35	Decapoda: Dendrobranchiata
Phyllodurinae	1	1	Decapoda: Gebiidea
Pseudioninae	53	236	Decapoda: Anomura, Astacidea, Axiidea, Brachyura, Caridea, Gebiidea
Entoniscidae	16	36	Decapoda: Anomura, Brachyura, Caridea, Gebiidea
Ionidae	1	8	Decapoda: Axiidea
Superfamily Cryptoniscoidea			
Asconiscidae	1	1	Peracarida: Mysida
Cabiropidae	14	34	Peracarida: Isopoda
Crinoniscidae	1	3	Cirripedia: Thoracica
Cryptoniscidae	8	30	Cirripedia: Rhizocephala Decapoda
Cyproniscidae	2	8	Ostracoda
Dajidae	18	56	Peracarida: Isopoda, Mysida. Euphausiacea Decapoda: Dendrobranchiata, Caridea
Entophilidae	2	2	Decapoda: Anomura, Axiidea
Hemioniscidae	3	8	Cirripedia: Acrothoracica, Thoracica
Podasconidae	2	4	Peracarida: Amphipoda

Data from World Marine, Freshwater and Terrestrial Isopod Crustaceans database (Boyko et al. 2008 onwards)

[a] The monotypic family Colypuridae is based on a single male and its host is unknown: it is not included here

(Fig. 3.2e). Males have less modified, symmetrical bodies and generally resemble the cryptoniscus larval form (Hosie 2008). Most cryptoniscoideans are parasitic castrators, and this appears to result from the energy burden placed on the host (Williams and Boyko 2012).

Cymothooidea

The superfamily Cymothooidea comprises a cluster of families with a range of life styles and feeding modes that show a transition from a free-living, scavenging–predatory life style (Cirolanidae) to obligate parasitism in the Cymothoidae (Poore and Bruce 2012; Smit et al. 2014). Members of families such as the Aegidae, Corallanidae, Leptanthuridae, Paranthuridae and Tridentellidae are generally regarded as micro-predators as they only temporarily attach to 'hosts' in order to feed, and then detach before digestion (see Wägele 1981, 1985). Cirolanids are either predators or scavengers, although some enter loose symbiotic relationships: *Cartetolona* Bruce, 1981, for example, inhabits the oral disc of crinoids and *Neocirolana hermitensis* (Boone, 1918) inhabits shells housing hermit crabs (Poore and Bruce 2012) and may act as brood predators feeding on the eggs of the hermit (Bruce 1994). None is considered parasitic. The Corallanidae contains mostly marine species but some occur in brackish and fresh waters. Most are predatory but some live in symbiotic relationships with invertebrates, including sponges and palaemonid shrimps, fishes, and turtles (Delaney 1989; Williams et al. 1996). All Aegidae are micro-predators of marine fishes, attaching temporarily to feed on blood or mucus before detaching. Some species of aegid genera such as *Rocinela* Leach, 1818 and *Syscenus* Harger, 1880, remain attached to fish hosts for extended periods, and it has been suggested that some *Syscenus* may attach permanently (Ross et al. 2001; Bruce 2009; Poore and Bruce 2012). A small number of aegids has been reported in association with invertebrates, including sponges and ascidians (Bruce 2009). Species of the monogeneric family Tridentellidae have been found in association with fishes: information on their feeding biology is limited (Bruce 2008) but their rasping and incisory mouthparts may be indicative of micro-predation on fish.

Three subfamilies of Cymothoidae were recognised by Brusca and Wilson (1991): Anilocrinae containing external scale parasites (Fig. 3.3a–c) (sometimes burrowing beneath the host's skin), Cymothoinae (buccal cavity parasites, Fig. 3.3d–f) and the Livonecinae (gill parasites, Fig. 3.3g–i). The monophyly of the Cymothoidae was supported by Ketmaier et al. (2007) but their analysis suggested that the more specialised mouth- and gill-inhabiting species are not necessarily derived from scale-dwelling ones as hypothesised by Brusca (1981) (see also Bruce 1990). The morphological analysis of Hadfield (2012) recovered the subfamily Anilocrinae as a well-supported terminal clade, with the buccal-inhabiting taxa (such as *Cymothoa* Fabricius, 1793 and *Ceratothoa* Dana, 1852 (Fig. 3.3e, f)) forming a sister clade to the Anilocrinae, while the gill-attaching genera were basal and did not form a clade (Hadfield 2012; Smit et al. 2014). More unusual attachment modes include burrowing beneath the skin of the host to create a pocket or capsule within the musculature, as exhibited by freshwater genera such as *Artystone* Schioedte, 1860, *Riggia* Szidat, 1948 and *Ichthyoxenus* Herklots, 1870, and by one marine genus, *Ourozeuktes* Milne Edwards, 1840. *Riggia paransensis* Szidat, 1948 is effectively endoparasitic and is found in the peritoneal or pericardial cavities of its curimatid fish hosts (Bastos and Thatcher 1997; Hadfield 2012).

Members of the Cymothoidae (Table 3.4) are all obligate parasites of fishes; most parasitise actinopterygian fishes, particularly in warm temperate and tropical seas, although they also occur in fresh water. Cymothoids are also found on elasmobranchs and a few have been reported from jellyfish, cephalopods, crustaceans and amphibians (e.g. Trilles and Öktener 2004; Ateş et al. 2006) although these may be accidental. The family currently comprises 369 valid species placed in 43 genera (Table 3.4), but the status of many genera is uncertain (Smit et al. 2014). Host–parasite specificity is high

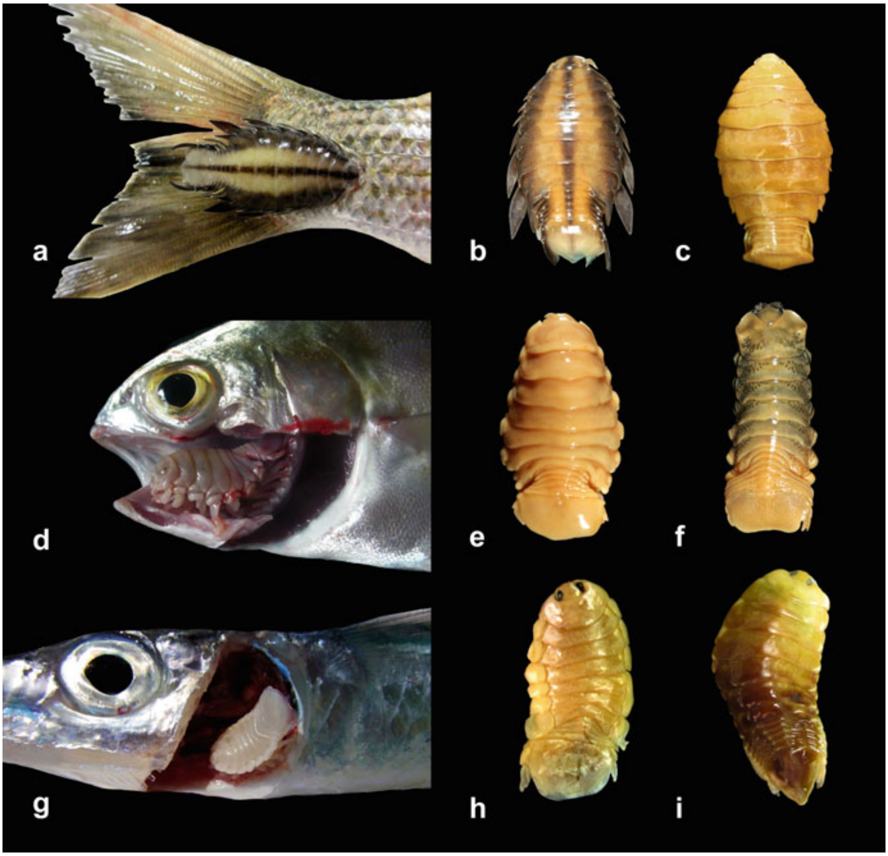

Fig. 3.3 Isopoda: Cymothoidae. (**a**) body surface cymothoid (*Nerocila monodi* Hale, 1940) on host; (**b**) *Nerocila* Leach, 1818; (**c**) *Anilocra* Leach, 1818; (**d**) "tongue biter" cymothoid (Cymothoa sodwana Hadfield, Bruce & Smit, 2013) attached in mouth of host; (**e**) *Cymothoa* Fabricius, 1793; (**f**) *Ceratothoa* Dana, 1852; (**g**) gill-inhabiting cymothoid (*Mothocya affinis* Hadfield, Bruce & Smit, 2015); (**i**) *Mothocya* Costa in Hope, 1851; (**j**) *Norileca* Bruce, 1990. Images © Kerry Hadfield and Nico Smit

in genera such as *Cymothoa*, *Idusa* Schioedte & Meinert, 1884 and *Mothocya* Costa in Hope, 1851, but relatively low in others, such as *Nerocila* Leach, 1818 and *Elthusa* Schioedte & Meinert, 1884 (Poore and Bruce 2012).

The site of attachment is reflected in the gross morphology of cymothoids. External and buccal cavity inhabiting taxa are usually symmetrical (Fig. 3.3b, c, e, f), while those inhabiting the gills or gill arches and operculum are often asymmetrical (Fig. 3.3h, i; Hadfield 2012). In cymothoids all seven pairs of pereopods are prehensile. The family is also characterised by the lack coupling setae on the endites of the maxilliped. Once an infective manca stage has found and attached to a suitable host it moults, loses its adaptations for swimming, and matures into an adult male. Cymothoids are protandric hermaphrodites, so after a period as a functional male, a cymothoid typically transforms into a female (Smit et al. 2014).

Table 3.4 Species richness, salinity regimes and hosts of genera of Cymothoidae (Isopoda). Data from World Marine, Freshwater and Terrestrial Isopod Crustaceans database (Boyko et al. 2008 onwards)

Genus	No. species	Salinity regime	Host group
Aegathoa Dana, 1853	2	Marine	Fish: Actinopterygii
Agarna Schioedte & Meinert, 1884	4	Marine	Fish: Actinopterygii
Amblycephalon Pillai, 1954	2	Marine	Fish: Actinopterygii
Anilocra Leach, 1818	50	Marine	Fish: Actinopterygii
Anphira Thatcher, 1993	4	Freshwater	Fish: Actinopterygii
Artystone Schioedte, 1866	3	Freshwater	Fish: Actinopterygii
Asotana Schioedte & Meinert, 1881	3	Freshwater	Fish: Actinopterygii
Braga Schioedte & Meinert, 1881	7	Freshwater	Fish: Actinopterygii
Catoessa Schioedte & Meinert, 1884	4	Marine	Fish: Actinopterygii
Ceratothoa Dana, 1852	30	Marine	Fish: Actinopterygii, Elasmobranchii
Cinusa Schioedte & Meinert, 1884	1	Marine	Fish: Actinopterygii
Creniola Bruce, 1987	3	Marine	Fish: Actinopterygii
Cterissa Schioedte & Meinert, 1884	2	Marine	Fish: Actinopterygii
Cymothoa Fabricius, 1793	49	Marine/ freshwater	Fish: Actinopterygii
Elthusa Schioedte & Meinert, 1884	32	Marine	Fish: Actinopterygii
Emetha Schioedte & Meinert, 1883	2	Marine	Fish: Actinopterygii
Glossobius Schioedte & Meinert, 1883	8	Marine	Fish: Actinopterygii
Ichthyoxenos Herklots, 1870	23	Marine/ freshwater	Fish: Actinopterygii
Idusa Schioedte & Meinert, 1884	3	Marine	Fish: Actinopterygii
Isonebula Taberner, 1977	2	Freshwater	Fish: Actinopterygii
Joryma Bowman & Tareen, 1983	4	Marine	Fish: Actinopterygii
Kuna Williams & Williams, 1986	1	Marine	Fish: Actinopterygii
Lathraena Schioedte & Meinert, 1881	1	Marine	Fish: Actinopterygii
Livoneca Leach, 1818	3	Marine	Fish: Actinopterygii, Elasmobranchii Mollusca: Cephalopoda [1 species]
Lobothorax Bleeker, 1857	3	Marine	Fish: Actinopterygii
Mothocya Costa in Hope, 1851	31	Marine	Fish: Actinopterygii
Nerocila Leach, 1818	42	Marine/ freshwater	Fish: Actinopterygii Reptilia [1 species]
Norileca Bruce, 1990	3	Marine	Fish: Actinopterygii
Olencira Leach, 1818	2	Marine	Fish: Actinopterygii
Ourozeuktes Milne Edwards, 1840	1	Marine	Fish: Actinopterygii
Paracymothoa Lemos de Castro, 1955	3	Freshwater	Fish: Actinopterygii

(continued)

Table 3.4 (continued)

Genus	No. species	Salinity regime	Host group
Philostomella Szidat & Schubart, 1960	1	Freshwater	Fish: Actinopterygii
Pleopodias Richardson, 1910	4	Marine	Fish: Actinopterygii
Plotor Schioedte & Meinert, 1881	1	Marine	Fish: Actinopterygii
Pseudoirona Pillai, 1964	1	Marine	Fish: Actinopterygii
Renocila Miers, 1880	18	Marine	Fish: Actinopterygii
Rhiothra Schioedte & Meinert, 1884	1	Marine	Fish: Actinopterygii
Riggia Szidat, 1948	5	Freshwater	Fish: Actinopterygii
Ryukyua Williams & Bunkley-Williams, 1994	2	Marine	Fish: Actinopterygii
Smenispa Özdikmen, 2009	2	Marine	Fish: Actinopterygii
Telothoa Schioedte & Meinert, 1884	4	Freshwater	Fish: Actinopterygii Crustacea: Decapoda
Tetragonocephalon Avdeev, 1978	1	Marine	Fish: Actinopterygii
Vanamea Thatcher, 1993	1	Freshwater	Fish: Actinopterygii

Gnathiidae

Gnathiid isopods have free-living, non-feeding adults that inhabit cavities in muddy sediments, in dead barnacles, or in sponges, but the juveniles feed on the blood of elasmobranch and actinopterygian fishes. Early juveniles, the unfed zuphea stage, have a thin non-calcified cuticle in the midsection of the pereon, which allows for engorgement while feeding on the blood of their hosts. An engorged juvenile (Fig. 3.4a) is commonly referred to as a “praniza larva”. The adult and juvenile stages of gnathiid isopods are highly polymorphic, and adult gnathiids exhibit strong sexual dimorphism (Fig. 3.4b, c). Currently there are 226 valid species but adult female gnathiids are almost indistinguishable at the species level. The existing taxonomy of the family is largely based on characters of adult males, as enumerated by Cohen and Poore (1994). The juveniles have large eyes, long setae on the pleopods and uropods, and five pairs of mouthparts (mandibles, paragnaths, maxillules, maxillipeds and gnathopods) which provide important features for differentiating between species.

Gnathiids are unique among the Isopoda in having a pereon with only five pairs of ambulatory pereopods, in contrast to the usual seven in other isopods. The second pereonal segment is also fused with the cephalothorax, and its limbs form an additional pair of mouthparts (= gnathopods) in the juvenile stages, which are used for attachment to the host. In adults the gnathopods are modified as pylopods. Adult males are characterised by the frontal forceps (Fig. 3.4b), formed from the development of anteriorly-directed mandibles (Smit and Davies 2004). In adult females (Fig. 3.4c) the mouthparts are reduced or absent, with no mandibles.

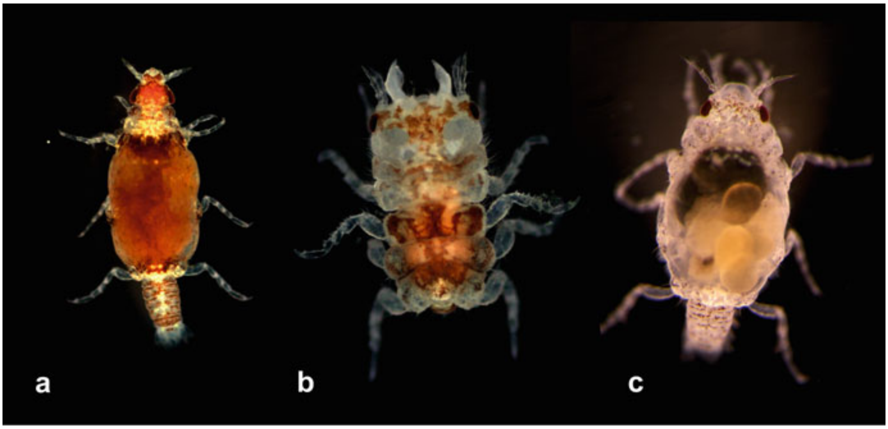

Fig. 3.4 Isopoda: Gnathiidae: *Gnathia pilosus* Hadfield, Smit & Avenant-Oldewage, 2008. (**a**) adult male showing enlarged, anteriorly-directed mandibles; (**b**) adult female, carrying developing eggs within swollen pereon; (**c**) praniza larva showing expanded midsection of pleon. Images © Kerry Hadfield

The Gnathiidae is classified within the Cymothooidea (Brandt and Poore 2003; Boyko et al. 2013) but some recent phylogenetic studies and studies on the juvenile stages have cast doubt on this (see Wilson et al. 2011). Gnathiids exhibit features that distinguish them from other cymothooideans: the lack of the characteristic frontal lamina, for example, serves to distinguish them from all except the Cymothoidae itself. Wilson (2009) cast doubt on the unity of Cymothoida after analysis of combined 18S rDNA and morphological data, although the taxon set for his study included only a single gnathiid (*Paragnathia formica* (Hesse, 1884)).

Life cycles have been fully elucidated in relatively few species, representing only four genera, *Caecognathia* Dollfus, 1901, *Elaphognathia* Monod, 1926, *Gnathia* Leach, 1814 and *Paragnathia* Omer-Cooper & Omer-Cooper, 1916. The life cycles of these four genera are broadly similar but all examples involve actinopterygian hosts (see Smit and Davies 2004); no life cycles are available for gnathiids feeding on elasmobranchs. Gnathiids are unique in having only three post-marsupial stages before the adult (Wilson et al. 2011). The zuphea stage, or unfed juveniles, are fully segmented and occur prior to feeding. Praniza juveniles (Fig. 3.4a) are fed or partially fed individuals showing considerable expansion of the body, facilitated by the elastic membrane of pereonal segment 5 (see Smit and Davies 2004; Wilson et al. 2011). Blood feeding occurs three times, once at each juvenile stage. The duration of feeding varies between species, from a few hours for juveniles feeding on teleosts (Grutter 2003; Smit et al. 2003) to several days for those feeding on elasmobranchs (McKiernan et al. 2005).

3.2.1.4 Tanaidacea

More than 1000 species of tanaids are known and these are all free-living or tube-dwelling detritivores with a single exception, *Exspina typica* Lang, 1968. This widespread deep-sea species has been repeatedly found within the body cavity and intestine of abyssal holothurians and it is known to actively tunnel into the body wall of its host (Alvaro et al. 2011).

3.2.2 Thecostraca

The Thecostraca comprises three main sub-groups, the Facetotecta, Ascothoracida and Cirripedia, with the latter consisting of the Acrothoracica, Thoracica and Rhizocephala. All adult thecostracans are sessile and are linked by the shared possession of a cypridoid larval stage, known variously as the cyprid in Cirripedia, the a-cyprid in Ascothoracida and as y-cypris in Facetotecta. The cypridoid larva has characteristic features such as lattice organs, which are synapomorphies for the Thecostraca as a whole (see Høeg et al. 2009). The Ascothoracida and Rhizocephala have independently adopted parasitism as a mode of life (Pérez-Losada et al. 2009), and the Facetotecta, known only from their larvae, are also presumed to have parasitic adults (Glenner et al. 2008). The Acrothoracica and the Thoracica are predominantly suspension feeders but many thoracicans live in symbiotic associations and a few have become parasitic.

3.2.2.1 Ascothoracida

The Ascothoracida comprises 104 valid species classified in 2 suborders, the Dendrogastrida and Laurida. The former comprises 48 species, all of which are parasites of echinoderms, while the 56 species within the latter predominantly use cnidarians as hosts (Table 3.5), with the exception of the synagogid genus *Waginella* Grygier, 1983, which is found on crinoid echinoderms. All ascothoracidans are marine and they are known from the intertidal to the deep sea.

The basic body plan of an adult ascothoracidan consists of a head plus an 11-segmented postcephalic trunk, all enclosed within a bivalve carapace, the valves of which contain gut diverticulae and the reproductive organs. The head carries prehensile clawed antennules with up to six expressed segments, plus an oral cone with associated piercing and sucking mouthparts. More transformed genera, such as *Ulophysema* Brattström, 1936 and *Dendrogaster* Knipovich, 1890 (Fig. 3.5), employ absorptive feeding through the modified integument of the carapace. The trunk bears six pairs of biramous swimming legs, plus genitalia in the adult male, and terminates in paired caudal rami. This basic organisation is best exhibited by the synagogid genera *Waginella* and *Synagoga* Norman, 1888, but most ascothoracids

Table 3.5 Classification, species richness and host utilisation of the Ascothoracida ($n = 104$)

Family and genus	No. species	Host group
Order Dendrogastrida		
Ascothoracidae		
Ascothorax Djakonov, 1914	8	Echinodermata: Ophiuroidea
Parascothorax Wagin, 1964	1	Echinodermata: Ophiuroidea
Ctenosculidae		
Ctenosculum Heath, 1910	1	Echinodermata: Asteroidea
Endaster Grygier, 1985	1	Echinodermata: Asteroidea
Gongylophysema Grygier, 1987	1	Echinodermata: Asteroidea
Dendrogastridae		
Bifurgaster Stone & Moyse, 1985	3	Echinodermata: Asteroidea
Dendrogaster Knipovich, 1890	31	Echinodermata: Asteroidea
Ulophysema Brattström, 1936	2	Echinodermata: Echinoidea
Order Laurida		
Lauridae		
Baccalaureus Broch, 1929	12	Cnidaria: Zoantharia
Laura Lacaze-Duthiers, 1865	3	Cnidaria: Zoantharia
Polymarsypus Grygier, 1985	1	Cnidaria: Zoantharia
Zoanthoecus Grygier, 1985	2	Cnidaria: Zoantharia
Petrarcidae		
Introcornia Grygier, 1983	2	Cnidaria: Scleractinia
Scleractinia*Petrarca* Fowler, 1889	8	Cnidaria: Scleractinia
Zibrowia Grygier, 1985	1	Cnidaria: Scleractinia
Synagogidae		
Cardomanica Lowry, 1985	3	Cnidaria: Alcyonacea
Flatsia Grygier, 1991	1	Unknown
Gorgonolaureus Utinomi, 1962	6	Cnidaria: Gorgonacea
Isidascus Moyse, 1983	1	Cnidaria: Alcyonacea
Sesillogoga Grygier, 1990	1	Cnidaria: Antipatharia
Synagoga Norman, 1888	5	Cnidaria: Antipatharia
Thalassomembracis Grygier, 1984	7	Cnidaria: Alcyonacea
Waginella Grygier, 1983	3	Echinodermata: Crinoidea

Data from World Ascothoracida database (Grygier 2018)

have modified bodies especially in the adult female. The trunk appendages and abdomen tend to be reduced, while the carapace is often enlarged to form a brood chamber. In highly transformed taxa, such as *Dendrogaster*, the brood chamber can be lobed or branched (Fig. 3.5a, b) and can attain lengths up to 16 cm, occupying much of the main body cavity of the starfish host (Grygier and Høeg 2005).

The more basal ascothoracids such as *Synagoga* are ectoparasitic, but most genera are meso- or endoparasitic. Mesoparasitic forms may be found in a body cavity of the host, such as *Ascothorax* Djakonov, 1914 species inhabiting the genital bursae of ophiuroids or in galls or cysts which open to the external environment,

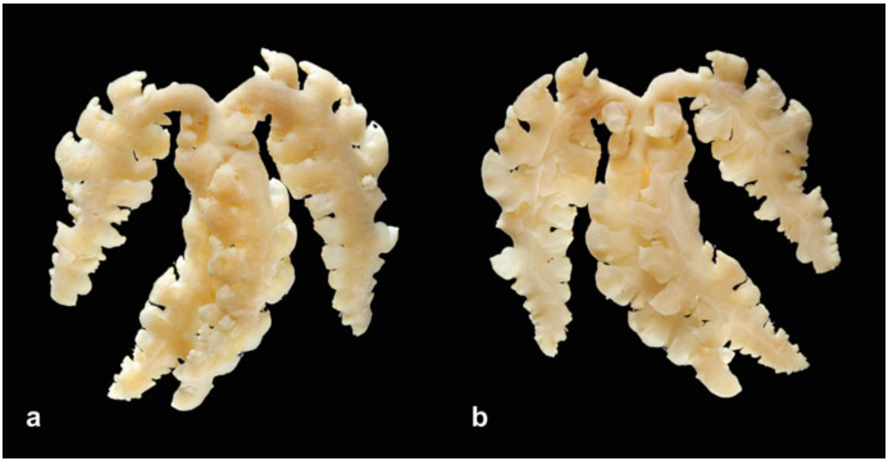

Fig. 3.5 Thecostraca: Ascothoracida. Adult holotype female of *Dendrogaster zoroasteri* Stone, 1987, showing lobate, branching brood chamber. (**a**) dorsal view, (**b**) ventral view. Images © Natural History Museum, London

such as *Gorgonolaureus* Utinomi, 1962 on its gorgonian hosts. The most highly modified forms are endoparasitic and these occur in galls in their scleractinian hosts (e.g. *Petrarca* Fowler, 1889) or in the body cavity of their echinoderm hosts (e.g. *Ulophysema* and *Dendrogaster*).

3.2.2.2 Facetotecta

The Facetotecta currently comprises 11 nominal species placed in a single, recently established genus, *Hansenocaris* Itô, 1985, based on free-swimming larvae. Prior to Îto (1985) the so-called y-larvae were not formally named, and it is clear that the species richness is considerably higher, given that Grygier (1991) recorded over 40 putative species at a single shallow coastal locality in the tropics. The y-nauplius moults into the y-cypris which has a cypridoid facies, with the body enclosed in a bivalved carapace and divided into a head bearing modified antennules and a ten-segmented postcephalic trunk bearing six pairs of biramous swimming legs anteriorly. Glenner et al. (2008) experimentally induced the y-cypris to moult into a vermiform ypsigon larva, which they inferred was the first parasitic stage, based on its resemblance to the vermigon stage of rhizocephalan cirripedes. However, in the absence of information on the presumed parasitic adults, the hosts are currently unknown.

3.2.2.3 Cirripedia

The cirripedes are extremely heterogeneous in adult body form but they share important larval characteristics. The detailed analysis by Høeg et al. (2009) showed that all cirripedes share the possession of paired frontolateral horns on the nauplius stage and numerous detailed features of the cyprid larva including lattice organ 2 with a large, anteriorly located terminal pore, antennule with attachment disc covered with microvilli, and rudimentary or absent abdomen. These features serve as apomorphies shared by the Acrothoracica, Thoracica and Rhizocephala. The acrothoracicans burrow into calcareous substrates and lack shell plates but they are typical suspension feeders. Of the other two groups, the Rhizocephala is wholly parasitic while the Thoracica (including the iblomorphs) are predominantly suspension feeders but include many commensals and a few parasitic forms.

Rhizocephala

The Rhizocephala is a well-defined monophyletic group within the Cirripedia (Pérez-Losada et al. 2009). All rhizocephalan barnacles are parasitic and the main hosts are decapod malacostracans (Fig. 3.6a–c), in particular members of the Brachyura and Anomura but also including some Caridea and Axiidea. In addition, a few species parasitise other malacostracans, from the Stomatopoda, Isopoda and Cumacea, while the four species of Chthamalophilidae are found on thoracican barnacle hosts (Table 3.6). There are two orders, Akentrogonida and Kentrogonida, distinguished by the absence or presence of a kentrogon in the infective cyprid larva, respectively. However, recent studies (see Glenner et al. 2010) suggest that the Akentrogonida are more derived and emerge from within the Kentrogonida and therefore that the latter is paraphyletic. Currently 288 valid species are recognised and classified in ten families (Table 3.6). Virtually all species are marine but there are exceptions: *Polyascus gregaria* (Okada & Miyashita, 1935) occurs on the riverine crab *Eriocheir japonicus* (De Haan, 1835), but does not release its free-swimming larvae until it returns to the estuary to breed, and the genera *Sesarmaxenos* Annandale, 1911 and *Ptychascus* Boschma, 1933 are found on semiterrestrial crabs and have abbreviated development in which the free nauplius phase is lacking (Andersen et al. 1990).

Adult female rhizocephalans have highly transformed bodies consisting of an external reproductive sac (the externa) connected to a system of branching rootlets that ramify within the host and absorb nutrients (Høeg and Lützen 1985). The form of the rootlet system (the interna) is variable: typically it infiltrates through the body and may even penetrate the limbs of the host. Nutrients are absorbed through the delicate cuticle and transported along the lumen of the rootlets and into the externa. The externa (Fig. 3.6a–d) contains the visceral mass, the nervous system in the form of a ganglion and the reproductive apparatus. It is bounded by an extensive mantle, enclosing a mantle cavity opening to the environment typically by a single mantle

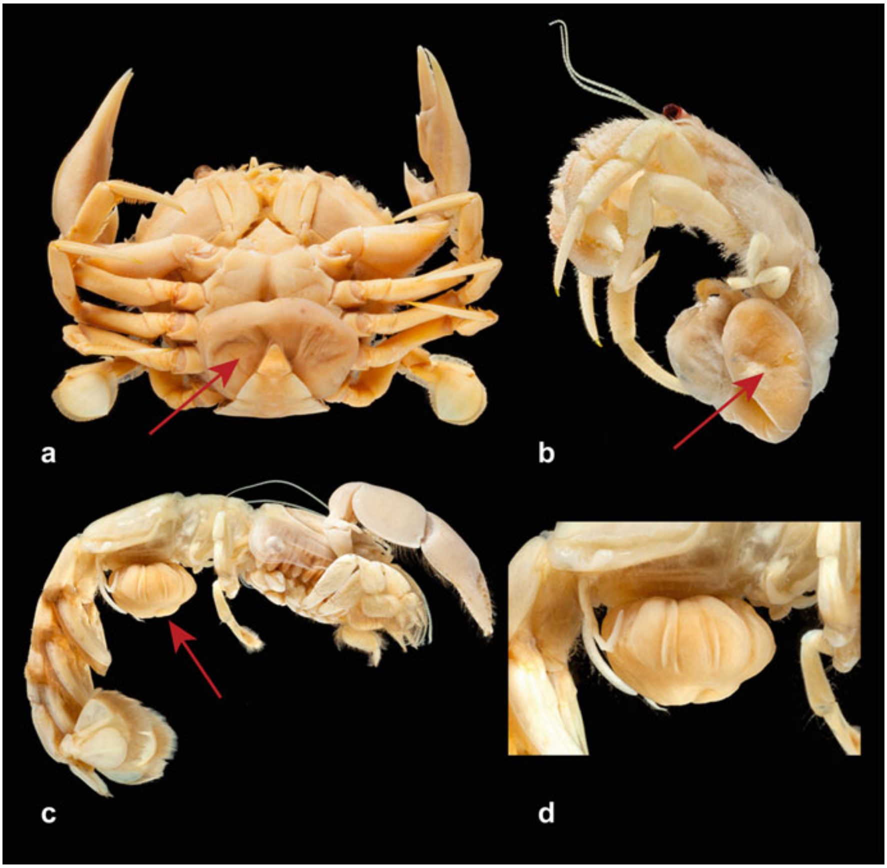

Fig. 3.6 Thecostraca: Rhizocephala. (**a**) externa of *Sacculina carcini* Thompson, 1836 (*arrow*), beneath abdomen of crab (*Liocarcinus holsatus* (Fabricius, 1798)); (**b**) externa of *Peltogaster paguri* Rathke, 1842, attached laterally (*arrow*) on pleon of hermit crab (*Pagurus bernhardus* (Linnaeus, 1758)); (**c**) externa of *Parthenopea subterranea* Kossmann, 1874, attached ventrally (*arrow*) on pleon of mud-shrimp (*Pestarella tyrrhena* (Petagna, 1792)); (**d**) externa of *Parthenopea subterranea.* Images © Natural History Museum, London

opening. The ovaries are paired and discharge eggs into the mantle cavity via paired collateric glands which produce a secretion that binds the eggs together. The externa also contains one or a pair of seminal receptacles, formerly thought to be testes, but now known to contain spermatogenic cells implanted by male trichogon larvae (Yanagimachi 1961; Høeg et al. 2005). The life cycles of akentrogonids differ in several respects from those of kentrogonids (Bocquet-Vedrine 1957; Diechmann and Høeg 1990) and were summarised by Glenner et al. (2010). The complex life histories of the Rhizocephala are dealt with in Chap. 9 of this volume.

Species of the sacculinid genus *Polyascus* Glenner, Lützen & Takahashi, 2003 produce multiple externae on a single rootlet system within the host, and these

Table 3.6 Species richness of Rhizocephala and host taxa

Family and genus	No. species	Host group
Order Akentrogonida		
Chthamalophilidae		
Bocquetia Pawlik, 1987	1	Cirripedia: Balanomorpha
Boschmaella Bocquet-Védrine, 1968	2	Cirripedia: Balanomorpha
Chthamalophilus Bocquet-Védrine, 1957	1	Cirripedia: Balanomorpha
Clistosaccidae		
Clistosaccus Lilljeborg, 1861	1	Decapoda: Anomura
Sylon Sars, 1870	1	Decapoda: Caridea
Duplorbidae		
Arcturosaccus Rybakov & Høeg, 1992	1	Peracarida: Isopoda
Cryptogaster Bocquet-Védrine & Bourdon, 1957	1	Peracarida: Cumacea
Duplorbis Smith, 1906	3	Peracarida: Isopoda
Mycetomorphidae		
Mycetomorpha Potts, 1912	2	Decapoda: Caridea
Polysaccidae		
Polysaccus Høeg & Lützen, 1993	2	Decapoda: Axiidea
Thompsoniidae		
Diplothylacus Høeg & Lützen, 1993	4	Decapoda: Brachyura
Jensia Boyko & Williams in Hiller, Williams & Boyko, 2015	2	Stomatopoda. Decapoda: Caridea
Thompsonia Kossmann, 1872	5	Decapoda: Anomura, Brachyura
Thylacoplethus Coutière, 1902	13	Stomatopoda. Decapoda: Anomura, Brachyura, Caridea
Family uncertain		
Pirusaccus Lützen, 1985	1	Decapoda: Anomura
Order Kentrogonida		
Lernaeodiscidae		
Lernaeodiscus Müller, 1862	8	Decapoda: Anomura
Septodiscus Van Baal, 1937	1	Decapoda: Anomura
Triangulopsis Guérin-Ganivet, 1911	1	Decapoda: Anomura
Triangulus Smith, 1906	6	Decapoda: Anomura
Parthenopeidae		
Parthenopea Kossmann, 1874	2	Decapoda: Axiidea
Peltogastridae		
Angulosaccus Reinhard, 1944	1	Decapoda: Anomura
Boschmaia Reinhard, 1944	1	Decapoda: Anomura
Briarosaccus Boschma, 1930	4	Decapoda: Anomura
Cyphosaccus Reinhard, 1958	4	Decapoda: Anomura
Dipterosaccus van Kampen & Boschma, 1925	2	Decapoda: Anomura
Galatheascus Boschma, 1929	2	Decapoda: Anomura

(continued)

Table 3.6 (continued)

Family and genus	No. species	Host group
Ommatogaster Yoshida & Osawa, in Yoshida, Osawa, Hirose & Hirose, 2011	1	Decapoda: Anomura
Peltogaster Rathke, 1842	16	Decapoda: Anomura
Peltogasterella Krüger, 1912	4	Decapoda: Anomura
Pterogaster Van Baal, 1937	2	Decapoda: Anomura
Septosaccus Duboscq, 1912	4	Decapoda: Anomura
Temnascus Boschma, 1951	1	Decapoda: Anomura
Tortugaster Reinhard, 1948	3	Decapoda: Anomura
Trachelosaccus Boschma, 1928	1	Decapoda: Caridea
Sacculinidae		
Drepanorchis Boschma, 1927	5	Decapoda: Brachyura
Heterosaccus Smith, 1906	15	Decapoda: Brachyura
Loxothylacus Boschma, 1928	28	Decapoda: Brachyura
Polyascus Glenner, Lützen & Takahashi, 2003	3	Decapoda: Brachyura
Ptychascus Boschma, 1933	2	Decapoda: Brachyura
Sacculina Thompson, 1836	129	Decapoda: Brachyura
Sesarmaxenos Annandale, 1911	2	Decapoda: Brachyura

Data from World Register of Marine Species (WoRMS 2018)

originate by asexual reproduction from a single infective cypris larva (Glenner et al. 2003). Asexual propagation by means of budding has arisen independently several times within the Rhizocephala: in a few species in two families of kentrogonids, Sacculinidae and Peltogastridae, and in three families of akentrogonids.

Thoracica

The Thoracica is the largest taxon within the Thecostraca and it currently contains over 1400 valid species, the vast majority of which are sessile suspension feeders—typical barnacles. The sessile or acorn barnacles form a monophyletic group, the Sessilia, which comprises the asymmetrical Verrucomorpha and the Balanomorpha. The classification of the pedunculate or stalked barnacles is in a state of flux since the most recent analysis (Rees et al. 2014) failed to recover two of the major traditional pedunculate taxa, the Scalpellomorpha and Lepadomorpha, as monophyletic groups. Many thoracican barnacles live in symbiotic relationships: for example, pyrgomatids inhabit scleractinian corals; *Koleolepas* Stebbing, 1900 is associated with sea anemones; many *Acasta* Leach, 1817 species are associated with sponges; *Poecilasma* Darwin, 1852 and *Octolasmis* Gray, 1825 species with decapod crustaceans; and *Alepas* Rang, 1829 species with pelagic cnidarians. In their review of Taiwanese pyrgomatids, Chan et al. (2013) referred to these barnacles as episymbionts on their coral hosts. However, undischarged coral nematocysts have been found in the barnacle gut and there is some evidence that the barnacles might ingest organic matter and zooxanthellae expelled by the coral (Achituv et al. 1997). In addition, the pyrgomatid *Hoekia* Ross & Newman, 1973 has been reported using its cirri to feed on host tissue (Ross and Newman 1969), and Thamrín et al. (2001) reported a decrease in fecundity of host polyps adjacent to specimens of *Cantellius pallidus* (Broch, 1931). Several of these thoracican lineages have scattered representatives that have crossed over the line into parasitism.

Heteralepadomorph pedunculate barnacles typically live in symbiotic associations, many inhabiting the gills of decapods, and they typically have reduced or absent valves. Most heteralepadomorphs are treated as commensals, but *Koleolepas* species participate in a tripartite symbiosis; they live on gastropod shells inhabited by hermit crabs and carrying sea anemones. They are typically attached beneath the pedal disc of the anemone and feed by cropping its tentacles (Yusa and Yamato 1999).

So the sessile epibiontic mode of life, living attached to or partly embedded in a host, has led to obligate symbioses with host taxa, and it appears that on numerous occasions thoracican barnacles have exploited the host as an available food source and have thus moved from a commensal to a parasitic life style. A few thoracican barnacles have switched more dramatically from the ancestral suspension feeding to a clearly parasitic mode of life. These can use either vertebrates or invertebrates as hosts: for example, *Anelasma squalicola* Darwin, 1852 is found on deep-sea sharks, typically embedded in the skin behind the dorsal fin (Rees et al. 2014), while *Rhizolepas* Day, 1939 species are parasitic on marine polychaete hosts (Day 1939). Both *Anelasma* Darwin, 1852 and *Rhizolepas* have an atrophied suspension-feeding apparatus and absorb nutrients from the host via an embedded rootlet system.

3.2.3 Tantulocarida

All tantulocaridans are minute ectoparasites of marine crustacean hosts (Table 3.7) and they have been found in all temperature regimes from the poles to the tropics, and over an enormous range of depths from shallow coastal waters to the deep ocean (Mohrbeck et al. 2010). They attach permanently to the outer surface of their crustacean host by means of the adhesive oral disc of the tantulus (Fig. 3.7a), the infective larval stage (Boxshall and Lincoln 1987). Tantulocaridans exhibit varying degrees of host specificity: members of the family Basipodellidae occur only on copepod hosts, the Doryphallophoridae occur only on isopod hosts and the Microdajidae and Onceroxenidae only on tanaids, in contrast to the Cumoniscidae which have been reported from a wide range of peracaridan (Amphipoda, Cumacea, Isopoda and Tanaidacea), ostracod and copepod hosts. The main asexual cycle was elucidated by Boxshall and Lincoln (1987), who also described the sexual male, and the sexual cycle was completed by the discovery of the sexual female by Huys et al. (1993). The sexual adults probably inhabit the hyperbenthic zone, just above the sea bed. The free-living larval phase was studied in detail by Huys (1991).

Table 3.7 Species of Tantulocarida ($n = 38$) and their hosts

Family and species	Host group
Basipodellidae	
Basipodella atlantica Boxshall & Lincoln, 1983	Copepoda: Harpacticoida: Tisbidae
Basipodella harpacticola Becker, 1975	Copepoda: Harpacticoida: Cletodidae
Hypertantulus siphonicola Ohtsuka & Boxshall, 1998	Copepoda: Siphonostomatoida: Asterocheridae
Nipponotantulus heteroxenus Huys, Ohtsuka & Boxshall, 1994	Copepoda: Calanoida: Pseudocyclopiidae
Polynyapodella ambrosei Huys, Møbjerg & Kristensen, 1997	Copepoda: Harpacticoida: Cerviniidae
Polynyapodella thieli Martinez Arbizu & Petrunina, 2017	Unknown (free in sediment)
Rimitantulus hirsutus Huys & Conroy-Dalton, 1997	Copepoda: Harpacticoida: Argestidae
Serratotantulus chertoprudae Savchenko & Kolbasov, 2009	Copepoda: Harpacticoida: Cletodidae
Stygotantulus stocki Boxshall & Huys, 1989	Copepoda: Canuelloida: Canuellidae, Tisbidae
Cumoniscidae (syn. Deoterthridae)	
Amphitantulus harpiniacheres Boxshall & Vader, 1993	Amphipoda: Phoxocephalidae
Aphotocentor styx Huys, 1991	Unknown (free in sediment)
Arcticotantulus kristenseni Knudsen, Kirkegaard & Olesen, 2009	Copepoda: Harpacticoida: Ectinosomatidae
Arcticotantulus pertzovi Kornev, Tchesunov & Rybnikov, 2004	Copepoda: Harpacticoida: Ectinosomatidae
Boreotantulus kunzi Huys & Boxshall, 1988	Copepoda: Harpacticoida: Cylindropsyllidae
Campyloxiphos dineti Huys, 1990	Copepoda: Harpacticoida: Zosimidae
Coralliotantulus coomansi Huys, 1991	Copepoda: Canuelloida: Longipediidae
Cumoniscus kruppi Bonnier, 1903	Cumacea: Leuconidae
Deoterthron dentatum Bradford & Hewitt, 1980	Ostracoda: Myodocopida: Cypridinidae
Deoterthron lincolni (Boxshall, 1988)	Copepoda: Harpacticoida: Miraciidae
Dicrotrichura tricincta Huys, 1989	Unknown (free in sediment)
Itoitantulus misophricola Huys, Ohtsuka, Boxshall & Itô, 1992	Copepoda: Misophrioida: Misophriidae
Tantulacus coroniporus Martinez Arbizu & Petrunina, 2017	Unknown (free in sediment)
Tantulacus dieteri Mohrbeck, Martinez Arbizu & Glatzel, 2010	Unknown (free in sediment)
Tantulacus hoegi Huys, Andersen & Kristensen, 1992	Unknown (free in sediment)
Tantulacus karolae Mohrbeck, Martinez Arbizu & Glatzel, 2010	Unknown (free in sediment)
Tantulacus longispinosus Mohrbeck, Martinez Arbizu & Glatzel, 2010	Unknown (free in sediment)

(continued)

Table 3.7 (continued)

Family and species	Host group
Doryphallophoridae	
Doryphallophora aselloticola (Boxshall & Lincoln, 1983)	Isopoda: Haploniscidae
Doryphallophora harrisoni (Boxshall & Lincoln, 1987)	Isopoda: Macrostylidae
Doryphallophora megacephala (Lincoln & Boxshall, 1983)	Isopoda: Haploniscidae
Paradoryphallopora inusitata Ohtsuka & Boxshall, 1998	Isopoda: Haploniscidae
Microdajidae	
Microdajus aporosus Grygier & Sieg, 1988	Tanaidacea: Nototanaidae
Microdajus gaelicus Boxshall & Lincoln, 1987	Tanaidacea: Typhlotanaidae
Microdajus langi Greve, 1965	Tanaidacea: Anarthruridae, Leptognathiidae, Typhlotanaidae
Microdajus pectinatus Boxshall, Huys & Lincoln, 1987	Tanaidacea: Typhlotanaidae
Microdajus tchesunovi Kolbasov & Savchenko, 2010	Tanaidacea: Nototanaidae
Xenalytus scotophillus Huys, 1991	Unknown (free in sediment)
Onceroxenidae	
Onceroxenus birdi Boxshall & Lincoln, 1987	Tanaidacea: Agathotanaidae
Onceroxenus curtus Boxshall & Lincoln, 1987	Tanaidacea: Leptognathiidae

Data from World Register of Marine Species (Walter and Boxshall 2018)

The Tantulocarida was established by Boxshall and Lincoln in 1983 and remains a small taxon, currently comprising just 38 nominal species placed in 22 genera and 5 families (Table 3.7), although its true diversity is undoubtedly underestimated as these parasites are often overlooked because of their minute size (Mohrbeck et al. 2010).

Tantulocaridans have a double life cycle comprising sexual and asexual phases. The body of the adult asexual female consists of a minute head, neck, and an unsegmented sac-like trunk (Fig. 3.7a), and it attains a maximum length of about 1.5 mm (Boxshall and Vader 1993). The animal is secured to the cuticle of its host by an oral disc, about 12–15 μm in diameter. There is an absorptive rootlet system extending from the pore in the centre of the oral disc into the host (Petrunina et al. 2014). This female has no limbs and no genital apertures. The trunk of the female expands to accommodate the batch of developing tantulus larvae until they are released, apparently by rupture of the trunk wall (Boxshall and Lincoln 1987).

The body of the sexual female (Fig. 3.7b) consists of an anterior cephalothorax and a five-segmented postcephalic trunk and is typically less than 0.5 mm in length. The large cephalothorax carries a pair of sensory antennules but no mouthparts. The ovary is contained within the cephalothorax and a conspicuous median genital opening, interpreted as a copulatory pore, is present ventrally (Huys et al. 1993). The first two trunk segments each carry a pair of biramous thoracic legs, which

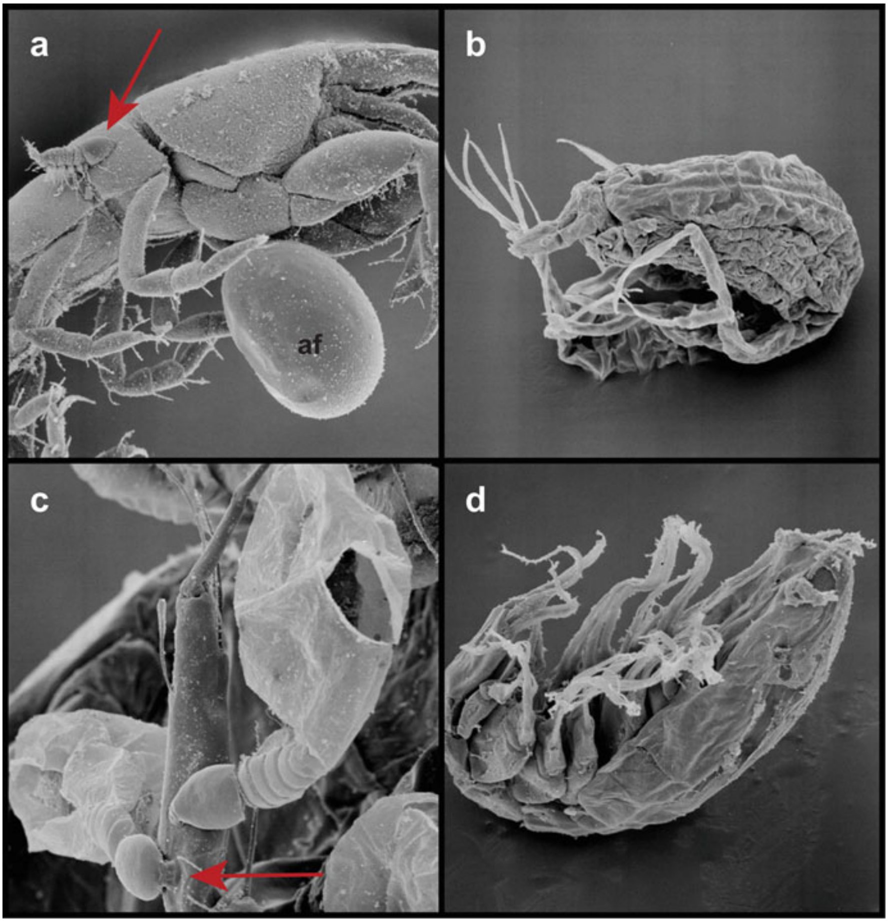

Fig. 3.7 Tantulocarida. (**a**) anterior end of tanaidacean host carrying tantulus larva (*arrow*) and asexual female (af) of *Microdajus pectinatus* Boxshall, Huys & Lincoln, 1988; (**b**) adult sexual female of *Itoitantulus misophricola* Huys, Ohtsuka, Boxshall & Itô, 1992, dissected out of trunk sac; (**c**) two empty expanded trunk sacs of Microdajus pectinatus attached by oral disc (arrow) of preceding tantulus stage; (**d**) adult sexual male of Microdajus pectinatus, dissected out of trunk sac. Images (**a**) and (**d**) © Natural History Museum, London; image (**b**) reproduced with permission from *Journal of Crustacean Biology*; image (**c**) reproduced with permission from *Systematic Parasitology*

appear to be used for grasping. The third and fourth segments are limbless, and the fifth segment bears paired, setose, caudal rami.

The adult male (Fig. 3.7c) resembles the sexual female in size and basic body plan, consisting of a large cephalothorax and six-segmented trunk. Males have more limbs: vestigial sensory antennules, six pairs of swimming legs (the first five biramous and the sixth uniramous), plus a well-developed median penis which is used to inseminate the sexual female. The male has paired clusters of chemosensory aesthetascs representing the antennules, which it is presumed to use to locate a receptive sexual female.

Knowledge of tantulocaridan biology is fragmentary. They spend most of their lives attached to their marine crustacean hosts. The tantulus larva functions as the infective stage in the life cycle, and free larvae can be common in marine sediments (Mohrbeck et al. 2010). The tantulus larva (Fig. 3.7a) has a body length between 85 μm and 180 μm and comprises a head, which has an oral disc but lacks any cephalic limbs, and a postcephalic trunk of eight segments, terminating in an anal segment bearing a pair of caudal rami. The first five trunk segments have biramous swimming legs and the sixth has a pair of uniramous legs. The setation and segmentation of the legs provide important taxonomic characters. How the infective larvae locate and attach to suitable hosts is poorly understood as they lack antennules and eyes, the main sensory interfaces of other crustaceans.

After infection the attached larva punctures the host cuticle using the oral stylet which is protruded through a pore in the centre of the oral disc. The cephalic musculature that operates the stylet subsequently degenerates (Huys 1991). The tantulus larva can develop into an asexual female, and the postcephalic trunk of the larva is shed, so the sac-like female remains attached by the adhesive oral disc of the preceding larval stage. Alternatively, in the sexual phase, the infective tantulus attaches by its oral disc and the trunk expands to form a sac (Fig. 3.7d) within which a single sexual adult, either male or female, develops.

3.2.4 Copepoda

Copepods are small but extremely abundant crustaceans which occur in every type of aquatic habitat. Free-living forms dominate the marine zooplankton community, and benthic copepods are second only to nematodes in abundance in the marine meiofauna. In fresh waters, copepods are abundant in both lotic and lentic epigean habitats, and they are often highly speciose in hypogean waters (Boxshall and Defaye 2008). Copepods also live in symbiotic association with hosts representing at least 14 marine metazoan phyla (Huys and Boxshall 1991; Boxshall and Halsey 2004).

Ten orders of copepods were recognised by Huys and Boxshall (1991) in their review of copepod phylogeny. However, the distinction between the Cyclopoida and Poecilostomatoida has become unclear. These two orders were treated as a single monophyletic group by Boxshall and Halsey (2004), and the recent molecular phylogenetic analysis by Khodami et al. (2017) provided robust evidence that the poecilostome lineage originated within the Cyclopoida. The validity of the order Monstrilloida was questioned in a phylogenetic analysis (Huys et al. 2007) which recovered this distinctive taxon as a lineage emerging from within the wholly parasitic order Siphonostomatoida, but the Monstrilloida is retained here as it was recovered as a distinct order in the multigene analysis of Khodami et al. (2017). Finally the monophyly of the largely free-living Harpacticoida has also been challenged (Dahms 2004; Schizas et al. 2015), and the polyarthran families were placed in a new order, the Canuelloida, on the basis of molecular evidence (Khodami et al. 2017). Parasites are known from five copepod orders: Cyclopoida (including the poecilostomes), Canuelloida, Harpacticoida, Monstrilloida and Siphonostomatoida. These five all belong to the superorder Podoplea.

Copepoda are amazingly diverse in body form, reflecting their diversity in mode of life. In podoplean copepods the body is primitively divided into broad anterior prosome and slender posterior urosome by an articulation located between the fourth and fifth pedigerous somites. The prosome is five-segmented, comprising the cephalosome and four free pedigerous somites, and the urosome is primitively six-segmented in both sexes, comprising the fifth pedigerous somite, the genital somite and four limbless abdominal somites. In podoplean copepods the majority of adult females have a maximum of five expressed urosomites resulting from fusion at the final moult stage of the genital and first abdominal somites to form a genital double-somite. The last abdominal somite bears the anus and paired caudal rami. The cephalosome consists of the five-segmented cephalon with its standard complement of five paired limbs, plus the maxilliped-bearing first thoracic somite. This basic body plan is retained in many parasitic copepods, but others have profoundly transformed adult bodies (Figs. 3.8, 3.9, and 3.10), lacking any expressed body segmentation and with their paired appendages heavily modified or completely lost (Huys and Boxshall 1991). In some parasites the metamorphosis can be so extreme that their identity as copepods can only be ascertained by features of the larval stages or by molecular diagnostics.

Copepod antennules are a single axis limb with up to 27 expressed segments which carry an array of setae and aesthetascs which collectively represents the main sensory interface of a copepod. In most podoplean copepods, some-to-many of the intersegmental articulations along the antennule are not expressed during development, resulting in a shortened limb with reduced segmentation (Boxshall and Huys 1998). The antenna is primitively biramous, although in most parasitic copepods the exopod is highly reduced or lost. The endopod forms the main axis of the limb, and it commonly bears hooks or claws towards the tip and is important in securing attachment to the host. The mandibles comprise a proximal coxal gnathobase and a distal palp which is primitively biramous but often secondarily lost. The form of the mandible and its position relative to the labrum and the paragnaths (or labium) are important taxonomic characters and vary significantly between orders. The maxillules are primitively biramous with a one-segmented exopod, but in most parasitic forms the exopod is lost and the entire limb is reduced and uni- or bilobate. The maxilla is uniramous and consists of the protopodal part which primitively carries endites and a distal endopod. In many parasites the endites are lost, setation is reduced, and the maxillary endopod carries distal claw involved in feeding or attachment to the host. The maxilliped is also uniramous, and in most parasitic copepods it is clawed and aids in attachment to the host. All these cephalosomic limbs can be reduced or even lost in the most derived parasitic forms (Huys and Boxshall 1991).

The first four pairs of swimming legs of copepods each consist of a broad protopodal part bearing two rami, both of which are primitively three-segmented.

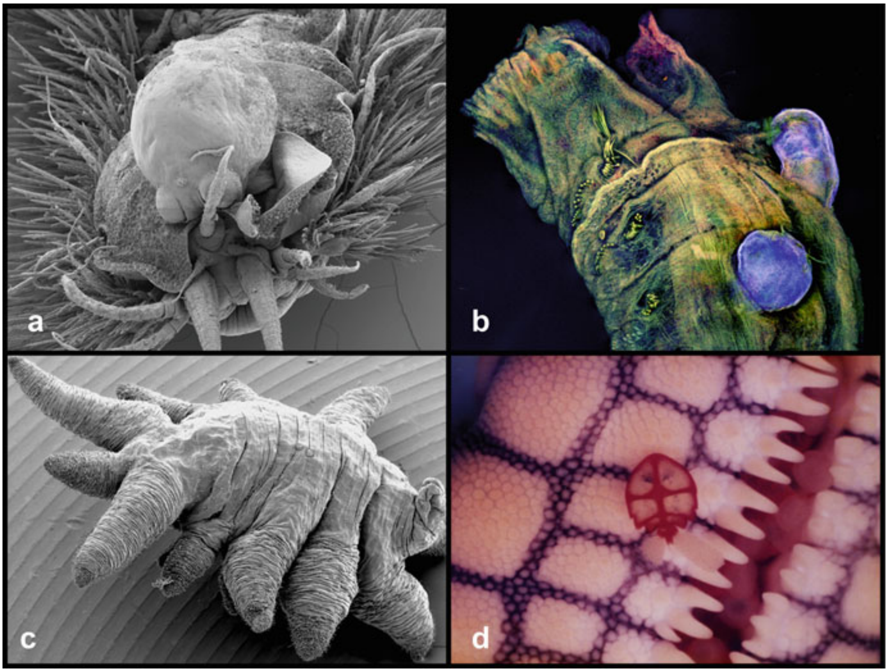

Fig. 3.8 Copepoda, Cyclopoida, from invertebrate hosts. (**a**) adult *Herpyllobius polynoes* (Krøyer, 1863) attached to head of polynoid worm host; (**b**) two embedded females of *Jasmineiricola mackiei* Boxshall, O'Reilly, Sikorski & Summerfield, 2015 on sabellid worm host; (**c**) adult female of *Achelidelphys papuensis* Boxshall & Marchenkov, 2007, dorsolateral; (**d**) *Sipadania celerinae* Humes & Lane, 1993 on asteroid echinoderm host. Images (**a**)–(**c**) © Natural History Museum, London; image (**d**) courtesy of Arthur Humes

The two members of a limb pair are permanently united by fusion to an intercoxal sclerite, thus ensuring that they always move in unison. Intercoxal sclerites are present even in the earliest copepodid larvae and their presence is diagnostic of the Copepoda. In podopleans, the fifth pair of legs, which is carried on the first urosomite, is usually reduced by loss of the endopod. Copepod swimming legs are armed with specific arrays of spines and setae: the number and arrangement of which provide important taxonomic characters at all levels of classification from order to species. The ancestral segmentation and setation patterns of all appendages have been hypothesised for each of the ten orders (Huys and Boxshall 1991; Boxshall and Huys 1998).

All copepod appendages can exhibit sexual dimorphism, but typically this is most commonly found in the antennules, maxillipeds and fifth swimming legs. The precise pattern of sexual dimorphism is highly variable and typically reflects the mechanisms involved in mate guarding and spermatophore transfer during mating (Boxshall 1990a). Female podoplean copepods typically carry their eggs in paired egg sacs, which are extruded from paired genital apertures. Egg sacs are carried by the female until ready to hatch, and the presence of paired egg sacs is a useful clue to

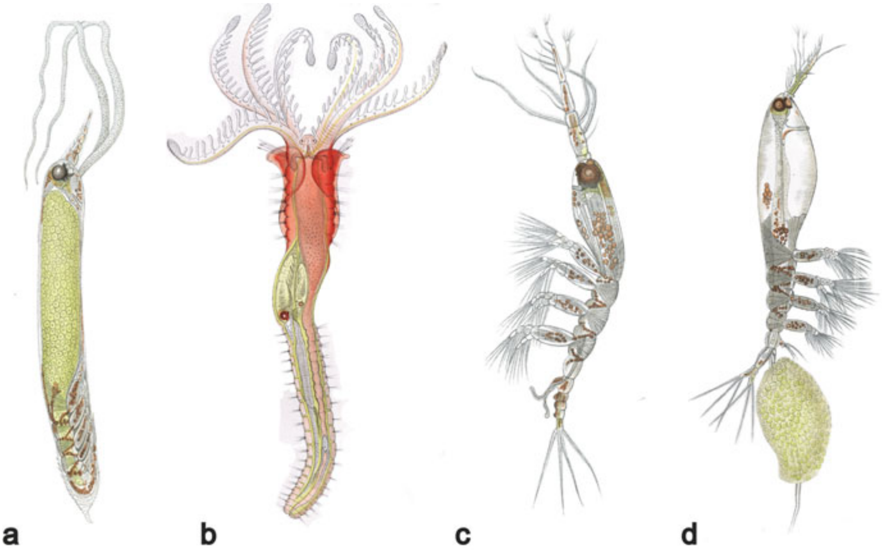

Fig. 3.9 Copepoda, Monstrilloida. (**a**) development stage dissected out from polychaete host; (**b**) developing *Cymbasoma danae* (Malaquin, 1896) within polychaete host (*Salmacina dysteri* (Huxley, 1855)); (**c**) adult male of *C. danae*, showing lack of mouthparts and paired elongate spermatophores; (**d**) adult female of *C. danae* carrying egg mass on ovigerous spines. Images modified from Malaquin (1901)

the identity of highly transformed or mesoparasitic copepods that lack any other morphological characteristics. Males typically produce paired spermatophores which are transferred onto the female during mating.

3.2.4.1 Cyclopoida (Including the Poecilostomes)

The Cyclopoida, as constituted by Boxshall and Halsey (2004), includes the poecilostomes (formerly the order Poecilostomatoida) and contains a mix of free-living and symbiotic copepods, including the most species-rich family within the Copepoda, the largely free-living, freshwater-inhabiting Cyclopidae. A total of 80 families or family-level groupings (sensu Boxshall and Halsey 2004) comprise species that live in symbiotic associations with a wide range of host taxa (Table 3.8). About 2690 cyclopoid species are symbionts, and the majority of these are probably best categorised as parasitic, although in many cases data on their biology are lacking. There is little formal subdivision of the Cyclopoida, although the phylogenetic analysis by Khodami et al. (2017) recovered the poecilostome lineage as a monophyletic group embedded within the traditional Cyclopoida (sensu Huys and Boxshall 1991).

The range of hosts used by cyclopoids is astonishing (Table 3.8). They occur on almost all classes of molluscs, especially bivalves and gastropods (including pteropods), but also on cephalopods, chitons, scaphopods and even a caudofoveate (Boxshall and

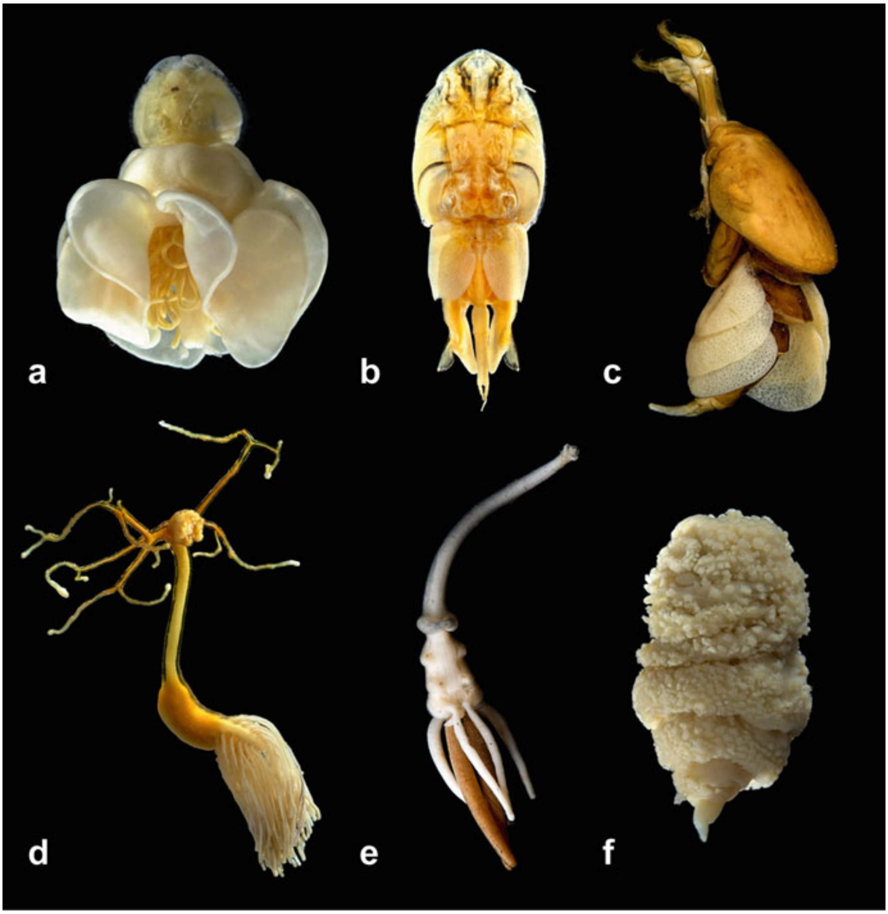

Fig. 3.10 Copepoda, from fish hosts. (**a**) dorsal adult female of *Avitocaligus assurgericola* Boxshall & Justine, 2005; (**b**) dorsal adult female of *Gloiopotes hygomianus* Steenstrup & Lütken, 1861; (**c**) lateral adult female of *Anthosoma crassum* (Abildgaard, 1794); (**d**) adult female of *Lernaeolophus sultanus* (Milne Edwards, 1840); (**e**) adult female of *Brachiella thynni* Cuvier, 1830, with dwarf male attached; (**f**) adult female of *Sarcotaces* sp. Images © Natural History Museum, London

O'Reilly 2015). At least 18 families, many of them with highly transformed bodies, occur exclusively on polychaete hosts (Fig. 3.8a, b), and it is likely that the diversity of copepods parasitic on polychaetes has been significantly underestimated (Kim et al. 2013; Boxshall et al. 2015). Large families such as Anchimolgidae (139 species) and Rhynchomolgidae (268 species) occur predominantly on scleractinian corals, and cyclopoids also occur on alcyconaceans, antipatharians, gorgonians, anemones, scyphozoans and hydroids (Humes 1985). Several large families utilise fish as hosts including Bomolochidae, Chondracanthidae and Taeniacanthidae in marine waters, Lernaeidae in freshwater and Ergasilidae across all salinity regimes from fresh to brackish and fully

Table 3.8 Species richness and host taxa of families and family-level groupings (*sensu* Boxshall and Halsey 2004) of parasitic Cyclopoida (Copepoda)

Family	No. genera	No. species	Host group
Akessonia-group	4	4	Sipuncula
Anchimolgidae	32	139	Cnidaria: Scleractinia
Anomoclausiidae	1	1	Polychaeta
Antheacheridae	4	8	Cnidaria: Actiniaria
Anthessiidae	6	57	Mollusca: Bivalvia, Gastropoda. Fish [1 species]
Archinotodelphyidae	2	5	Ascidiacea
Ascidicolidae	8	12	Ascidiacea
Axinophilus-group	2	3	Mollusca: Bivalvia, Gastropoda
Bomolochidae	20	142	Fish: Actinopterygii
Botryllophilidae	7	66	Ascidiacea
Bradophilidae	3	3	Polychaeta
Buproridae	1	2	Ascidiacea
Catiniidae	5	11	Polychaeta, Sipuncula
Chitonophilidae	9	16	Mollusca: Gastropoda, Polyplacophora
Chondracanthidae	51	193	Fish: Actinopterygii, Elasmobranchii
Chordeumiidae	6	12	Echinodermata: Ophiuroidea
Clausidiidae	11	98	Porifera, Mollusca, Polychaeta, Cnidaria, Crustacea
Clausiidae	9	36	Polychaeta
Corallovexiidae	2	10	Cnidaria: Scleractinia
Cucumaricolidae	1	2	Echinodermata: Holothuria
Echiurophilidae	2	3	Echiura
Endocheres Bocquet & Stock, 1956	1	1	Mollusca: Gastropoda
Enterognathidae	4	7	Echinodermata, Hemichordata
Enteropsida	5	43	Ascidiacea
Entobiidae	1	4	Polychaeta
Erebonasteridae	5	10	Mollusca, Polychaeta, unknown
Ergasilidae [all salinity regimes]	29	261	Fish: Actinopterygii, Elasmobranchii. Mollusca [3 species]
Eunicicolidae	2	3	Polychaeta, Porifera
Fratiidae	1	1	Ascidiacea
Gadilicolidae	1	1	Mollusca: Scaphopoda
Gastrodelphyidae	2	10	Polychaeta
Gonophysema-group	4	4	Ascidiacea
Herpyllobiidae	4	27	Polychaeta
Intramolgidae	1	1	Ascidiacea
Iveidae	1	3	Hemichordata (Enteropneusta)
Jasmineiricolidae	1	1	Polychaeta
Kelleriidae	1	18	Various invertebrates

(continued)

Table 3.8 (continued)

Family	No. genera	No. species	Host group
Lamippidae	10	53	Cnidaria: Octocorallia
Leaniricolidae	1	1	Polychaeta
Lernaeidae [freshwater]	17	131	Fish: Actinopterygii
Lichomolgidae	30	154	Mollusca, Echinodermata, Ascidiacea
Macrochironidae	4	33	Cnidaria, (Echinodermata, Ascidiacea, Fish [1 species each])
Makrostrotidae	1	2	Fish: Actinopterygii
Mantridae	3	3	Mollusca: Bivalvia
Mesoglicolidae	1	1	Cnidaria
Micrallectidae	1	2	Mollusca: Pteropoda
Myicolidae	8	23	Mollusca: Bivalvia
Mytilicolidae	4	14	Mollusca: Bivalvia
Nereicolidae	7	19	Polychaeta
Notodelphyidae	51	202	Ascidiacea
Octophiophora-group	2	2	Polychaeta
Octopicolidae	1	3	Mollusca: Cephalopoda
Ophelicola Laubier, 1978	1	2	Polychaeta
Ozmanidae	1	2	Mollusca: Gastropoda
Philichthyidae	9	91	Fish: Actinopterygii
Philoblennidae	5	11	Mollusca: Gastropoda
Phyllodicolidae	2	3	Polychaeta
Pionodesmotidae	1	2	Echinodermata: Echinoidea
Polyankyliidae	2	4	Polychaeta
Praxillinicolidae	1	1	Polychaeta
Pseudanthessiidae	6	59	Echinodermata, Mollusca, Polychaeta, Nemertea, Turbellaria
Rhynchomolgidae	44	268	Cnidaria, Mollusca, Echinodermata
Sabelliphilidae	9	25	Polychaeta
Saccopsidae	1	4	Polychaeta
Serpulidicolidae	5	8	Polychaeta
Shiinoidae	2	9	Fish: Actinopterygii
Spiophanicolidae	1	2	Polychaeta
Splanchnotrophidae	6	31	Mollusca: Nudibranchia
Strepidae	1	1	Cnidaria
Synapticolidae	9	50	Echinodermata: Holothuria, Echinoidea
Synaptiphilidae	3	9	Echinodermata: Holothuria, Echinoidea
Taeniacanthidae	21	121	Fish: Actinopterygii, Elasmobranchii. Echinodermata: Echinoidea
Telsidae	1	2	Fish: Actinopterygii
Teredicola-group	4	14	Mollusca
Thamnomolgidae	3	4	Cnidaria: Antipatharia, Gorgonacea
Thaumatopsyllidae	4	5	Echinodermata

(continued)

Table 3.8 (continued)

Family	No. genera	No. species	Host group
Vahiniidae	1	2	Cnidaria: Antipatharia
Ventriculinidae	2	3	Sipuncula
Xarifiidae	5	93	Cnidaria: Scleractinia
Xenocoelomatidae	2	3	Polychaeta

Data from World of Copepods database (Walter and Boxshall 2018)

marine. In total 948 cyclopoid species parasitise fish: most are ectoparasites on the gills and body surface, but the Philichthyidae comprises 91 species that typically inhabit the lateral line canals of their hosts, and 1 genus of Ergasilidae inhabits the urinary bladder of its fish host (Rosim et al. 2013). At least 7 families of cyclopoids use ascidiaceans as hosts, the largest being Notodelphyidae (Fig. 3.8c) with over 200 valid species. All classes of echinoderms serve as hosts to cyclopoids (Fig. 3.8d), although species utilising crinoids are relatively scarce. Finally, a few cyclopoid copepods occur in association with crustaceans, hemichordates, enteropneusts, phoronids, nemerteans and turbellarians (Table 3.8). Very few cyclopoids have been reported from sponges.

The antenna of parasitic cyclopoids is typically clawed, and the exopod is most commonly absent but in more basal forms can be represented by a vestigial segment bearing a maximum of three setae. Cyclopoids have an oral zone defined anteriorly by a distinct labrum, which is typically incised medially in poecilostomes. The mandible can vary from a basal type with a large coxal gnathobase and a biramous palp, as present in the Archinotodelphyidae and Mantridae, for example, to the falcate tapering blade typical of most associated families in the poecilostome lineage. The maxillules, maxillae and maxillipeds each exhibit a range in form, from unmodified limbs of the basal podoplean type to reduced or highly modified limbs, or can be absent. Swimming legs 1 to 4 are as in other copepods, but the absence of an inner seta on the first exopodal segment of all legs was highlighted by Huys and Boxshall (1991) as a characteristic of the poecilostomes within the Cyclopoida. The trend towards oligomerisation is strongly expressed in several lineages, and the end-point of such a trend is exemplified by Herpyllobiidae (Fig. 3.8b), members of which have no limbs and no expressed body segmentation in the adult female. The oligomerisation can follow different paths, as in Thaumatopsyllidae which have lost their antennae and all mouthparts from mandibles to maxillipeds while retaining typical segmented cyclopiform adult bodies.

Sexual dimorphism is expressed in the antennules: primitively males have geniculate antennules on both sides which they use for holding onto females during mating, but in many more derived families the geniculations are lost, and antennulary dimorphism takes the form of subtle differences in setation patterns. In such derived families, especially those in the main poecilostome lineage, males tend to hold onto females using their maxillipeds which tend to be robust subchelate limbs, while those of the female are often vestigial or absent. Extreme sexual dimorphism is shown in numerous families: in the fish-parasitic Chondracanthidae, for example, the relatively large females have dwarf males which they supply with nutrients via the nuptial organs (Østergaard and Boxshall 2004). Female cyclopoids typically produce paired multiseriate egg sacs.

3.2.4.2 Canuelloida

The basal, polyarthran families, the Longipediidae and Canuellidae, were excluded from the Harpacticoida and placed in a distinct new order by Khodami et al. (2017). Both families are predominantly free-living, but the Canuellidae contains a cluster of species that live as loose symbionts, residing within the gastropod shells inhabited by hermit crabs (Ho 1988), as well as *Echinosunaristes bathyalis* Huys, 1995 which inhabits the rectum of a deep-sea spatangoid echinoderm.

3.2.4.3 Harpacticoida

After the transfer of the basal Polyarthran families to a new order, the Harpacticoida now comprises those families formerly placed in the Oligarthra. The systematics of the harpacticoids is unstable, and the composition of several large families is in a state of flux since too few molecular data are currently available to resolve the many uncertainties. Harpacticoids are predominantly free-living and benthic forms, although a few lineages have independently colonised the zooplankton community of the oceanic water column. A significant number of harpacticoids have also entered into close symbiotic associations with a wide variety of hosts, and some have become parasitic. The most common pattern is to find isolated species or small clusters of parasitic species nested within larger free-living taxa. A good example is the clade of nine genera and 13 species within the otherwise free-living family Tisbidae, all nine are parasitic and use cephalopod molluscs as hosts. These are often highly transformed species, lacking expressed body segmentation and exhibiting reductions in appendages; however, they typically retain traces of the characteristic first swimming leg of the tisbids.

The family Balaenophilidae comprises just two species, one living on the baleen plates of cetaceans and the other on marine turtles and manatees. These species have often been regarded as commensals, although studies of gut contents reveal that they appear to scrape epidermal cells from the host and thus might be regarded as parasites (Ogawa et al. 1997).

The Cancrincolidae include species that inhabit the gill chambers of land crabs. The phylogenetic relationships of this family were explored by Huys et al. (2009) who found it to constitute a specialised terminal branch within the Ameiridae. It currently comprises four genera and seven species which live in association with terrestrial and semiterrestrial crabs belonging to the families Gecarcinidae, Grapsidae, Sesarmidae and Varunidae. Their nearest relatives within the Ameiridae appear to be *Nitocra* Boeck, 1865 species, several of which live in association with freshwater decapods, sometimes on the gills and body surface but often in the burrows (Huys et al. 2009).

The classification of the cluster of taxa comprising the subfamily Donsiellinae has been unstable; estimates of its phylogenetic affinities have migrated from the Laophontidae via the Thalestridae to the Pseudotachidiidae (Willen 2006). It comprises 5 genera and 12 species which are typically associates of the wood-boring or macroalgal isopod genus *Limnoria* Leach, 1814 or live in decaying wood occupied by species of *Limnoria*. The precise nature of the symbiosis in these donsiellines is uncertain: they may be inquilines or commensals.

Numerous other parasites and close symbionts can be found scattered across the different families of Harpacticoida (Boxshall and Halsey 2004) including the following: *Xouthous parasimulans* (Médioni & Soyer, 1967) (Pseudotachidiidae) is an associate of a bryozoan; *Neoscutellidium yeatmani* Zwerner, 1967 (Idyanthidae) occurs on the gills of a zoarcid fish; *Scutellidium patellarum* Branch, 1974 (Tisbidae) was reported from five species of limpets; *Metis holothuriae* (Edwards, 1891) (Metidae) lives in association with a holothurian host; *Porcellidium* Claus, 1860 (Porcellidiidae) species are reported as external associates of echinoids and hermit crabs; *Amphiascus* Sars, 1905 (Miraciidae) species are known to live in association with marine lobsters and crabs; and numerous members of the Laophontidae are symbionts including species of *Harrietella* Scott, 1906 (in wood bored by *Limnoria* and by the shipworm *Teredo* Linnaeus, 1758), *Microchelonia* Brady, 1918 (on holothurians), *Laophonte* Philippi, 1840 (on cnidarians, bryozoans and crustaceans), *Hemilaophonte* Jakubisiak, 1932 and *Paralaophonte* Lang, 1948 (on majoid spider crabs); *Mictyricola* Nicholls, 1957 (on the crab *Mictyris* Latreille, 1806); and *Coullia* Hammond, 1973, *Xanthilaophonte* Fiers, 1991 and *Robustunguis* Fiers, 1992 (on xanthid crabs). Huys (2016) estimated that 172 species of harpacticoids were symbionts, although this total included species living in association with Cyanobacteria, macroalgae and sea grasses.

3.2.4.4 Monstrilloida

Montrilloids are parasites with a life cycle that consists of a dispersal phase (early naupliar stages), an infective nauplius stage, the endoparasitic post-naupliar stages (Fig. 3.9a) and the free-living but non-feeding adults. The adults are found in marine plankton and can be locally common. The known hosts of the parasitic larval stages include polychaetes (Fig. 3.9b) and both gastropod and bivalve molluscs (Malaquin 1901; Pelseneer 1914; Suárez-Morales et al. 2010). The Monstrilloida was originally established by Sars (1901) and was retained as a distinct order by Huys and Boxshall (1991) and Boxshall and Halsey (2004), but the analysis of Huys et al. (2007), based on morphological and molecular data, suggested that monstrilloids emerged from within the Siphonostomatoida. This proposal has not yet received wide acceptance, and more evidence is needed. The Monstrilloida is treated as a distinct order here. A second family with a similar pattern of missing cephalosomic limbs, the Thaumatopsyllidae, was formerly included in the Monstrilloida but was transferred to the Cyclopoida by Huys and Boxshall (1991).

There are currently 166 valid species of monstrilloids classified in six genera and placed in a single family, the Monstrillidae. Most monstrilloid species are known only from their distinctive planktonic adults. The prosome of adult monstrilloids (Fig. 3.9c, d) consists of an elongate cephalothorax incorporating the first pedigerous somite, plus three free pedigerous somites. The only prosomal limbs present are the sexually dimorphic antennules and four pairs of biramous swimming legs on the pedigerous somites. The antennae and the entire set of mouthparts from mandibles to maxillipeds are lost in both sexes. A simple tubular process with an apical opening, present on the midventral surface of the cephalothorax, may represent the vestigial mouth of the adult. The segmentation of the urosome varies with genus but comprises a maximum of three urosomites in the male and four in the female. The fifth legs are carried on the first urosomite and may be bilobed and setose, or reduced. The adult females have paired ovigerous spines associated with the genital aperture, and these carry masses of fertilised eggs (Fig. 3.9d). Males produce pairs of elongate spermatophores (Fig. 3.9c).

3.2.4.5 Siphonostomatoida

The Siphonostomatoida is a large and diverse order within the Podoplea containing approximately 2233 valid species classified into 40 families (Table 3.9). Currently there is no subordinal system for grouping these families although those parasitic on fish appear to form a single monophyletic lineage characterised by the stylet-like form of the mandible, which lacks any trace of the palp and typically has a series of marginal teeth on one side near the tip of the gnathobase. Most of these fish-parasitic families also lack any trace of the antennal exopod, with the exception of the Lernaeopodidae-Sphyriidae-Tanypleuridae group.

All siphonostomatoids are treated as parasitic although there is uncertainty about the feeding biology of members of the relatively basal family Dirivultidae. Dirivultids are typically members of hydrothermal vent and cold seep communities and have been collected in washings of various vent invertebrates, including tubicolous polychaetes and gastropod and bivalve molluscs, as well as in the gill chamber of decapod crustaceans and attached to the tentacular crown of the vestimentiferan polychaetes. However, Tsurumi et al. (2003) and Dinet et al. (1988) inferred that the loosely associated dirivultids exploit the bacteria growing on the surfaces of other invertebrates.

By far the commonest host group utilised by siphonostomatoids is the fishes (Fig. 3.10a–f), including agnathans, elasmobranchs, holocephalans and actinopterygians: in total 1544 species from 17 families use fishes as hosts (Table 3.9). All extant classes of echinoderms are exploited by siphonostomatoids: nine families, comprising 57 species in total, are found exclusively on echinoderms (Table 3.9), and some members of the generalist families Asterocheridae and Artotrogidae also use echinoderms as hosts. One family, the Nicothoidae, parasitises other crustaceans, including a leptostracan, several decapods, a wide range of peracaridans (amphipods, isopods, tanadiaceans, mysids and cumaceans) and some myodocopan ostracods (Boxshall and Halsey 2004). The other

Table 3.9 Species richness and host taxa of families of Siphonostomatoida (Copepoda)

Family	No. genera	No. species	Host group
Archidactylinidae	1	1	Fish: Agnatha
Artotrogidae	21	110	Ascidiacea, Bryozoa, Cnidaria, Porifera and many unknown
Asterocheridae	64	289	Bryozoa, Cnidaria, Echinodermata, Mollusca, Porifera, Urochordata
Brychiopontiidae	3	3	Echinodermata: Holothuria
Caligidae	30	508	Fishes: Actinopterygii, Elasmobranchii. Mollusca [1 species]
Calverocheridae	1	3	Echinodermata: Echinoidea
Cancerillida	6	14	Echinodermata: Ophiuroidea
Codobidae	1	1	Echinodermata: Ophiuroidea
Coralliomyzontidae	4	7	Cnidaria: Scleractinia
Dichelesthiidae	2	2	Fishes: Actinopterygii, Elasmobranchii
Dichelinidae	1	2	Echinodermata: Echinoidea
Dinopontiidae	2	5	Cnidaria, Porifera
Dirivultidae	13	53	various invertebrates
Dissonidae	2	13	Fishes: Actinopterygii, Elasmobranchii
Ecbathryontidae	1	1	Unknown
Entomolepididae	7	12	Porifera
Eudactylinidae	12	57	Fishes: Actinopterygii, Elasmobranchii
Hatschekiidae	9	163	Fishes: Actinopterygii
Hyponeoidae	3	3	Fishes: Actinopterygii
Kroyeriidae	3	25	Fishes: Elasmobranchii
Lernaeopodidae	48	334	Fishes: Actinopterygii, Elasmobranchii
Lernanthropidae	8	140	Fishes: Actinopterygii
Megapontiidae	1	9	Unknown
Micropontiidae	1	2	Echinodermata: Echinoidea
Nanaspididae	5	19	Echinodermata: Holothuria
Nicothoidae	22	137	Crustacea
Pandaridae	23	88	Fishes: Actinopterygii, Elasmobranchii
Pennellidae	24	148	Fishes: Actinopterygii. Mammals. Mollusca (developmental stages only)
Pontoeciellidae	1	1	Unknown
Pseudocycnidae	2	4	Fishes: Actinopterygii
Pseudohatschekiidae	1	2	Fishes: Actinopterygii
Rataniidae	1	2	Unknown
Scottomyzontidae	1	1	Echinodermata: Asteroidea, Echinoidea
Sphyriidae	9	39	Fishes: Actinopterygii, Elasmobranchii
Sponginticolidae	1	1	Porifera
Spongiocnizontidae	2	5	Porifera
Stellicomitidae	7	12	Echinodermata: Asteroidea
Tanypleuridae	1	1	Fishes: Actinopterygii
Trebiidae	1	16	Fishes: Elasmobranchii

Data from World of Copepods database (Walter and Boxshall 2018) two common host taxa are the sponges and cnidarians, especially the scleractinian corals. These corals host numerous asterocherid and artotrogid species, as well as families that are more host specific. It is interesting to note the virtual absence of parasitic siphonostomatoids from polychaetes and molluscs. There are no siphonostomatoids parasitic on polychaetes, although some dirivultids are loosely associated with polychaetes (see above). Very few siphonostomatoids use molluscs as hosts: a single species of Caligidae, *Anchicaligus nautili* Stebbing, 1900, is found on *Nautilus pompilius* Linnaeus, 1758, some species of Pennellidae use pelagic molluscs as intermediate hosts but not as the final hosts, and one or two asterocherids and artotrogids are reported as associated with molluscs. These are rare exceptions.

Siphonostomatoids are characterised by the possession of a tubular mouth containing stylet-like mandibular gnathobases. The mouthtube is formed by the labrum (upper lip) and the labium, which represents the fused paragnaths (Boxshall 1990b). The antennae and maxillipeds are typically subchelate in form and serve to attach these copepods to their hosts as in sea lice (Family Caligidae) (Fig. 3.10a, b). The maxillae are also often subchelate, but they are more variable: one interesting variant is the ribbon-like maxillae of *Naobranchia* Hesse, 1863, which are used to secure attachment by encircling the gill filaments of their fish host. Body form in the siphonostomatoids is extremely variable: basal families such as the Asterocheridae and Dirivultidae retain the basic podoplean body tagmosis and segmentation patterns, while most members of highly derived families such as the Pennellidae (Fig. 3.10d) and Sphyriidae have females that undergo a profound metamorphosis, so the adults express no body segmentation and exhibit different tagmosis patterns.

Sexual dimorphism is strongly expressed within the Siphonostomatoida. In more basal families, such as the Asterocheridae, adult males typically have geniculate antennules used for grasping the female during mating. In more derived families, including all the fish parasites, this geniculation is not expressed, and males tend to grasp females using the antennae and/or the maxillipeds, which often show special modifications. Extreme sexual dimorphism is shown in families such as Lernaeopodidae (Fig. 3.10e) and Sphyriidae, which have dwarf adult males that live attached to the larger and often highly metamorphic females. Females typically produce paired egg sacs which are primitively multiseriate, but in a large cluster of fish-parasitic families, the egg sacs are uniseriate strings and the eggs themselves are flattened and discoid.

3.2.5 Branchiura

Most branchiurans, commonly called fish lice, are ectoparasites of fishes, although *Dolops ranarum* (Stuhlmann, 1892) and a few species of *Argulus* Müller, 1785 have been reported from amphibians, including salamanders and tree frogs, as well as tadpoles (Poly 2003). Most species live in freshwater (Table 3.10) and may occur at high density in artificial water bodies such as reservoirs and ornamental fish ponds. Nearly 40 species of *Argulus* infest brackish and coastal marine fishes, but they

Table 3.10 Diversity and habitat usage of all valid species of Branchiura ($n = 155$)

Genus	Freshwater	Marine/brackish	Total species
Argulus Müller, 1785	88	39	127
Chonopeltis Thiele, 1900	13	0	13
Dipteropeltis Calman, 1912	2	0	2
Dolops Audouin, 1837	13	0	13

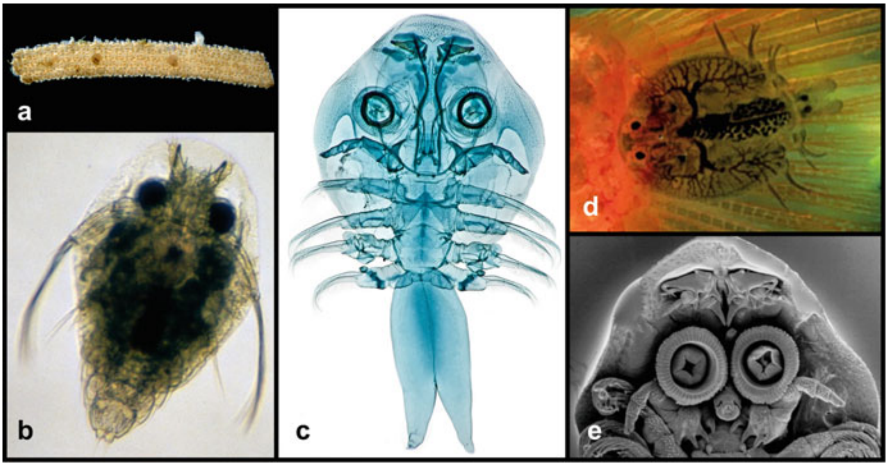

Fig. 3.11 Branchiura. (**a**) egg rows of *Argulus foliaceus* (Linnaeus, 1758); (**b**) free-swimming larval stage of *Argulus foliaceus*; (**c**) adult male of *Argulus personatus* Cunnington, 1913, ventral view showing "respiratory areas" and secondary sexual modification of posterior swimming legs; (**d**) adult female of *Argulus foliaceus* on host, showing blood-filled gut diverticulae extending through lateral carapace lobes; (**e**) head of *Argulus foliaceus* showing paired maxillulary suckers. Images © Natural History Museum, London

rarely occur offshore. Adults periodically leave their hosts to deposit eggs (Fig. 3.11a) on submerged hard substrates. These hatch into a free-swimming larval stage (Fig. 3.11b) in *Argulus*.

The Branchiura were classified with the copepods throughout the nineteenth and early twentieth centuries, but research by Thiele (1904) and Martin (1932) provided evidence supporting the recognition of this group as equal to and distinct from the Copepoda (see Møller 2009 for summary). The Branchiura is a small taxon, currently comprising 155 valid species classified in four genera (Table 3.10) placed in a single family, the Argulidae.

All branchiuran fish lice are parasitic, and they have a strongly dorsoventrally flattened body, which gives them a low profile when attached to their host. They range in body length from a few mm to a maximum of 30 mm (Møller 2009). The body (Fig. 3.11c) comprises a head of five segments and a postcephalic trunk comprising a four-segmented thoracic region carrying four pairs of laterally directed swimming legs and a short, unsegmented abdomen. The abdomen terminates in paired lobes separated by a median anal cleft, within which lie the paired caudal rami.

The head is covered with a dorsal cephalic shield which is produced into well-defined lateral carapace lobes, which typically extend over the swimming legs. In some species of *Argulus*, they may extend further, to cover the entire abdomen, but in species of *Chonopeltis* Thiele, 1900 the carapace lobes are usually short and do not cover the swimming legs. In *Dipteropeltis* Calman, 1912 the carapace lobes form enormous wing-like extensions. The carapace lobes contain highly branched gut caeca (Fig. 3.11d) which are often visible through the body wall (Overstreet et al. 1992). Ventrally the carapace lobes carry two pairs of so-called respiratory areas (Fig. 3.11c), the shape and arrangement of which are important taxonomic characters. These areas of specialised integument appear to be involved in regulation of internal body fluids (Haase 1975) and have little to do with gaseous exchange. Paired compound eyes are located on either side of the dorsal midline on the anterior part of the carapace.

Branchiurans typically have nine pairs of limbs, five cephalic and four thoracic. In *Argulus* the anterior-most limb, the antennule, comprises a robust two-segmented basal part and a two-segmented distal part bearing setae (Rushton-Mellor and Boxshall 1994). The basal part is heavily sclerotized, and both segments usually carry curved hook-like processes (Fig. 3.11e) which help these ectoparasites secure themselves to the surface of their hosts (Gresty et al. 1993). In *Dolops* the proximal segment is hooked as in *Argulus*, but the distal part of the antennule is reduced (Fryer 1969). In *Dipteropeltis* the structure of the antennule is poorly known but appears to comprise a proximal swollen part without hooks and cylindrical distal part bearing setae (Neethling et al. 2014): in *Chonopeltis* the entire antennule is absent.

The antenna is uniramous in the adult, lacking any trace of an exopod. In *Argulus* and *Dolops* it is five-segmented and the first segment (coxa) is heavily sclerotized and carries a stout hooked process proximally. The other four segments are cylindrical and setose, and this limb is primarily sensory in function although the process on the coxa probably assists in securing attachment of the parasite by preventing it from being dislodged (see Gresty et al. 1993). There is uncertainty about the separation of the coxa in *Dipteropeltis*, but the endopod also consists of three setose segments (Møller and Olesen 2010). In *Chonopeltis* the antenna is four-segmented; all segments are cylindrical and setose.

Adult branchiurans have a proboscis-like, sucking mouth tube with an apical mouth opening enclosed by an upper labrum and a lower sternal outgrowth sometimes referred to as the labium. Paired labial stylets lie within the mouth opening and may produce secretion with a pre-digestive function. The length of the mouth tube varies: it is long in *Argulus* and *Dipteropeltis* and short in *Chonopeltis* and *Dolops* (Møller 2009). The adult mandibles consist of the coxal gnathobase only and are positioned at the tip of the mouth tube. They lie concealed within the mouth opening except during feeding (Gresty et al. 1993). A mandibular palp is present in the earliest developmental stage of some *Argulus* (Rushton-Mellor and Boxshall 1994) but is lost in subsequent stages. In *Argulus* and *Dipteropeltis* there is a retractable stylet, the pre-oral spine, located on the ventral cephalic surface just anterior to the mouth tube. It is used to penetrate the skin of the host and inject a toxin, causing severe local pathological effects (Kabata 1970; Gresty et al. 1993). No pre-oral stylet is present in *Chonopeltis* and *Dolops*.

The paired maxillules are the main attachment organs. In early larvae the maxillules are uniramous with barbed apical claws, but by the fifth instar a powerful muscular sucker develops in the protopodal part of each limb, and the distal clawed part atrophies over the next few moults (Rushton-Mellor and Boxshall 1994). All adult branchiurans have sucker-like maxillules (Fig. 3.11e) except members of the freshwater genus *Dolops*, which retain clawed maxillules into the adult phase. Branchiuran maxillae are uniramous, lacking an exopod and comprise six segments. The first segment usually carries three spinous processes along its posterior margin; their shape and associated ornamentation can be useful taxonomic characters. The apical segment carries two small claws at its tip in three genera, the exception being *Dolops* which has an offset sixth segment bearing several small hooks (Møller and Olesen 2010).

The four pairs of thoracic swimming legs are biramous and directed laterally. In *Dolops* and most *Argulus* the first and second legs carry a dorsal flagellum originating on the exopod close to its base (Boxshall and Jaume 2009). The second, third and fourth legs are variously modified in the male (Fig. 3.11c) and are used for transferring sperm to the female during mating. The precise form of the lobes on these legs provides taxonomic information, important for species identification.

The sexes are separate in Branchiura, and the abdomen contains paired testes in males and paired seminal receptacles in females. Sperm are elongate, filiform and motile, and their ultrastructure has provided evidence of close phylogenetic affinity between Branchiura and Pentastomida (Wingstrand 1972). In *Dolops* sperm transfer is by means of spermatophores, but in the other genera sperm are transferred directly to the paired seminal receptacles of the female.

3.2.6 *Pentastomida*

Modern pentastomids, or tongue worms, are obligate parasites at all stages of their life cycle. Their definitive hosts are vertebrates, most frequently reptiles (snakes, crocodiles, turtles and lizards), but they also are found in amphibians, birds and mammals including humans (Table 3.11). Intermediate hosts include these same taxa, as well as fishes, and larval stages of *Raillietiella* Sambon, 1910 species have been found in terrestrial insects (Christoffersen and De Assis 2013). In the genus *Reighardia* Ward, 1899 transmission is direct and does not involve an intermediate host. Adult pentastomids are bloodsuckers (on reptiles and sea bird hosts) or feed on mucus and sloughed cells (on mammalian hosts) (Böckeler 2005).

Fossils from the late Cambrian to early Ordovician have been described as larval pentastomids, and conodonts (early vertebrates) were considered to be their likely hosts (e.g. Waloszek et al. 2006; Castellani et al. 2011). However, Siveter et al. (2015) recently described a fossil from the Silurian, *Invavita piratica*, which they interpreted as an adult pentastomid ectoparasitic on a myodocopan ostracod. We find the evidence in support of this interpretation to be equivocal. The fossil is star-shaped with five short processes plus a much longer process identified as the trunk; the short process opposite the trunk is identified as the "snout", and the remaining four processes are interpreted as two pairs of limbs, as retained by pentastomids. In addition to the ostracod host and the ectoparasitic mode of life, our difficulties in accepting *Invavita* as a pentastomid include the snout and trunk are in different planes, so all five short processes lie in a single plane, but the trunk originates and is directed more dorsally (the trunk and snout represent the main body axis, and in all pentastomids this axis lies in a single plane); the paired limbs are relatively longer than in modern pentastomids, and no apical hooks were found (the two pairs of hooks are a diagnostic feature of all pentastomids), so, given that the preservation had captured details of very fine setation on the host limbs, it seems incongruous that the strongly chitinised hooks were not preserved. The morphology of *Invavita* is more reminiscent of a whip-like body attached via a star-shaped holdfast, and we reject the hypothesised pentastomid affinities of this fossil.

Two different classification schemes are available for the Pentastomida. Christoffersen and De Assis (2013, 2015) recognised four orders, Cephalobaenida, Raillietiellida, Reighardiida and the Porocephalida, whereas Poore (2012) recognised only two, the Cephalobaenida (including the Raillietiellidae and Reighardiidae as family level taxa) and the Porocephalida. The Porocephalida can be distinguished from the other three orders by the position of the two pairs of hooks: in porocephalids they are arranged in a single row posterior to the mouth, whereas the other orders have hooks arranged in anterior and posterior pairs (Fig. 3.12a, b). There are currently 130 valid Pentastomida species classified in seven families (Table 3.11).

Adult pentastomids are vermiform (Fig. 3.12c) and the body length of females is typically in the 1–2 cm range, although they may attain lengths up to 16 cm. They attach themselves within the respiratory tract of their final vertebrate host by means of two pairs of cuticular hooks. These hooks can be located on the ventral surface of the head (Fig. 3.12a, b) or can be carried on reduced appendages as in *Cephalobaena* Heymons, 1922 (Almeida et al. 2006). The hooks are retractile in *Porocephalus* Humboldt, 1812 (Fig. 3.12b). The body is usually cylindrical and superficially annulated, and in adults is indistinctly divided into a head and limbless trunk. The ventral mouth is located close to the anterior margin of the head and it is surrounded by papillae and numerous sensillae and gland openings. The gut is complete in almost all genera and terminates in a posteriorly located anus. The sexes are separate and in both sexes the reproductive organs are extensive, occupying much of the space within the trunk. There is a single gonopore located close to the head-trunk junction. Fertilisation is internal and the sperm is filiform, resembling that of the Branchiura (Wingstrand 1972).

Table 3.11 Classification, species richness and host utilisation of the Pentastomida ($n = 130$)

Family	No. species	Definitive host group
Order Cephalobaenida		
Cephalobaenidae		
Cephalobaena Heymons, 1922	1	Reptiles (snakes)
Order Raillietellida		
Raillietiellidae		
Raillietiella Sambon, 1922	43	Reptiles, amphibians, birds
Yelirella Spratt, 2010	1	Mammals (marsupials)
Order Reighardiida		
Reighardiidae		
Hispania Martinez, Criado-Fornelio, Lanzarot, Fernández-Garcia, Rodriguez-Caabiero & Merino, 2004	1	Birds
Reighardia Ward, 1899	2	Birds
Order Porocephalidae		
Linguatulidae		
Linguatula Frölich, 1789	4	Mammals
Neolingatula von Hoffner in von Hoffner, Rack & Sachs, 1969	1	Mammals
Porocephalidae		
Armillifer Sambon, 1922	8	Reptiles (snakes), mammals
Cuberia Kishida, 1928	2	Reptiles (snakes)
Elenia Heymons, 1932	1	Reptiles (lizards)
Gigliolella Chabaud & Choquet, 1954	1	Reptiles (snakes)
Kiricephalus Sambon, 1922	6	Reptiles (snakes), amphibians (frogs)
Parasambonia Stunkard & Gandal, 1968	2	Reptiles (snakes)
Porocephalus Humboldt, 1812	9	Reptiles (snakes, lizards), mammals
Waddycephalus Sambon, 1922	10	Reptiles (snakes)
Sebekiidae		
Agema Riley, Hill & Huchzermeyer, 1977	1	Reptiles (crocodilians)
Alofia Giglioi in Sambon, 1922	8	Reptiles (crocodilians)
Diesingia Sambon, 1922	2	Reptiles (chelonians)
Leiperia Sambon, 1922	3	Reptiles (crocodilians)
Levisunguis Curran, Overstreet, Collins & Benz, 2014	1	Reptiles (chelonians)
Pelonia Junker & Boomker, 2002	1	Reptiles (chelonians)

(continued)

Table 3.11 (continued)

Family	No. species	Definitive host group
Sambonia Noc & Giglioli, 1922	5	Reptiles (lizards)
Sebekia Sambon, 1922	12	Reptiles (crocodilians)
Selfia Riley, 1994	1	Reptiles (crocodilians)
Subtriquetridae		
Subtriquetra Sambon, 1922	4	Reptiles (crocodilians)

Data from Poore (2012) and Curran et al. (2014)

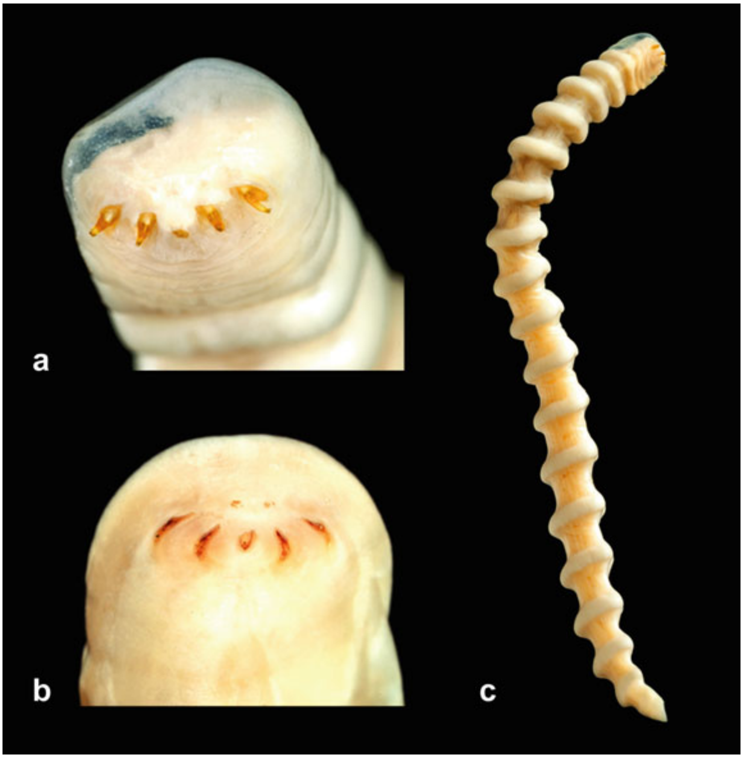

Fig. 3.12 Pentastomida. (**a**) head of *Armillifer armillatus* (Wyman, 1845), ventral showing anterior hooks and mouth opening; (**b**) head of *Porocephalus brasilicus* Riley & Self, 1979, ventral showing paired hooks retracted into sockets; (**c**) *Armillifer armillatus*, 9.3 cm long adult. Images © Natural History Museum, London

3.2.7 Ostracoda

The Ostracoda is a highly speciose group with an extensive fossil record and it contains two large extant orders, the Podocopa and Myodocopa. Numerous species of ostracods live in close symbiotic associations and a few have been treated as parasites. The podocopan family Entocytheridae, for example, consists of 220 species of obligate symbionts which utilise malacostracan crustaceans as hosts (Mestre et al. 2014). Most entocytherids are symbionts of freshwater crayfish (Decapoda: Cambaridae, Parastacidae and Astacidae); one lives in association with a pseudothelphusid crab, a few species live in association with wood-boring limnoriid, sphaeromatid and cirolanid isopods, and one is associated with an amphipod. The latter, *Sphaeromicola dudichi* (Klie, 1938), is the only marine entocytherid, and its host is the wood-boring *Chelura terebrans* Philippi, 1839. Mestre et al. (2014) found that while 73 species of entocytherid had been reported from only a single host species, their frequency distribution of host usage showed a long tail of species with lower specificity, with a maximum of 64 host species recorded for *Entocythere elliptica* Hoff, 1944. Entocytherids usually attach to setae along the pleon and around the bases of the pereopods, maxillipeds, chelae and antennae of their crayfish hosts, as well as under the rostrum (Williams et al. 2011). They can also occur inside the branchial chamber of the host. The feeding biology of entocytherids is poorly known but, despite their obligate relationship with the host and their specificity towards the host, they are considered to be commensals (see Hobbs and Peters 1977).

Harding (1966) concluded that the myodocopan cypridinids *Photeros parasitica* (Wilson, 1913) and *Sheina orri* Harding, 1966 found on the gills and in the nasal cavities of elasmobranch and actinopterygian fishes were parasitic, but Cohen (1983) suggested that they were scavengers on injured or unhealthy fish. A study of *Sheina orri* on the gills of a shark (Bennett et al. 1997) demonstrated that the ostracods were typically found in small pockets between adjacent gill filaments and caused tissue damage and distortion of gill lamellae. Even though they were unable to confirm that the ostracods had ingested shark tissue, Bennett et al. (1997) concluded that *Sheina orri* was parasitic.

3.3 Patterns of Diversity of Parasitic Crustacea

3.3.1 Morphological Trends

Huys and Boxshall (1991) noted that the dominant evolutionary trend in copepods is oligomerisation expressed as fusion of body somites and reduction and loss of appendage segments and setal elements. In parasites, such a trend can culminate in extreme morphological simplification, as exhibited by terminal taxa of several different parasitic lineages within the Copepoda. Examples of such extreme morphological reduction include mesoparasites such as the siphonostomatoid families Pennellidae

(Fig. 3.10d) and Sphyriidae and cyclopoid families Herpyllobiidae (Fig. 3.8a) and Chitonophilidae, as well as endoparasites, such as derived members of the Philichthyidae (Fig. 3.10f), Iveidae and Chordeumiidae (Boxshall and Halsey 2004).

The adoption of a parasitic mode of life is associated with extreme oligomerisation in several other highly derived parasitic crustacean taxa, so that similar patterns of morphological simplification are observable. Within the Thecostraca, for example, both sexes of rhizocephalans show extreme morphological simplification, with no traces of body segmentation or any vestiges of paired limbs retained the adults. The endoparasitic ascothoracid *Dendrogaster* (Fig. 3.5) shows similar extreme modification. In the Isopoda, the endoparasitic bopyroidean family Entoniscidae and crytponiscoidean families Cabiropidae and Crinoniscidae all have adult females that lose segmentation and have reduced limbs, but the males are typically less modified.

Sexual size dimorphism is often very pronounced in parasitic crustaceans. In bopyroidean and cryptoniscoidean isopods, for example, the females are larger and more highly transformed than the males. In cryptoniscoideans the males essentially retain the body form of the cryptoniscus larva (Hosie 2008). In most parasitic copepods, the females are larger than the males, although there are exceptions. The copepod family Chondracanthidae is noted for having dwarf males (Kabata 1979), but more detailed analysis showed a trend within the family towards increasing sexual size dimorphism. Østergaard et al. (2005) showed that both sexes are driving this sexual size dimorphism, with chondracanthid females probably selected for high fecundity leading to large body size (i.e. giant females), while males are probably selected for small size (i.e. dwarf males).

3.3.2 Patterns Through Time

3.3.2.1 Fossils and Traces

Fossil parasitic crustaceans are relatively rare (Klompmaker and Boxshall 2015). One species of parasitic copepod is known as a body fossil from the Cretaceous: *Kabatarina patersoni* Cressey & Boxshall, 1989 was recovered from a fossil actinopterygian fish, *Cladocyclus gardneri* Agassiz, 1841, from the Romualdo Member of the Santana Formation of the Serra do Araripe in northern Brazil (Cressey and Patterson 1973; Cressey and Boxshall 1989). *Kabatarina* Cressey & Boxshall, 1989 is currently classified in the family Dichelesthiidae, a family that also contains two other monotypic genera of fish parasites (Boxshall and Halsey 2004). Both sexes of *Kabatarina* were preserved in calcareous nodules and minute details of the segmentation and setation of the limbs are visible on the fossils.

Ten nominal species of pentastomids have been described from the Late Cambrian to Early Ordovician (Waloszek et al. 2006; Castellani et al. 2011). These fossils are typically small, less than 0.8 mm, and have mostly been interpreted as larvae. They had undergone Orsten-type phosphatisation which captured fine detail of surface ornamentation as well as the presence of the two pairs of hooks, diagnostic of all modern pentastomids. Sanders and Lee (2010) suggested that these early Palaeozoic arthropods parasitised small fish-like marine vertebrates, such as conodonts. However, the interpretation of *Invavita piratica*, which is ectoparasitic on a fossil myodocopan ostracod from the Silurian (Siveter et al. 2015), as an adult pentastomid, would suggest that early pentastomids used marine arthropods as hosts. We do not accept this interpretation for the reasons outlined in Sect. 3.2.6. As indicated by Siveter et al. (2015), this novel host association would not preclude a mid-to-late Palaeozoic terrestrialisation of pentastomids during the vertebrate radiation on land.

No body fossils of bopyroidean isopods are known but pronounced swellings of the branchial chamber of fossil decapods are widely accepted to represent swellings induced by parasitic isopods. These traces are the best known example of parasitism by crustaceans from the fossil record, dating back to the Jurassic (see Klompmaker et al. 2014). Wienberg Rasmussen et al. (2008) referred to them as bopyriform swellings, but Klompmaker et al. (2014) expressed doubt that these are all caused by bopyrids and referred to them as isopod-induced swellings. They named this embedment structure as an ichnotaxon, *Kanthyloma crusta* Klompmaker, Artal, van Bakel, Fraanjie & Jagt, 2014, and it currently has about 90 host species, mostly fossil true crabs (Brachyura) and squat lobsters (Anomura) (Klompmaker and Boxshall 2015).

Radwańska and Radwańska (2005) interpreted large external cysts (of the “Halloween pumpkin-mask” type) on Jurassic echinoids as probably of copepod origin, due to their similarity to cysts with multiple openings induced by siphonostomatoid copepods on some modern hydrocorals (see Zibrowius 1981). These authors also accepted the copepod attribution of the trace fossil *Castexia douvillei* Mercier, 1936, described as cysts penetrating the test of Middle Jurassic echinoids (Mercier 1936).

3.3.2.2 Invasive Parasitic Crustaceans

Non-native populations of hosts typically carry an impoverished parasite fauna compared to that of the host population within its original range, and among the factors potentially responsible for this are historic host population bottleneck events, and the possibility that the small size of the founder population may eliminate parasites by sampling effects (Torchin et al. 2002). Despite the generally low level of parasitisation of invasives, there are a few examples of parasitic crustaceans that have been introduced along with their hosts. The common European rhizocephalan *Sacculina carcini* Thompson, 1836 has been introduced into waters off Myanmar, probably transported by international shipping together with its invasive host crab, *Carcinus maenas* (Linnaeus, 1758) (see Boschma 1972). The bopyrid isopod *Orthione griffenis* Markham, 2004 was apparently introduced from Asia into waters off the west coast the USA in the 1980s. This alien parasite has been implicated in the collapse of populations of its gebiidean decapod host, *Upogebia pugettensis* (Dana, 1852), in mudflats along the Pacific coast (Dumbauld et al. 2011).

The eastern Mediterranean is an exceptional situation: it has been profoundly impacted by invasive species coming through from the Red Sea via the Suez Canal, and there are now numerous examples of parasitic crustaceans co-invading the Mediterranean with their Red Sea hosts. El-Rashidy and Boxshall (2010, 2011, 2012a, b, 2014) have documented seven species of parasitic copepods that are of Indo-West Pacific origin and which have co-invaded the Mediterranean with their Red Sea fish hosts. Similarly, Galil and Lützen (1995) reported the presence of the invasive rhizocephalan *Heterosaccus dollfusi* Boschma, 1960 on its invasive decapod host *Charybdis longicollis* Leene, 1938, in eastern Mediterranean waters. El-Rashidy and Boxshall (2011) noted that, in the case of the copepod *Hatschekia siganicola* El-Rashidy & Boxshall, 2011 on the gills of the rabbitfish *Siganus luridus* (Rüppell, 1829), there was no evidence that the host population had undergone any bottleneck event and inferred that the numbers of immigrant host fishes were probably large. The lack of such bottlenecks may explain why the eastern Mediterranean is exceptional, with numerous parasite species co-invading with their hosts. El-Rashidy and Boxshall (2010) also documented the first example of host switching of invasive Red Sea parasites, the copepods *Mitrapus oblongus* (Pillai, 1964) and *Clavellisa ilishae* Pillai, 1962 switching from their original invasive hosts onto a native Mediterranean fish, *Sardinella aurita* Valenciennes, 1847.

3.3.3 Host Usage by Parasitic Crustacea

Parasitic crustaceans utilise an extraordinary range of marine metazoan phyla as hosts, and the highest level of host diversity is exhibited by the copepods, which are reported from hosts representing 14 phyla (Table 3.12). No other fully parasitic taxon approaches this level: hyperiid amphipods use three phyla of gelatinous metazoans as hosts (chordates (= salps), ctenophores and cnidarians), while gammarideans can be found on another two (echinoderms and chordates); thoracican barnacles utilise hosts from three phyla (cnidarians, annelids and chordates); isopods use hosts from two phyla (chordates and arthropods); ascothoracidans use two phyla (cnidarians and echinoderms); pentastomids use two phyla (arthropoda and chordates); although only larval stages occur in arthropods, rhizocephalans and tantulocaridans both use arthropods only, while branchiurans occur only on chordates. Decapods live in symbiotic association with hosts from at least five phyla, Annelida, Chordata (tunicates), Cnidaria, Echinodermata and Mollusca, but in many instances the nature of the association is equivocal.

Table 3.12 Summary of host usage by parasitic Crustacea

Host group	Parasite taxa
Porifera	Copepoda (Cyclopoida, Siphonostomatoida)
Ctenophora	Amphipoda (Hyperiidea)
Cnidaria	
Anthozoa	
Hexacorallia	Ascothoracida, Copepoda (Cyclopoida, Siphonostomatoida), Decapoda, Thoracica
Octocorallia	Ascothoracida, Copepoda (Cyclopoida, Siphonostomatoida)
Cubozoa	Copepoda (Cyclopoida)
Hydrozoa	Amphipoda (Hyperiidea), Copepoda (Cyclopoida)
Scyphozoa	Amphipoda (Hyperiidea), Copepoda (Cyclopoida)
Platyhelminthes	Copepoda (Cyclopoida)
Nemertea	Copepoda (Cyclopoida)
Sipuncula	Copepoda (Cyclopoida)
Annelida: Polychaeta	Copepoda (Cyclopoida, Monstrilloida), Thoracica
Mollusca	
Caudofoveata	Copepoda (Cyclopoida)
Polyplacophora	Copepoda (Cyclopoida)
Bivalvia	Copepoda (Cyclopoida, Monstrilloida, Siphonostomatoida), Decapoda
Gastropoda	Copepoda (Cyclopoida, Harpacticoida, Monstrilloida, Siphonostomatoida)
Scaphopoda	Copepoda (Cyclopoida)
Cephalopoda	Copepoda (Cyclopoida, Harpacticoida, Siphonostomatoida) Isopoda (Cymothooidea)
Phoronida	Copepoda (Cyclopoida)
Bryozoa	Copepoda (Cyclopoida, Harpacticoida, Siphonostomatoida)
Brachiopoda	Copepoda (Cyclopoida)
Arthropoda	
Hexapoda	Pentastomida (larvae)
Crustacea	
Leptostraca	Copepoda (Siphonostomatoida)
Stomatopoda	Rhizocephala
Euphausiacea	Isopoda (Cryptoniscoidea)
Decapoda	Copepoda (Cyclopoida, Harpacticoida, Siphonostomatoida), Isopoda (Bopyroidea, Cryptoniscoidea, Cymothooidea), Rhizocephala
Peracarida	Copepoda (Harpacticoida, Siphonostomatoida), Isopoda (Cryptoniscoidea), Rhizocephala, Tantulocarida
Thecostraca	Isopoda (Cryptoniscoidea), Rhizocephala
Copepoda	Tantulocarida, Isopoda (larvae)
Ostracoda	Copepoda (Siphonostomatoida), Isopoda (Cryptoniscoidea), Tantulocarida
Echinodermata	
Crinoidea	Ascothoracida, Copepoda (Cyclopoida, Siphonostomatoida)

(continued)

Table 3.12 (continued)

Host group	Parasite taxa
Asteroidea	Ascothoracida, Copepoda (Cyclopoida, Siphonostomatoida)
Holothuroidea	Copepoda (Cyclopoida, Harpacticoida, Siphonostomatoida), Decapoda, Tanaidacea
Echinoidea	Ascothoracida, Copepoda (Cyclopoida, Canuelloida, Siphonostomatoida), Amphipoda, Decapoda
Ophiuroidea	Ascothoracida, Copepoda (Cyclopoida, Siphonostomatoida)
Hemichordata	Copepoda (Cyclopoida)
Chordata	
Urochordata	
Ascidiacea	Copepoda (Cyclopoida, Siphonostomatoida)
Thaliacea	Amphipoda (Hyperiidea), Copepoda (Cyclopoida)
Vertebrata	
Agnatha	Copepoda (Siphonostomatoida)
Elasmobranchii	Copepoda (Cyclopoida, Siphonostomatoida), Isopoda (Cymothooidea), Thoracica, Amphipoda
Actinopterygii	Branchiura, Copepoda (Cyclopoida, Harpacticoida, Siphonostomatoida), Amphipoda, Isopoda (Cymothooidea), Pentastomida (larvae)
Amphibia	Branchiura, Copepoda (Cyclopoida), Pentastomida
Reptilia	Copepoda (Harpacticoida), Isopoda (Cymothooidea), Pentastomida
Birds	Pentastomida
Mammalia	Amphipoda (Cyamidae), Copepoda (Cyclopoida, Harpacticoida, Siphonostomatoida), Pentastomida

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Chapter 4
Adaptations and Types of Crustacean Symbiotic Associations

Jo G. Van As and Liesl L. Van As

Abstract Crustacean symbionts occur in all the oceans and in all the river systems and wetlands of the world. In the ocean, they are associated with almost all the invertebrate phyla and the vertebrate classes of fish, reptiles, birds and marine mammals. In freshwater, the crustacean associations are mainly with fish and some amphibian tadpoles. In almost every order of the Crustacea, there are species in some kind of association with other species. Associations range from facultative to highly specialised parasitism where the parasite undergoes total morphological adaptation, becoming metabolically completely reliant on the host for its survival. The crustacean associations are grouped into six categories: epibiosis, inquilinism, commensalism, mutualism, parasitism and eusociality. The most diverse category, parasitism, is subdivided into ectoparasites, mesoparasites, endoparasites, parasitic castrators, parasitoidism and sponge hotels, the latter to accommodate the complex crustacean association with sponges. In the category eusociality, the social behaviour of snapping shrimps is examined. The concluding sections discuss some interesting observations and deductions on parasitic crustacean parasite adaptations and associations using the subclass Branchiura, of which all the species are parasites of fish and amphibian tadpoles, as a case study due to the available information and expertise of the authors on this group.

4.1 Introduction

Living creatures on earth comprise an amazingly diverse assembly of species that all rely on associations with other living creatures. These associations fall under the collective term symbiosis, which was first used by De Bary (1879). Most, but not all,

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scientists agree symbiosis refers to any conceivable association and interaction between organisms. Over many decades various attempts have been made to classify the different types of symbiotic relations, and it would serve no purpose reviewing the vast array of literature, but at least a selected few should be mentioned: Baer (1952), Dales (1957), Hopkins (1957), Margulis (1971), Cheng (1973), Fricke (1975), Monod (1976), Boucher et al. (1982), Huys and Boxshall (1991), Rohde (2005), Poulin (2007) and Trilles and Hipeau-Jacquotte (2012). For the purpose of this chapter, we refer to symbiosis ("living together") as the biological interaction between different organisms living in close physical association, where at least one organism benefits (also see Sect. 4.8 for a glossary of terms).

Within ecosystems, organisms live in habitats, some in very specific habitats and others less so. In *The Science of Life*, an encyclopaedia published by Wells et al. (1934), in a chapter on habitats and their inhabitants, the following description is provided: "There remains one further major habitat, which is neither earth, air nor water but rather fish, flesh and fowl". All living creatures provide a habitat for other creatures to colonise, and it is very often our terminology that fails to describe the relationship of the association.

The symbiotic relationship where one organism benefits at the expense of another is referred to as parasitism (see Sect. 4.6.5). Mites living and feeding on plants are regarded as parasites, but monkeys living in trees and feeding on their fruits are not regarded as parasites, and yet both fit the classical definition of parasitism that focuses on effects such as profit or harm and even damage (Trilles and Hipeau-Jacquotte 2012). Amongst crustacean parasites, a group of major importance are the copepods. Descriptions of copepod species associated with fish, usually but not always, provide some information on the host species and location of the infestation. In the case of copepods and most crustaceans associated with fish, there is little doubt that it is always parasitic and even low infestations can seriously harm and kill the host. Descriptions of copepods and other crustaceans from marine invertebrate hosts very often do not provide host data, in some cases because hosts cannot be identified. This is often the case with ascidian and sponge hosts, or otherwise it is because this information is unknown due to the method of collection. For examples see Smit and Van As (2000) and Smit et al. (2000) where the hosts of parasitic larvae of a new and a redescription of a known species of gnathiid, respectively, are also listed as unknown.

Whilst scouring the vast volume of literature on crustaceans associated with an enormous diversity of marine and freshwater creatures, it became evident that the systematics of many groups of both symbionts and hosts are in flux and sometimes very confusing. With molecular systematics now becoming increasingly more accessible as a tool in parasitology and taxonomy in general, we will be experiencing an increase in this flux for some time to come. There is a general acknowledgement that alpha taxonomy and systematics of the groups should be based on a holistic approach where as many parameters as possible should be considered.

Parasitologists very often use the words "associated with" if the specific nature of the association is unknown or uncertain. Unfortunately, this is the case in the vast majority of associations, in particular those between crustacean symbionts with marine invertebrates. The term association refers to affiliation between living organisms. It does not imply that it is an equal partnership; in fact, it is almost certainly never equally beneficial to the different consorts.

Many parasitologists work in the medical and veterinary environments, studying parasites and disease-causing pathogens with the purpose of curing the host and eliminating the parasite. Some scientists studying naturally occurring symbioses may be referred to as parasitologists but should rather be referred to as "symbiontologists". This word does not appear in the *Oxford English Dictionary*, but it had already been coined more than 50 years ago by Noble and Noble (1961). It was not widely accepted as it may create the impression that the scientific interest only relates to the symbionts and not the hosts. It does sometimes crop up in recent papers such as Boscaro et al. (2012). Alternatively, the term "symbiology" was suggested by Russell (1967), but this also did not stick and therefore did not make it into the dictionaries. In this chapter, the term symbionts and symbiosis will be used unless there is enough evidence to specifically identify the association.

4.2 Host Range of Crustacean Symbiotic Associations

Crustacean symbionts in the ocean are associated in some way with almost all invertebrate phyla, including other arthropods, as well as all the marine vertebrates: fish, reptiles, birds and mammals (Rohde 2005; Trilles and Hipeau-Jacquotte 2012). In freshwater, crustaceans are mostly associated with fish, but there are isolated examples of lernaeid copepods associated with tadpoles in South Africa (Robinson and Avenant-Oldewage 1996), adult frogs and tadpoles of the foothill yellow-legged *Rana boylii* Baird, 1854, in California, USA (Kupferberg et al. 2009), and even aquatic larvae of insect species of Ephemeroptera and Trichoptera in Oklahoma, USA (McAllister et al. 2011). A new cyclopoid copepod *Eucyclops bathanalicola* Boxshall & Strong, 2006 was described from a gastropod endemic to Lake Tanganyika (Boxshall and Strong 2006). The subclass Branchiura comprises only four genera; all are fish parasites (mostly from freshwater fishes but about 40 species of the genus *Argulus* Müller, 1785, are found on marine and estuarine fishes). Some branchiurans have been reported from salamanders and alligators (Ringuelet 1943; Piasecki and Avenant-Oldewage 2008). Poly (2003) described a new species *Argulus ambystoma* Poly, 2003 from a salamander *Ambystoma dumerilii* (Dugès 1870). The original description of *Dolops ranarum* (Stuhlmann, 1891), the only species of this genus in Africa, was from a tadpole. Most of the reports of lernaeids on non-piscine hosts are the opportunistic *Lernaea cyprinacea* Linnaeus, 1758, originally from Asia, but it has invaded practically the whole world via the global introduction of Asian carp species.

4.3 Hosts and Transmission

4.3.1 Hosts

The term host usually refers to the physically larger associate, but as in most symbiotic terms, it also encompasses a broad spectrum. A permanent host is one on (or in) which all the life cycle stages of the symbiont live obligatory. A definitive host is one on (or in) which the reproductive stages of the symbiont will reside. Intermediate host refers to a host in which only some stages of the life cycle reside, generally larval stages. In complex life cycles, there could be two or even more intermediate hosts in a single cycle. Some intermediate hosts are also vectors of parasites that transmit parasitic diseases to mostly vertebrates (see Chap. 7 of this volume). Vectors can be active vectors, such as argulids transmitting larvae of dracunculoid nematodes to fish (Moravec et al. 1999), or passive vectors such as gnathiids that are transmitting blood protozoa when eaten by other fish after taking blood meals from infected fish in tidal pools (Davies and Smit 2001).

A rule of thumb is that internal adults (endoparasites) usually infect spaces in the host that have a way out for their eggs or larvae to escape, such as in the digestive or urinary systems of host fish. Infection is used in reference to internal parasites and infestation to ectoparasites. With a few exceptions, tissue-dwelling parasites are usually larval forms that require the intermediate host to fall prey to the final or definitive hosts in which they will become adults. Parasitic crustaceans evolved special anatomical adaptations to overcome this challenge; these are classified as mesoparasites (see Sect. 4.6.5). In some cases, the larval parasites can manipulate their intermediate host's behaviour so that the host becomes exposed, therefore increasing its vulnerability to predation in order for the parasite to become adults in the predator host. This occurs commonly amongst trematodes, particularly in the genus *Diplostomum* von Nordmann, 1832 (Van As et al. 2012; Grobbelaar et al. 2014). Amongst crustaceans the rhizocephalans parasitise a crab host by invading all body tissues and changing the host behaviour. In some hosts, the crustacean parasite will effectively castrate the host, either temporarily or in most cases permanently (Lafferty and Kuris 2009).

4.3.2 Transmission

In all the amazingly diverse crustaceans, including free-living and symbiotic forms, the first larval stage is in most cases a nauplius (Fig. 4.1a) (Martin et al. 2014). In some cases, as in the Branchiura, the eggs hatch into a more advanced stage, having passed the nauplius stage during embryonic development (Fig. 4.1b–d). In the case of *Dolops* Audouin, 1837, the hatchlings resemble the adults in miniature form (Avenant et al. 1989a) (Fig. 4.1c). In the Branchiura, the cephalic appendages include the antennules (greatly reduced to a small cluster of setae in *Chonopeltis* Thiele, 1900), the antennae and the maxillulae. The latter undergo transformation from hooklike structures in the larvae to become large disc-shaped suckers in the adults of *Chonopeltis* (Fig 4.2a–d) and *Argulus* (see Van As and Van As 1996). This remarkable process is regarded as a biological novelty; during the ontogeny the maxillulae, which is a suction disc, originates from the cross-boundary area of the first and second podomeres of the larval maxillulae, which is a hook (Kaji et al. 2011, 2012). The biological function of the mouthpart remains the same, i.e. attachment to

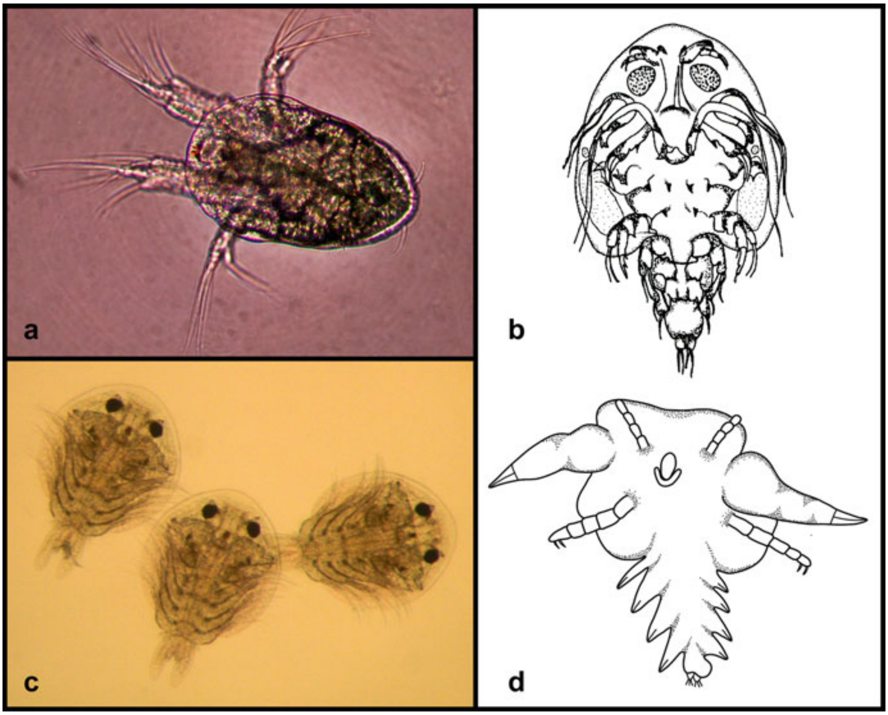

Fig. 4.1 First larval stages. (**a**) *Lamproglena* von Nordmann 1832 nauplius; (**b**) *Argulus japonicus* Thiele, 1900; (**c**) *Dolops ranarum* (Stuhlmann, 1891) larvae; and (**d**) *Chonopeltis lisikili* Van As & Van As, 1996 first larval stage. Image (**b**) redrawn from Lutsch and Avenant-Oldewage (1995)

the host, whilst the functional morphology undergoes comprehensive transformation. In *Chonopeltis lisikili* Van As & Van As, 1996, egg-bearing subadults with fully developed suction discs and nonfunctional remnants of hooks were recorded, and later fully developed females without any remnants of hooks were found in the Okavango Delta in Botswana (Van As and Van As 1996, 2015). In adult *Dolops* the maxillulae remain large prominent hooks, similar to those of the larvae. In some species of Caligidae, a novel characteristic is displayed in the lunule that consists of paired cuplike structures on the frontal plates. The lunule originates from a modification of the marginal membranes during ontogeny (Kaji et al. 2012).

At least in a few species, the first nauplius is already parasitic as is the case in all the species of the copepod order Monstrilloida. In some species there are up to six morphologically distinct nauplius stages, as well as five or six copepodite stages. Most copepod infestations of mesoparasites only start in the final copepodite stage and probably after copulation had taken place; the female will undergo post-mating metamorphosis and embeds as a mesoparasite (Schminke 2007; Martin et al. 2014).

In some mesoparasitic copepods, the head and a large part of the thorax are embedded and in many species even deep into the tissue of the host. In the lernaeid copepods, only the head is embedded with the body and egg sacs always external so

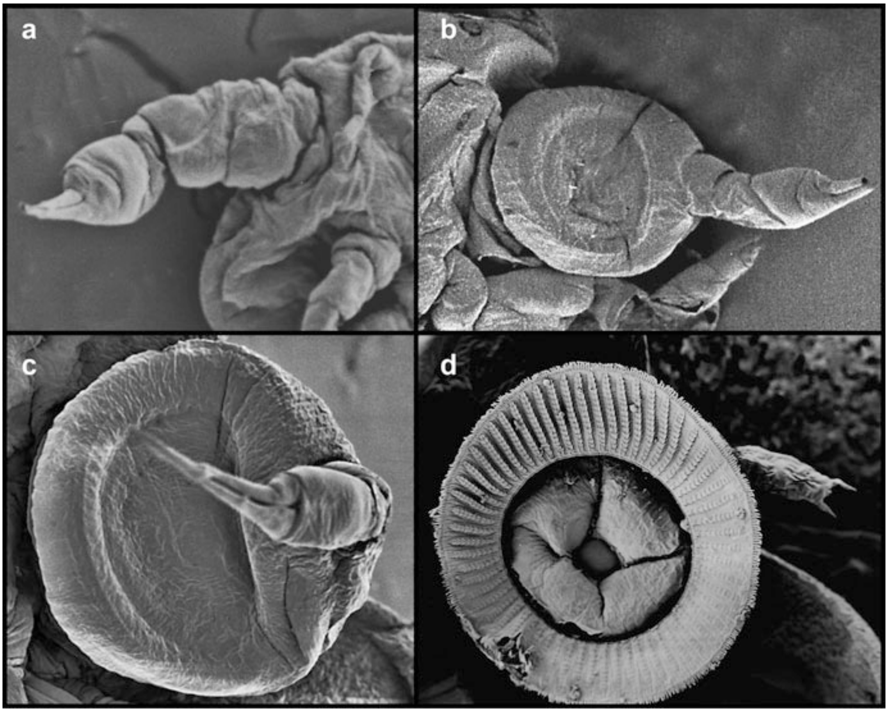

Fig. 4.2 Ontogeny of the maxillulae of *Chonopeltis lisikili* Van As & Van As, 1996. (**a**) Second larval stage, (**b**) fourth stage, (**c**) seventh stage and (**d**) subadult stage with remnant of claw still viable

that the nauplius larvae can escape into the water. The Pennellidae is one of the major families of parasitic copepods found on marine fishes and cetaceans. The family currently contains 148 species (24 genera) with a large part of the body embedded deep in the body of a large variety of marine fish hosts (Uyeno et al. 2015). Some species of the genus *Cardiodectes* Wilson, 1917 even penetrate into organs such as the heart of their fish host, but the eggs sacs remain external (Grobler et al. 2001).

4.4 The Origin of Symbiotic Associations

Unlike the origin of life, which we now understand was most likely a one-off event, the origin of symbiosis was not so straightforward. The very existence of eukaryotic cells, as elegantly proposed by Margulis (1970, 1993), came about through symbiosis. Although her revolutionary idea was harshly criticised initially, it is now well accepted as mainstream science (López-Garíca and Moreira 1999). Symbiotic life strategies are so successful that they occur in some form throughout all domains of life. It is also widely accepted that all forms of symbiosis, including parasitism, evolved independently in different groups and that it happened many times even within the same taxa (De Meeûs and Renaud 2002; Poulin 2007). Crustacean symbioses have resulted from multiple evolutionary events that lead to associations that cover the entire spectrum of categories (Trilles and Hipeau-Jacquotte 2012).

There is little doubt that parasites, and for that matter all forms of symbiosis, originally evolved from free-living organisms, but there are certainly some prerequisites for these associations to be consummated. The potential symbionts had to be preadapted in different ways to initiate the association. Their limbs must have had some hooks or other means to attach to the host. The mouthparts of the ancestral species, probably from a free-living predator, must have been able to take meals from the host tissue or blood. The idea of the need for preadaptive traits in precursors of parasites is an old idea first used in the 1950s by Rothschild and Clay (1952). According to Poulin (2007), this is essential for transition to a parasitic association. There had to be opportunity; the ancestral symbiont (including all possible types of associations) had to share the same microhabitat, even if only for a short time. Once the association was established, natural selection would gradually modify the attachment and feeding organs, as well as the life cycle and behaviour of the symbiont, over time to best fit the new environment on the external surface or in the internal organs of the host. Most extant and at least some extinct parasitic crustaceans produce a nauplius larva which is released into the water (Martin et al. 2014). In many parasitic crustaceans, these larvae, carried by water movement, go through several nauplius and copepodite stages before settling on a host. This opens the opportunity for crustacean parasites to explore new associations in much the same way as digenean trematodes, where the intermediate host is usually a snail. The snail releases cercariae intended to infect fish (Grobbelaar et al. 2014) which will try to penetrate any vertebrate, including humans, causing fish-borne zoonotic trematode infections (Hung et al. 2013).

Very often the adaptation will involve a regression or orthogenesis towards a more specialised relationship where the parasite forfeits a trait, often found in mesoparasitic copepods. This process was regarded as primitive in the early days of exploration (Poulin 1995). This was influenced by the view that has become known as Cope's rule. Cope (1896) concluded that if organisms of a particular taxon adopt a parasitic life strategy it is irreversible. This also cultivated the anthropocentric notion that parasites and parasitic strategies are "degenerate" and do not have any significant status in the evolution or ecology of the system in which they are found (Jackson 2014). All casual associations, including temporary parasitism such as found amongst argulids, do not necessarily evolve into a more complicated and permanent association. Temporary associations are not necessarily the beginning of an association that will gradually become more permanent.

Amongst the crustacean symbionts, there are species that are found associated with a variety of hosts (referred to as low host specificity). Crustaceans, such as some copepods and at least one branchiuran, are also known to have broad host ranges. The fish parasite *Lernaea cyprinacea* has been recorded from different fish species (Piasecki and Avenant-Oldewage 2008) and has also been recorded from aquatic insect larvae (McAllister et al. 2011). This could lead to a way of establishing new host models and for species radiation to occur within those particular symbiotic taxa.

Preadaptive symbionts could, in this way, establish associations with unusual hosts that may result in a new lineage of host and/or parasite association that could be fine-tuned over time by natural selection.

In coastal marine waters, ponds, lakes and pans in temperate and arid areas, many planktonic organisms, mostly crustaceans, have evolved the ability to produce diapausal eggs or stages that overcome unfavourable conditions (Hairson and Bohonak 1998). Association with a larger animal, especially if the symbiont becomes metabolically dependent on the host, could provide another way of adapting to variable conditions, obtaining food and decreasing the risk of desiccation and predation. Hairson and Bohonak (1998), in a review of reproductive strategies and copepod invasion of inland waters, concluded that diapause played a pivotal role in the successful colonising of inland waters. They also noted that of the 22 families of copepods found in inland waters, 12 either exhibit parasitism or diapause, and what is particularly significant is that there are no copepod taxa that exhibit both. We infer that the evolutionary pressure exerted by fluctuating conditions could have favoured the origin of copepod parasitism on fish.

Translocation of alien hosts and their parasites to virgin territory may provide a case study of transition to “parasitism in progress” (Poulin 2007). There may be such a potential transition in progress in South Africa, albeit not involving a crustacean parasite but rather an alien crustacean host. Du Preez and Smit (2013) recorded finding the Australian freshwater crayfish “redclaw” *Cherax quadricarinatus* (Van Martens, 1868) in natural waters of a game reserve in South Africa. These redclaw crayfish were infested with a nonindigenous temnocephalan flatworm parasite. Both crayfish and temnocephalan were in full breeding condition. The freshwater crayfish and its parasites do not occur naturally in Africa. The brachyuran crabs that include the freshwater crabs of Africa do not display any grooming behaviour (Bauer 1981) and will therefore be highly susceptible to infestations of temnocephalans. The response of the alien crayfish to local aquatic parasites could be interesting to study in the future.

4.5 Human Association with Parasites

Parasites of anatomically modern humans have had very little evolutionary time to coevolve; therefore any parasitic infection or infestation of humans has a negative impact from a great inconvenience to life-threatening. Parasites infecting humans include slightly more than 100 species, of which only the head louse *Pediculus humanus capitis* Linnaeus, 1758 and body louse *P. humanus corporis* Linnaeus, 1758 are strictly true obligate human parasites (Kittler et al. 2003). The rest evolved together with prehumans or are zoonotics originating from wild and later domestic animals. These infections are almost always life-threatening, and it is therefore no wonder that humans have such negative connotations with parasites. Although there are records of the isopod *Rocinela signata* Schioedte & Meinert, 1879, attacking human divers and even extracting blood from the wounds (see Garzón-Ferreira 1990), there are no true crustacean parasites of humans. Crustaceans are, however, instrumental in the transmission of a human parasite. A planktonic cyclopoid copepod acts as vector for the Guinea worm *Dracunculus medinensis* (Linnaeus, 1758). The copepod carriers of the larvae are swallowed whilst drinking water, usually from wells dug in arid environments.

4.6 Crustacean Symbiotic Associations

Symbiotic associations between organisms is a continuum of biotic interactions of which no two are exactly the same, none following the same route or necessarily came about along the same evolutionary pathway (Poulin 1995, 2007). It is also a dynamic process that changes over time depending on the life cycle stage of the symbionts involved, the behaviour of the host and the environmental conditions. What scientists usually do by attempting to define these relationships is taking snapshot pictures of a spot in the continuum and fixing the particular association in a specific situation.

This section attempts to summarise the different types of symbiotic associations of crustaceans based primarily on the classical approach by Monod (1976). It is also supplemented from other works already mentioned above, including the six basic strategies proposed by Poulin (2011). These are parasitoids, parasitic castrators, directly transmitted parasites, trophically transmitted parasites, vector-transmitted parasites and micropredators. In the same paper, Poulin also makes a case for the multiple origins of crustacean symbionts. The approach in this chapter will include the hosts and endeavours to understand the relationships from an ecological approach.

Crustacean symbionts are not a uniform group. Some parasitic groups are very old and date back at least 400 million years, as confirmed by Siveter et al. (2015) in describing a 425 million years old, perfectly preserved adult specimen of a pentastomid, still attached to its ostracod host. Crustaceans have radiated to fill almost all conceivable niches in the ocean, including symbiotic relationships with most of the phyla of oceanic animals. Due to the limitations of space, this account cannot provide a comprehensive review of all the associations of crustacean symbionts, neither can it include examples covering the total spectrum.

4.6.1 Epibiosis

This condition, although not considered to be a symbiotic interaction, describes an association worth discussing here and refers to one organism settling on another (see Chap. 8 of this volume). The settler is referred to as an epibiont and the host the basibiont. It applies to animals settling on other animals (epizoons), or any other living creature, such as plants in freshwater and chromists in the ocean (epiphytes). Epibiosis refers to living organisms attached to other living organisms, as used by

Robin et al. (2013) and not as used by Taylor and Wilson (2002), namely, as organisms attached to hard substrates. The attachment of small organisms to larger ones is common. When it is simply a brief association for the purpose of transportation, it is referred to as phoresy. In some cases, this could be the beginning of more permanent associations, and some parasites existing today could have evolved from phoretic ancestors. Even crustacean fish parasites such as *Dolops ranarum* are often the transporters of sessiline ciliophorans (Van As and Van As 2015). In the marine environment, one of the best-known examples is barnacle settlement on cetaceans. This includes species of the stalked barnacle of the genus *Lepas* Linnaeus, 1758 which attaches to almost anything floating and are often found on driftwood (Fig. 4.3a), attached to boats and ships, and also to cetaceans (Fig 4.3b). They could be considered as phoretic and are usually only a slight irritation to their hosts; however *Lepas* spp. has been implicated as partially responsible for die-off of dolphins during the early 1990s where they were found attached to the teeth of the dolphins (Aznar et al. 1994).

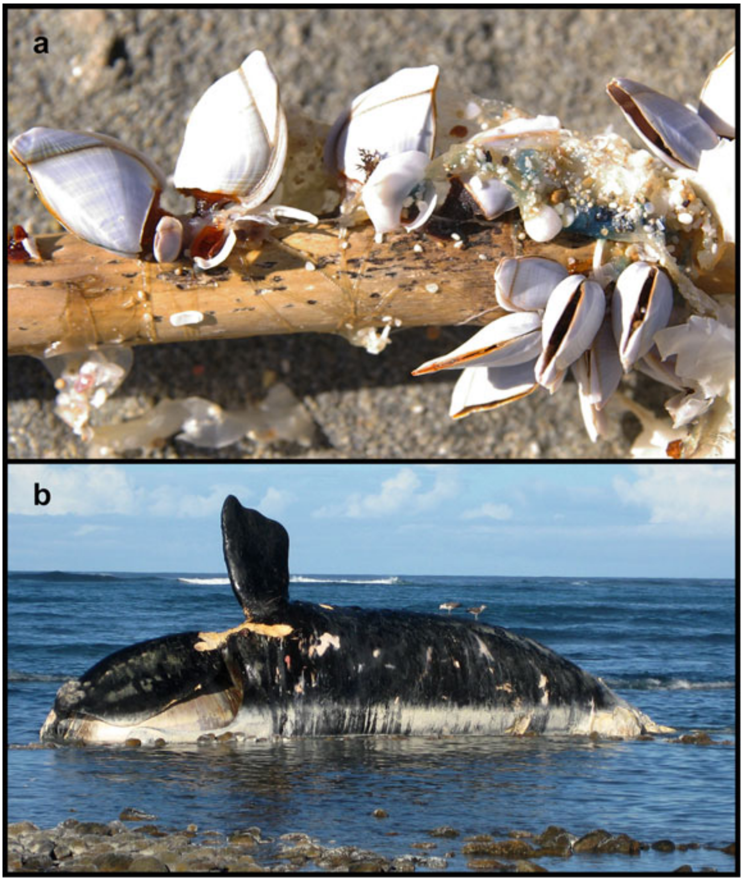

Fig. 4.3 (**a**) Goose barnacles of the genus *Lepas* Linnaeus, 1758 on driftwood. (**b**) Baleen whale beached along the coast of South Africa

4.6.2 Inquilinism

This apparently simple association refers according to Fraaye and Jäger (1995) to the condition where one organism lives within another using the host as a place of refuge, even after its death. This type of association is known in the fossil record from the Upper Jurassic (Robin et al. 2013). Inquilinism is best illustrated by hermit crabs (superfamily Paguroidea), which by their typical nature as mobile inhabitants of protective shells of dead molluscs (Fig. 4.4), where the dead molluscs provide multiple opportunities for a variety of co-inhabitants. The association between the hermit crab and remnants of former living molluscs would certainly not qualify to be included as parasites; nevertheless, it still represents an obligate association albeit with a body part of a dead animal. This association fits neatly into the definition of metabiosis, where one organism creates conditions for others to survive in, even though it is posthumously. This association provides countless opportunities for squatters, as well as a long list of parasites (about 150 species from 9 different phyla and 17 potential parasites from 5 phyla). The confirmed crustacean parasites include about 30 parasitic barnacles and more than 80 species of isopods, as well as several harpacticoid species (Ho 1988). The total number of parasites and potential parasites associated with hermit crabs exceeds 170 different species (Williams and McDermott 2004; McDermott et al. 2010). Representatives of the Copepoda order Harpacticoida also live associated with other animals. Their specific association is not clear; they appear not to be parasitic but utilise other animals as habitat. One such probable hitchhiker is the harpacticoid *Balaenophilus unisetus* Aurivillius, 1879,

Fig. 4.4 Hermit crabs escape midday sun hiding under the jetty of a coral island off the coast of Cuba

from the family Balaenophilidae, originally only found on the baleen plates of baleen whales by Vervoort and Tranter (1961) but was later also found on other whale species by Bannister and Grindley (1966). A second species of harpacticoid, *Balaenophilus umigamecolus* Ogawa, Matsuzaki & Misaki, 1997, was found on a sea turtle. It appears that it not only uses the turtle for transportation but also scrapes some of the epidermis from the neck of the turtle. This was found in an aquarium population of the turtle *Caretta caretta* (Linnaeus, 1758); thus it is not conclusive that they are parasites in the wild. Sea turtles have more than 200 species of epibionts that could fit into different association categories presented in this chapter. These are summarised by Frick and Pfaller (2013).

Some harpacticoids from the subfamily Donsiellinae live in burrows of wood-boring isopods of the genus *Limnoria* Leach, 1814. Species of the subfamily Cancrincolidae live in the gill chamber of marine as well as some land crabs, whilst some are also associated with cephalopod molluscs (Avdeev 1986).

4.6.3 Commensalism

The *Oxford English Dictionary* defines commensalism as relating or denoting an association between two organisms in which one benefits and the other derives neither benefit nor harm. The classic definition accepted by most biologists is the living together of two or more organisms in a bilateral relationship that is beneficial to the commensal but harmless for the other symbiont. Of all the categories of association, commensalism is probably the most controversial as it supposes an ecological state of equilibrium. Any bilateral association has costs and effects for the partners involved, sometimes perhaps only in the short term and in other cases over a longer period. A classic example relating to crustaceans is cleaning symbiosis, but that fits into other categories too and will be dealt with separately.

4.6.4 Mutualism

Mutualism is regarded as a bilateral relationship that involves reciprocity for both symbionts.

4.6.4.1 Cleaning Symbiosis

Cleaning symbiosis also attracted wide attention amongst the general public, mostly because of superb pictures of coral reef cleaning symbiosis continuously published in popular media. Cleaning behaviour in marine environments, especially in reef-dwelling fish species, is quite common but less known (or at least less reported) from freshwater. Ribbink and Lewis (1982) describe *Pseudotropheus* *crabro* (Ribbink & Lewis, 1982) which feeds on the branchiuran *Argulus africanus* Thiele, 1900, in Lake Malawi. Witte and Witte-Maas (1981) reported that some haplochromine species remove branchiurans from other species of fish, and Minshull (1985) reported observing juvenile *Labeo cylindricus* Peters, 1852, removing fungal growth from the red-breasted tilapia *Coptodon rendalli* (Boulenger, 1896).

Ayotunde et al. (2007) analysed the gut contents of 445 specimens of the African carp *Labeo coubie* Rüppell, 1832 and found a large percentage of the gut contained *Argulus* and *Dolops* remnants, as well as other benthic and planktonic copepods. These authors are of the opinion that cleaning behaviour amongst freshwater fishes is more common but less observed than those in marine environments.

Some cleaners are specialised in their feeding. The cleaner symbiont fish, *Labroides bicolor* (Fowler & Bean, 1928), has been observed to eat more than 1200 individual ectoparasitic crustaceans, mainly gnathiid isopods (Grutter 1996). It was also reported that some fish species spend about 30 min per cleaning session (Poulin and Grutter 1998). This implies that there must be some benefit for the fish's fitness if such a long period is allocated to visiting cleaning stations.

In a study of Branchiura in the Okavango Delta that extended over a period of 16 years by Van As and Van As (2015), the authors concluded that branchiurans are rare, especially members of the genus *Argulus*. During this period, a phylometroid nematode *Philometroides africanus* Moravec & Van As, 2001 was also collected and described with a high prevalence amongst the only infected host species, namely, the African pike *Hepsetus cuvieri* (Bloch, 1794). This was the first record of a phylometroid nematode parasite of Africa fish (Moravec and Van As 2001). The male and the vector of *P. africanus* are unknown, but *Argulus* species have been implicated as vector for other species of the Dracunculoidea (see Moravec et al. 1999). The prevalence of argulids in the Okavango is very low (Van As and Van As 2015), whilst the prevalence of the phylometroid nematode *P. africanus* is high. A possible explanation for the low prevalence of argulids is that members of the genus *Argulus* and *Dolops* are strong swimmers and frequently leave the host and could have done so during the collection of fish hosts. Another explanation for the low prevalence of argulids in the Okavango could possibly be that cleaner fish remove these ectoparasites. This possibility should be investigated.

4.6.5 Parasitism

In the case of parasitism, it will also be useful to start by referring to the *Oxford English Dictionary*. A parasite is defined as "an organism which lives in or on another organism and benefits by deriving nutrients at the other's expense". The term originated from the Greek word *parasitos* describing a person eating at another's table. Parasites are natural components of all ecosystems and of life itself. For the purpose of this chapter, we will adopt the concept of metabolic dependence as the password to be included in this category of true parasites. In most definitions of parasitism, the word "living on or in" and "damage or harm to the host" is mostly included. Excluding these words from the definition here is not intended to suggest that harm and even death of the host can and does not occur, but in many cases, it does not. Parasitism, or for that matter metabolic dependence, again could vary in the duration, which could be for a short period in the life cycle of the parasite or it could be a total obligate dependence of all life stages of the parasite as well as for their progeny.

4.6.5.1 Ectoparasites

All categories of crustacean ectoparasites use a wide range of microhabitats on their hosts, but the term generally refers to those that are found on the skin, gills and various orifices on the fish or invertebrate host, with an escape route to the external environment. This could also be only for a short period or even for only certain life stages of the parasite. We distinguish between permanent and transient ectoparasites, i.e. those that permanently remain associated with their host to those that spend only a short period on the external surface of their host.

Permanent Ectoparasites

The majority of freshwater crustacean parasites found associated with fish are ectoparasites, living on the skin of their host, such as some members of the branchiuran genus *Chonopeltis*. Those spending their entire life on the skin of the host contain pigments that resemble the host fish's pigmentation, for example, *Chonopeltis meridionalis* Fryer, 1964 (originally described as *C. koki* Van As, 1992; see Van As et al. 2017), found on the cyprinid *Labeo cylindricus* (Fig. 4.5a, b). Other branchiurans that live in the branchial cavity, i.e. *C. liversedgei* Van As & Van As, 1999, have no pigmentation and are never found on the gills itself, only on the interior surface of the operculum and the smooth surface of the branchial chamber (Van As and Van As 2015). All branchiuran species move around on their host but are mostly confined to specific areas. Those living in the branchial chamber are not found on the skin. The opportunistic, invasive *Argulus japonicus* Thiele, 1900, when found in heavy infestations, occur all over the host including the branchial chamber (Kruger et al. 1983) (Fig. 4.5c). At least *A. japonicus* and probably all the freshwater species leave the host at will and reattach to other hosts. They then are temporary ectoparasites.

Transient Ectoparasites

Sea lice are not "true lice" but parasitic copepods of the order Siphonostomatoida, family Caligidae (Fig. 4.6a, b). There are more than 30 genera within this family (Walter and Boxshall 2018). The genus *Lepeophtheirus* von Nordmann, 1832 and various species of *Caligus* Müller, 1785 are adapted to salt water, and some species are major ectoparasites of wild and farmed salmon where they feed on the mucus, epidermal tissue and blood of host fish. These parasites are also transient ectoparasites

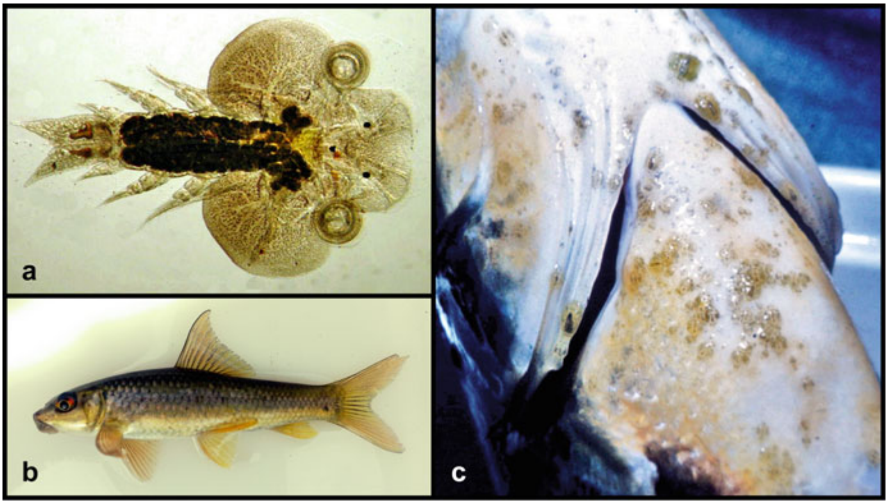

Fig. 4.5 (**a**) *Chonopeltis meridionalis* Fryer, 1964 collected from the Zambezi River, Namibia (syn. *C. koki*) is pigmented, corresponding to that of its host, *Labeo cylindricus* Peters, 1852; (**b**) *Labeo cylindricus* Peters, 1852; and (**c**) *Argulus japonicus* Thiele, 1900, infestation on the common carp, *Cyprinus carpio* Linnaeus, 1758. Image b © Wynand Malherbe

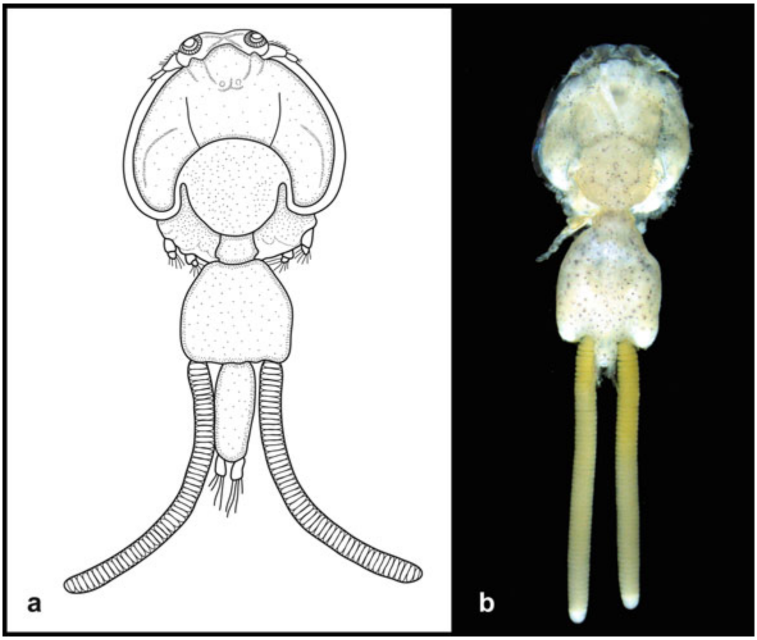

Fig. 4.6 Sea lice of the genus *Caligus* (order Siphonostomatoida) are ectoparasites, whilst some of their larval stages are free-living. Image (**a**) from Smit and Hadfield (2018); image (**b**) © Marliese Truter

with four chalimus stages, and the adults are all parasitic, whilst two nauplius larvae and two copepodites are free-living (Burka et al. 2011). In Chile, *Caligus rogercresseyi* Boxshall & Bravo, 2000, is the only species of this speciose genus that affects the salmon industry. The life cycle consists of two planktonic nauplius larvae. The third stage is an infective copepodite followed by four stages, young adults as well as the male and female that live and feed on the host (González and Carvajal 2003).

Other ectoparasites live on the gills, such as members of the genus *Ergasilus* von Nordmann, 1832, and attach with their modified antennae to the gill filaments (Fig. 4.7a–c). Members of the genus *Lamproglena* von Nordmann, 1832, attach

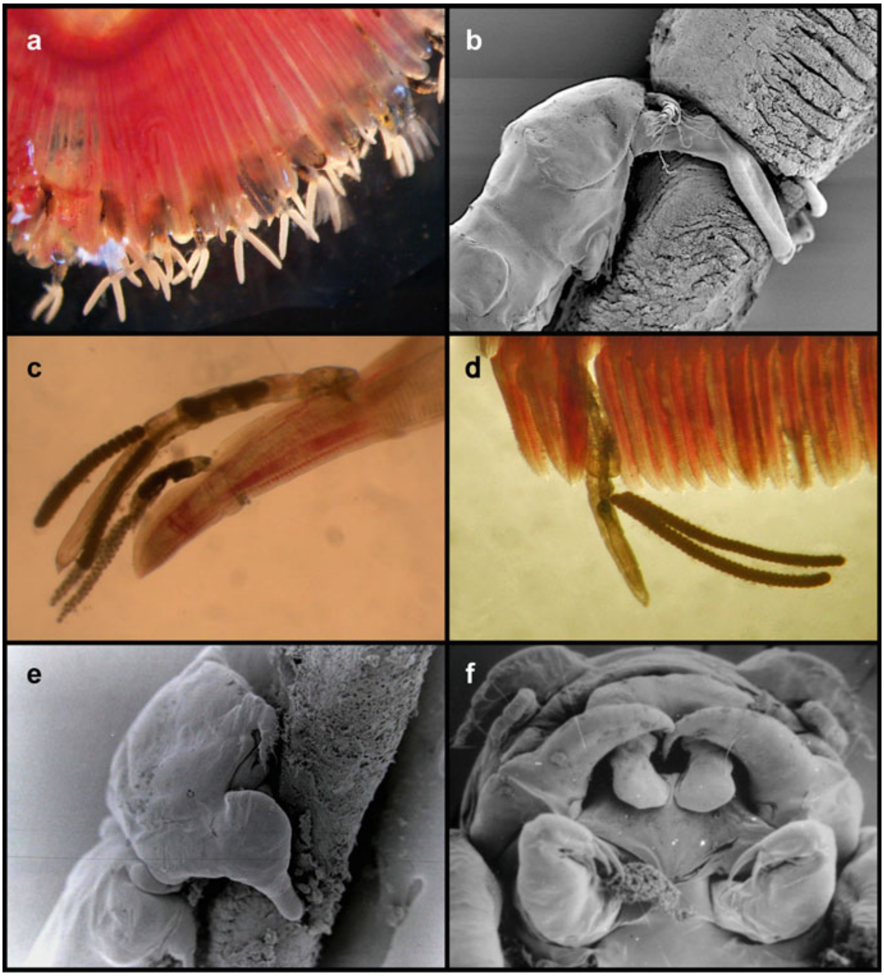

Fig. 4.7 (**a**) *Ergasilus* von Nordmann, 1832 attached to the gills of host fish, so that egg sacs extend past gill filament; (**b**) ergasilid attaches with adapted antenna; (**c**) both *Ergasilus* and *Lamproglena* von Nordmann, 1832 copepods on the same gill filament; (**d**) *Lamproglena* with egg sacs extending past gill filament of host fish; (**e**) *Lamproglena hepseti* Van As and Van As, 2007, extension of carapace aids in attachment; and (**f**) mouthparts of *L. hepseti*

with their modified maxillae (Fig. 4.7c–f). Usually the attachment site is such that the egg sac extends beyond the gill filament so that the newly hatched nauplius can escape without being entangled in the gill filaments. In the life cycle of species of the genus *Ergasilus* and *Lamproglena*, the larvae are free-swimming and only become parasitic after a few moults as copepodites. Copepodites of ergasilids are often found on the host but not attached to the gills as the antennae are not yet fully developed. They probably also do not yet feed on the host. In heavy infestations, more than one specimen can be found on the same gill filament (Fig. 4.7c). Ergasilids have also been recorded from the nasal cavity of piranhas in Brazil (Boeger and Thatcher 1988).

The information on the ectoparasite *Dolops* is based mostly on *D. ranarum*, of which the literature is summarised in Van As and Van As (2015), as not much is known about the biology of the South American and Tasmanian species. *Dolops* species are ectoparasites that can be found attached to the skin of the host, in the mouth, branchial cavities, and on the gills, where it leaves a lesion (Fig. 4.8). They are able to move around on the host, are capable of swimming, are probably able to leave the host to deposit eggs and are capable of infesting other hosts after depositing eggs on solid substrates. This is also most likely the case with all the species of *Argulus*, as well as the two known species of *Dipteropeltis* Calman, 1912 from South America.

Dipteropeltis hirundo Calman, 1912 was first described from specimens collected in southern Brazil, in the region of Matto Grosso (Calman 1912). Subsequently, *D. hirundo* was recorded in Brazil, Venezuela and Argentina by Thatcher (1991). Recently Neethling et al. (2014) redescribed *D. hirundo* (Fig. 4.9) and also described a new species *Dipteropeltis campanaformis* Neethling, Malta & Avenant-Oldewage, 2014 from material obtained from different museums. Not much is known about both *Dipteropeltis* spp. association with their hosts. They have been recorded from one species of the family Acestrorhynchidae, a piranha *Pygocentrus nattereri* Kern, 1860 of the family Characidae, including five other species and a species of the family Pimelodidae (see Luque et al. 2013). Comparing the mouthparts of *Dipteropeltis*

Fig. 4.8 *Dolops ranarum* (Stuhlmann, 1891), attached to the mouth of *Oreochromis mossambicus* (Peters, 1852)

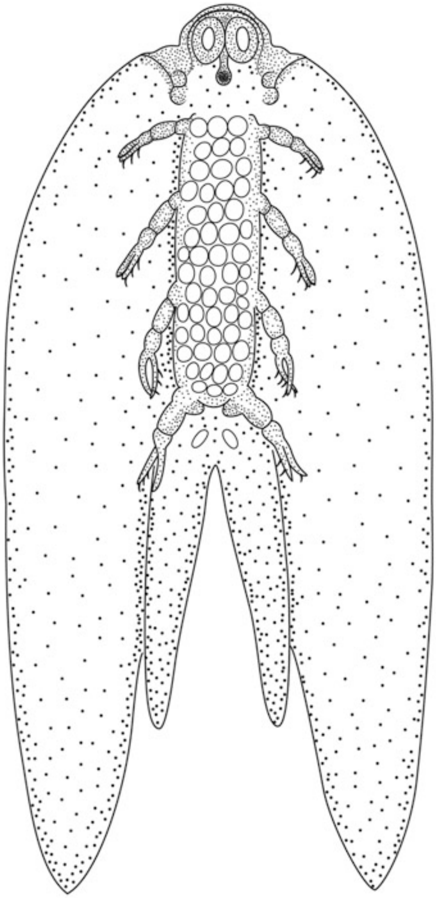

Fig. 4.9 *Dipteropeltis hirundo* Calman, 1912. Image of female redrawn from Neethling et al. (2014)

using scanning electron microscopy with those of other genera, Møller and Olesen (2010) came to the conclusion that *Dipteropeltis* is similar to that known for members of the genus *Argulus* in having a mouth cone, a pre-oral spine and a labial tubes. The labial tubes secrete anticoagulants during feeding (Saha et al. 2011). In Fig. 4.10, the mouthparts of *Argulus izintwala* Van As & Van As, 2001 (Fig. 4.10a, b) are compared with that of *Chonopeltis meridionalis* (syn. *C. koki*) (Fig. 4.10c, d) and *Dolops ranarum* (Fig. 4.10e, f). The oral spine and other features of the mouthparts described by Wadeh et al. (2008) and Møller and Olesen (2010) suggest that the feeding of *Dipteropeltis* is perhaps very similar to that of *Argulus.* The stylet and mouth tube are probably used to penetrate the host's integument and promote haemorrhaging to take a blood meal, so far only documented for a few species of *Argulus* (Swanepoel and Avenant-Oldewage 1992; Gresty et al. 1993). Based on this similarity, we infer that *Dipteropeltis* also feeds on blood. If the feeding is the same as in *Argulus* that takes blood meals from any part of the body of the fish host, *Dipteropeltis* spp. may also be temporary parasites that only attach when feeding. If this is indeed the case, it may also explain why so few specimens have been collected

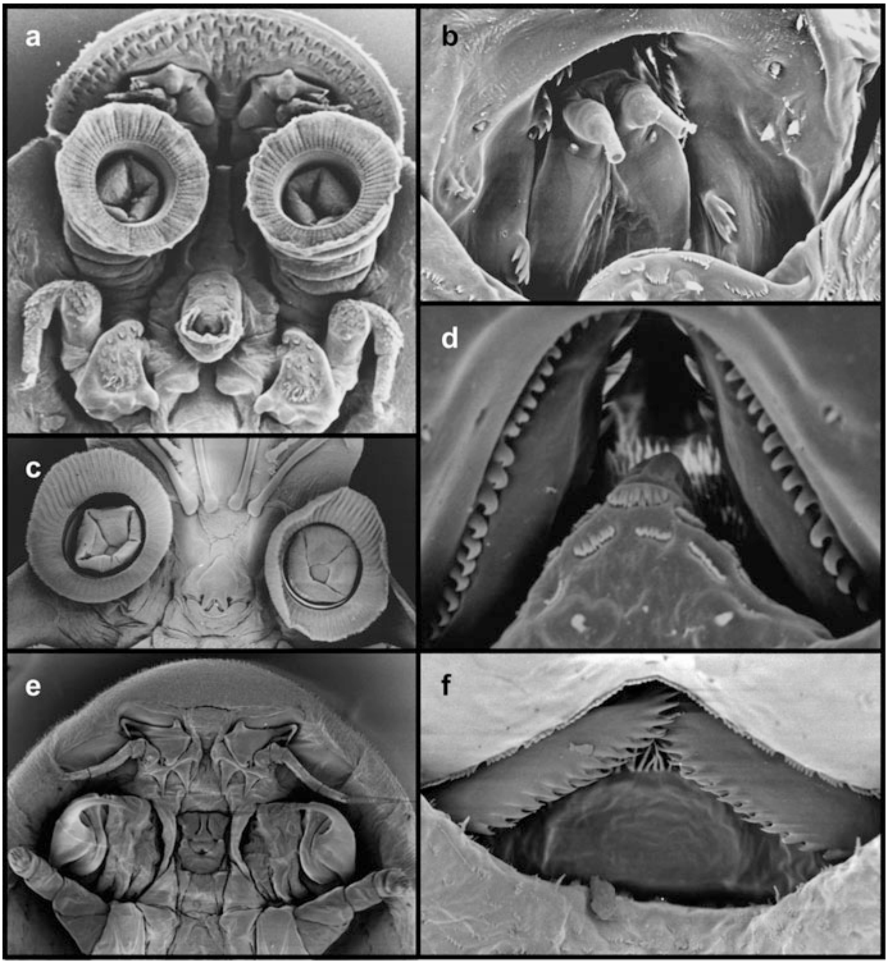

Fig. 4.10 Comparison of the mouthparts of *Argulus izintwala* Van As & Van As, 2001 (**a**, **b**); *Chonopeltis meridionalis* Fryer, 1964 (**c**, **d**); and *Dolops ranarum* (Stuhlmann, 1891) (**e**, **f**)

thus far. *Dipteropeltis hirundo* is so rare that since the original description more than 100 years ago, only 25–30 specimens have been collected (Møller and Olesen 2010), and to date the males still remain unknown. In a study of host-parasite interactions, Carvalho et al. (2003) examined more than 600 fish specimens in the Pantanal wetland in Brazil where they collected only a single specimen of *D. hirundo*. Likewise, Fontana et al. (2012) examined more than 440 specimens of 3 piranha species in the Pantanal and also only found a single female specimen of *D. hirundo*. If these branchiurans do leave the host after feeding, they must be strong swimmers to find a new host as is the case in *Dolops ranarum* and *Argulus* species. The legs of the two species of *Dipteropeltis* appear to be relatively small in the illustrations provided by Neethling et al. (2014), but the unusually large, elongated carapace may be used in swimming (Fig. 4.9).

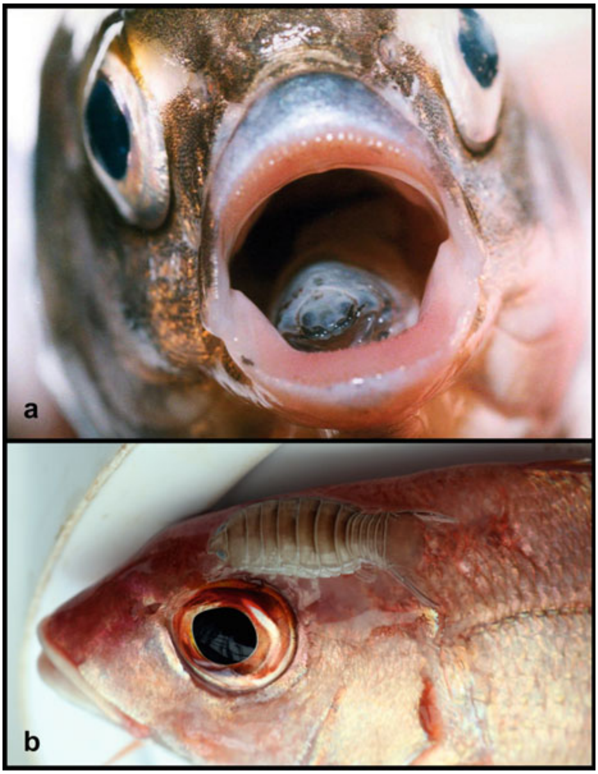

Fig. 4.11 (**a**) The tongue replacement isopod *Ceratothoa famosa* Hadfield, Bruce & Smit, 2014, and (**b**) ectoparasitic *Anilocra* sp. on a sea bream. Image (**b**) © Ruan Gerber

Transient ectoparasites could also settle on other organisms if they do not find their own host. In some cases they may even survive there, behaviour referred to as switching. This phenomenon is still poorly understood or studied. This could be an evolutionary pathway to establish new associations, and in some instances, we could be witnessing the beginning of a new primary relationship (Trilles and Hipeau-Jacquotte 2012). Some Cymothoidae isopods have been reported to settle on a variety of invertebrate hosts (Trilles and Öktener 2004) and are best known as tongue replacers of tidal pool fish, such as the famous *Ceratothoa famosa* Hadfield, Bruce & Smit, 2014 (Fig. 4.11a) (see Hadfield et al. 2014), whilst others are conspicuous ectoparasites of some common sea bream (Fig. 4.11b).

Protelian Parasitic Strategy

Amongst crustacean parasites, there are parasites of which only the larvae are parasitic and the adults free-living and nonfeeding. The example selected to illustrate this type of parasitism are members of the isopod family Gnathiidae.

Sponges as well as ascidians can play an important role in the life cycle of gnathiid isopods. Gnathiids have a protelian parasitic strategy with free-living adults and parasitic juveniles feeding on tissue fluids and blood of teleost and elasmobranch fishes. Of the more than 220 species of gnathiids, the life cycle of only 6 species have, to date, been studied in detail. The first species to be described from southern Africa was *Gnathia africana* Barnard, 1914 by Barnard (1914a, b) who found the resting larvae in different sponges and tunicates, as well as females in tubes of serpulid worms, as did Smit et al. (1999). The adult female was redescribed later by Smit et al. (2002). Smit et al. (2003) described the life cycle of this gnathiid from field observations as well as laboratory work. Although there are some minor differences in the life cycles of other gnathiids, in particular variations in moulting behaviour, the length of the cycle and the harem formation, they all follow more or less the same pattern.

In *G. africana*, the eggs develop into stage 1 zuphea larvae within 21 days at temperatures between 20 and 25 °C. They leave the female through the maternal marsupium and immediately search for a suitable tidal pool fish, which in this case is the klipfish *Clinus superciliosus* (Linnaeus, 1758). Comparing field observations with laboratory studies, it appears that the larvae do not show specificity to any attachment site. The feeding lasts for about 2 h during which the zuphea is transformed to the first praniza stage due to the expansion of the elastic part of the body between pereonites 3 and 5. The engorged praniza detaches from the fish to find shelter in sponges or tunicates. This process will be repeated three times, during which the unfed zuphea will attach to a fish, taking a blood meal lasting from 2 to 10 h, during which the zuphea will be transformed into an engorged praniza. Male larvae moult into adults between 8 and 10 days after final feeding and females after approximately 17 days (see Fig. 4.12a–d). Fertilisation of eggs takes place a day after females moult to maturity, and the release of larvae takes place between 2 and 3 weeks later. The entire cycle is completed in approximately two months.

In the case of *G. africana*, it appears that the cycle continues throughout the year, similar to the cycle of *Elaphognathia cornigera* (Nunomura, 1992) which has four cycles per year as described by Tanaka and Aoki (2000), the 2-year cycle of *Caecognathia calva* (Vanhöffen, 1914) as described by Wägele (1987, 1988) and the 1-year cycle of *Paragnathia formica* (Hesse, 1864) as described by Monod (1926). It is uncertain why the cycles differ so much. Tanaka and Aoki (2000) argue that the multiple cycles of *E. cornigera* could be explained by the warmer temperature of the ocean around Japan. *Gnathia africana* occurs in areas where the water temperature varies from 9 to 26 °C and yet maintains a continuous cycle throughout the year (Smit et al. 2003).

In *Paragnathia formica* and *Caecognathia calva*, the males gather females and larvae in "harems" in the same sponge, but this does not appear to be the case in *G. africana* as no males and females were collected in the same sponge (Smit et al. 2003). Some gnathiid larvae, and sometimes adults, also use (amongst other refugia) sponges and tunicates as asylum hosts. The redescription and life cycle of *G. africana* were based on material collected from sponges of the genera *Hymeniacidon* Bowerbank, 1858, and *Polymastia* Bowerbank, 1862 (see Smit et al. 1999, 2003). Many descriptions are based on material from museum collections (Hadfield and Smit 2008); light traps (Farquharson et al. 2012); suspending fish in cages on the coral reef

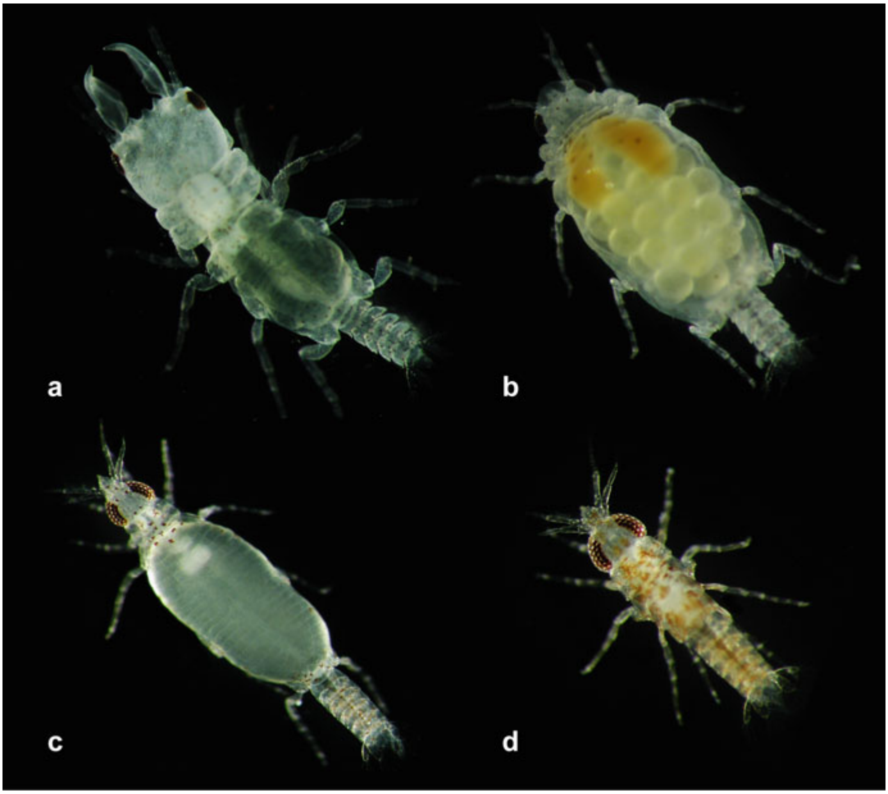

Fig. 4.12 Life stages of the gnathiid isopod *Gnathia falcipenis* Holdich & Harrison, 1980. (**a**) Adult male, (**b**) gravid female, (**c**) praniza, and (**d**) zuphea. Images © Nico Smit

(Farquharson et al. 2012); collecting larvae directly from the fish (Coile and Sikkel 2013); or following the method used by Smit and Basson (2002), to obtain adults by removing mature larvae from fish and maintaining them in containers with sea water until they moulted into adults (Hadfield et al. 2008). The fact is that very few papers on gnathiids even mention what the asylum host is, and we cannot say for sure that there are live animals that act as asylum hosts for the nonfeeding praniza larvae and adults. Tidal pools and coral reefs provide countless hiding places for small organisms, but if available, sponges would provide ideal hiding places in their canals. Sponges further have aposematic agents protecting them and their lodgers against predation.

There are, however, also other crustaceans with these life strategies. The entire copepod order Monstrilloida (Fig. 4.13a–d) are protelian parasites with all the larval stages parasitic, including the first nauplius stage that finds a polychaete or mollusc and burrows into the host tissue. Development of all the copepodite stages, probably five (Boxshall 2005), is completed in the host. The final copepodite leaves the host and moults into the nonfeeding adult that probably has a planktonic dispersal. Species of the Thaumatopsyllidae have a similar life cycle and were originally placed in the order

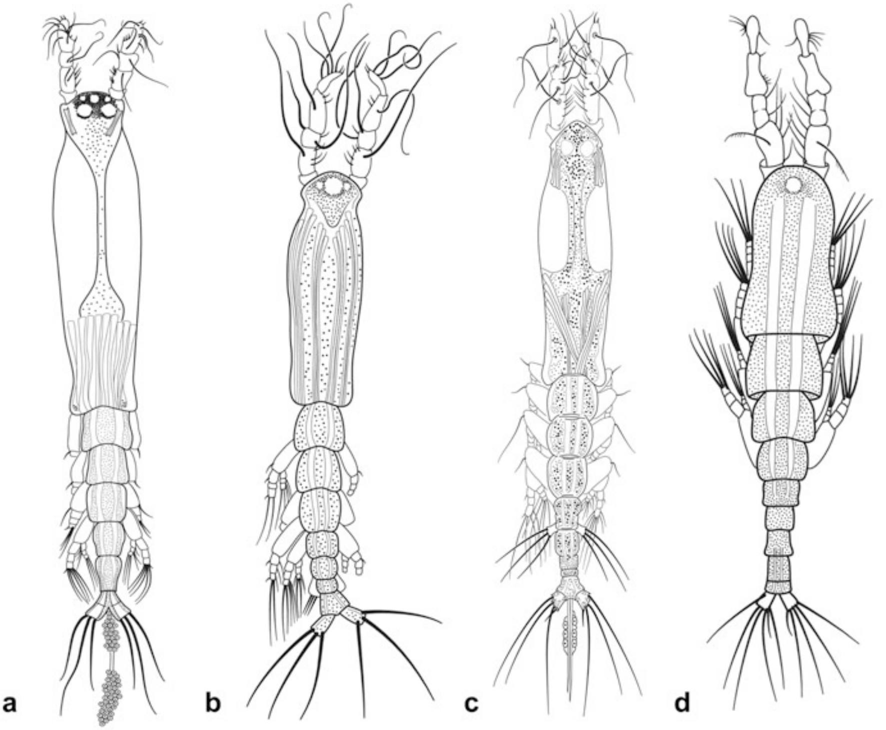

Fig. 4.13 Generalised body plan and different body shapes of Monstrilloida: (**a**) female *Cymbasoma cocoense* Suarez-Morales & Morales-Ramırez, 2009; (**b**) male *Cymbasoma quadridens* Davis, 1947; (**c**) female *Monstrillopsis igniterra* Suárez-Morales, Ramírez & Derisio, 2008; and (**d**) *Monstrilla patagonica* Suárez-Morales, Ramírez & Derisio, 2008. Images redrawn and adapted from Suárez-Morales (2011) with the author's permission

Copepoda, but even in the original description, Sars already expressed some doubt as to the inclusion of this family in the Copepoda. Ho et al. (2003) created a new order to accommodate these crustaceans, Thaumatopsylloida, and described both sexes of this parasite from a brittle star. The World Register of Marine Species (WoRMS) does not accept this order, placing them under the order Cyclopoida. This implies that the subclass Copepoda now only includes nine orders (Boxshall and Halsey 2004). The phylogenetic position of the Monstrilloida was examined by Huys et al. (2007) and found to fall within the clade of the Siphonostomatoida.

4.6.5.2 Mesoparasites

This category is perhaps the most defined group of parasites and occurs in all oceans as well as in all types of freshwater habitats. These crustacean parasites undergo a complete transformation in the parasitic adult stage, with no resemblance to their copepodite stage or the basic cyclopiform body plan. Only one family, the Lernaeidae, contains species that are mesoparasites on freshwater fish. This includes the genus *Lernaea* Linnaeus, 1758 with a worldwide distribution. Usually only the head or anchor is embedded in the fish tissue, which is encapsulated by host tissue (Fig. 4.14a). There are about 55 species worldwide, of which more than half are found in Africa. None, except the introduced species *L. cyprinacea*, is usually pathogenic. This lernaeid, like *Argulus japonicus*, has been distributed throughout the world and can result in mortalities if there are high infestations (Fig. 4.14b). Endemic lernaeids, like *Lernaea hardingi* Fryer, 1956 (Fig. 4.14c), have never been reported to cause mortalities.

Other examples of lernaeid mesoparasites are members of the genus *Afrolernaea* Fryer, 1956 (Fig. 4.15a, b). There are only six species endemic to Africa (Van As 1983; Oldewage 1994). They are slender and about as long as the gill filament of the

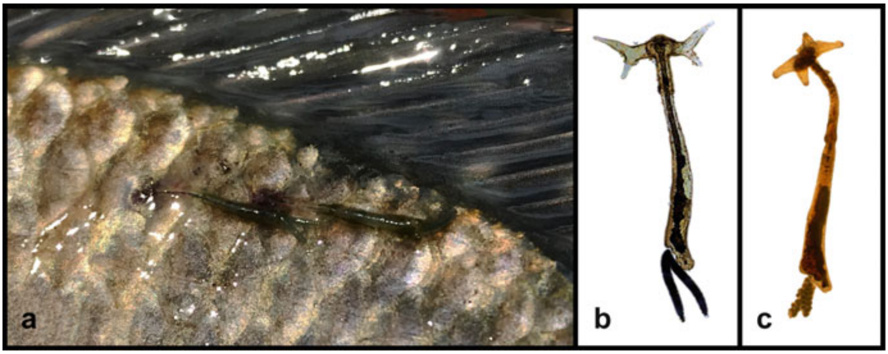

Fig. 4.14 (**a**) Anchor worms attached to the host fish; (**b**) exotic *Lernaea cyprinacea* Linnaeus, 1758; and (**c**) endemic African species *L. hardingi* Fryer, 1956

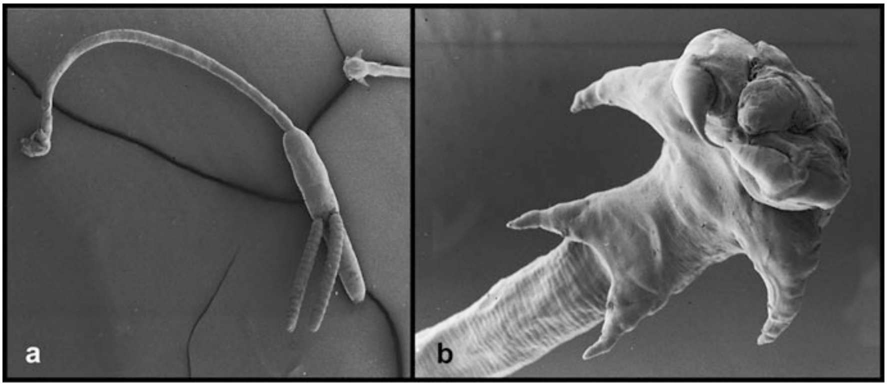

Fig. 4.15 Mesoparasites *Afrolernaea mormyroides* Van As, 1983, (**a**) female, (**b**) the head of this copepod is embedded into the cartilage of the gill arch with the neck, and part of the thorax extending along the gill filament, the abdomen and egg sacs extends beyond the filaments

mormyrid fish that they usually parasitise. Their anchor is embedded in the cartilage of the gill arch and 2 egg strings, consisting of about 30 eggs, and extended beyond the gill filaments. Each of the eggs is in a different stage of development, and the nauplius stages are released one by one. They never occur in large numbers. Other genera of mesoparasites are *Lernaeagiraffa* Zimmermann, 1922 and *Opistholernaea* Yin, 1960 (Paperna 1996). Opistholernaeids are found in the mouth or on the interior of the operculum. They penetrate deeper than any of the other African mesoparasites, often into the back of the eye socket where they can cause blindness. The head is encapsulated in a large cyst. During a visit to a fish farm in Namibia, the authors of this chapter found that almost all of the farmed cichlids were infested with this parasite (Fig. 4.16a–d).

Pennellid copepods comprise about 148 species that are all very large and include the largest copepod in the world, i.e. *Pennella balaenopterae* Koren & Danielssen, 1877, reaching a length of 30 cm. They are mesoparasites of cetaceans (Yamaguti 1963; Kabata 1979; Abaunza et al. 2001), mostly associated with whales (about 20 species) but also found on dolphins and pinniped elephant seals (Vecchione and Aznar 2014). Pennellids were first reported from elephant seals *Mirounga angustirostris* Gill, 1866 by Dailey et al. (2002). These large copepods are also parasites of a variety of pelagic and benthic fish species (Ohtsuka et al. 2007), such as swordfish *Xiphias gladius* Linnaeus, 1758 reported by Wunderlich and Sant'anna (2014). Pennellid copepods have also been found associated with the sunfish (*Mola* Koelreuter, 1766 species) that display an

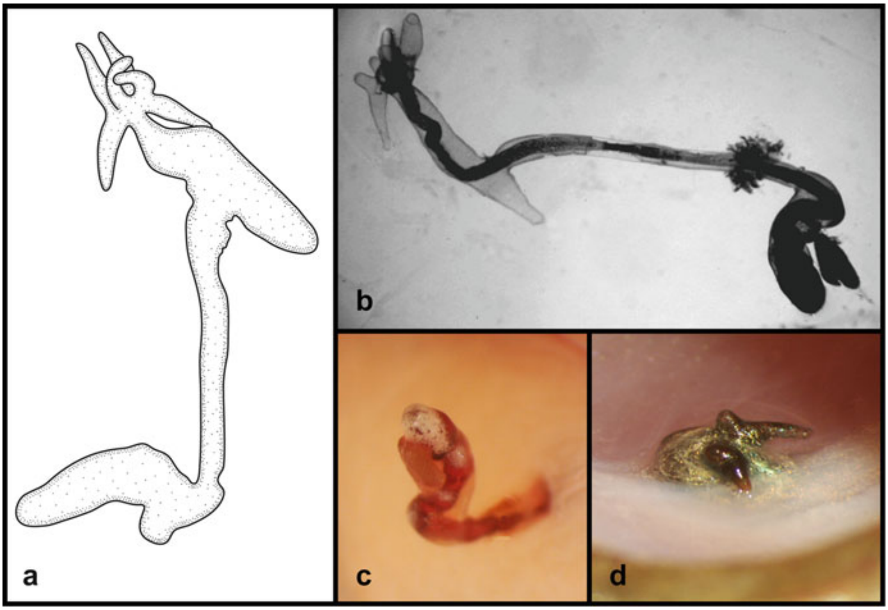

Fig. 4.16 (**a**–**b**) Mesoparasites *Opistolernaea laterobranchialis* (Fryer, 1959) (**c**) penetrate deep into their fish host body with only the abdomen protruding; (**d**) the anchor is encapsulated in this case behind the eye ball in the eye socket. Image (**a**) from Smit and Hadfield (2018)

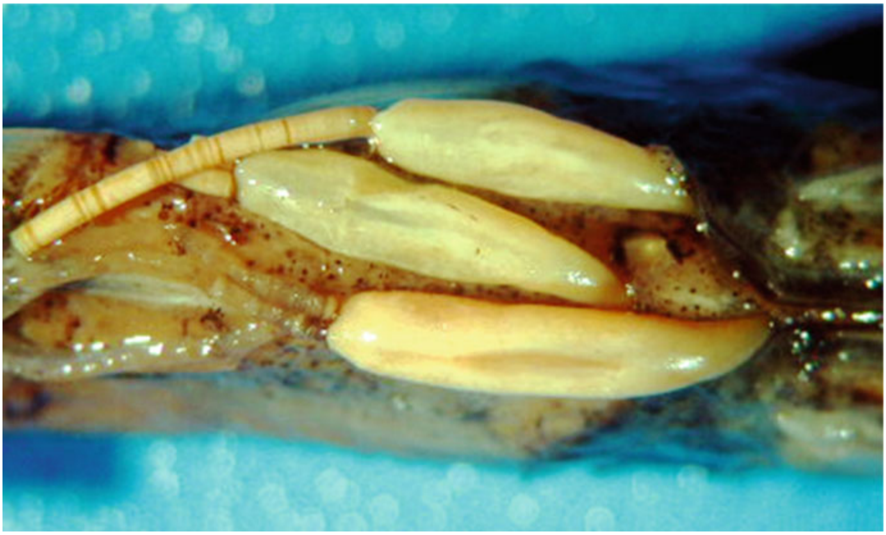

Fig. 4.17 Mesoparasites of the genus *Cardiodectes* Wilson C.B., 1917, penetrate the heart of their lanternfish host

interesting behaviour of “basking”, turning on its side allowing birds to pick the large copepods from their bodies (Abe and Sekiguchi 2012; Abe et al. 2012). These pennellids insert their cephalothorax into the body surface of the host and eventually anchor themselves in the musculature or organs. Some species of the genus *Cardiodectes* Wilson, 1917 burrow into the heart of their hosts, lanternfishes of the family Myctophidae. Most of the body protrudes from the host. Copepodites infest the mantle cavity of the planktonic mollusc *Janthina globosa* Swainson, 1822 where they pass through several copepodite stages to maturity. After fertilisation has taken place, the fertilised female will swim out of the mollusc’s mantle cavity to find a lanternfish host to which it attaches at a spot near the heart. It burrows through the skin and penetrates the heart (Perkins 1983; Grobler et al. 2001) (Fig. 4.17).

4.6.5.3 Endoparasites

Endoparasites are species that mature within the organs or tissues of its host’s body rather than the epidermis. Members of the Copepoda family Ergasilidae are mostly gill parasites of fishes, with a few species parasitic on the skin of the host, e.g. *Neoergasilus japonicus* (Harada, 1930) and *Ergasilus labracis* (Krøyer, 1864). Rosim et al. (2013) describe a new genus and species from the urinary bladder of freshwater fishes from the families Cichlidae and Erythrinidae from Brazil. They named it *Urogasilus brasiliensis* Rosim, Boxshall & Ceccarelli, 2013. There may be more such discoveries from freshwater environments, bearing in mind that only about 11% of the about 4000 fish species of Brazil have been investigated for fish parasites (Eiras et al. 2011).

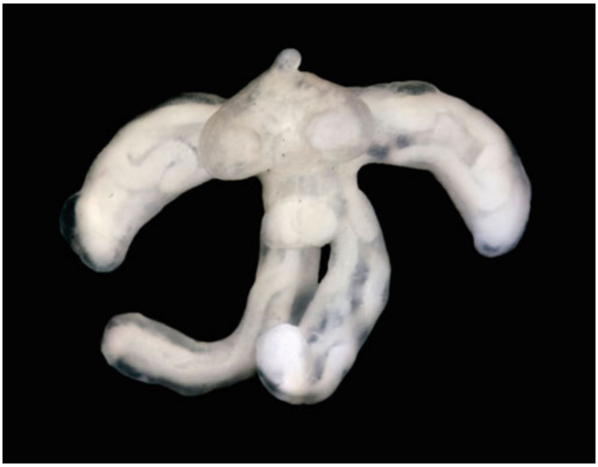

Fig. 4.18 Male *Golfingicola abyssalis* Schwabe & Maiorova, 2015, endoparasitic copepod of peanut worms. Image © Enrico Schwabe

Endoparasitic copepods are common amongst marine invertebrates, but the specific association is often unknown. For example, Schwabe and Maiorova (2014) describe a new genus and species of an endoparasitic copepod from a peanut worm (Sipuncula), *Golfingia muricaudata* (Southern, 1913). Males (Fig. 4.18) and females spend their entire adult lives in the peanut worm.

4.6.5.4 Parasitic Castrators

In a review paper on parasitic castration, Lafferty and Kuris (2009) provide a comprehensive list of all the parasitic genera that have species that are responsible or capable of castrating their host. This broad spectrum of parasites includes representatives of the Protozoa, Cnidaria, Orthonectida (mesozoan parasites of other invertebrates), Platyhelminthes, Nematoda, Mollusca and Strepsiptera (an insect order). The list also includes Crustacea: seven genera of Copepoda, Cirripedia (genera of the Rhizocephala and Ascothoracica), some Brachyura crab genera, and two isopod families. Of these, at least a few species, but in some cases all species, of those taxa are parasitic castrators. Copepod-induced castration has occurred in some marine fishes, polychaetes, nudibranchs and peanut worms. Cirripede castration has been found in deepwater sharks, decapod crabs and echinoderms. Isopod castration has been reported in other crustaceans and in fishes by some cymothoids. *Pinnotheres* Bosc, 1802 (pea crabs), cause castration in mussels.

Crustacean endoparasites in marine crabs are diverse. Many species of crabs are infected by sacculinids (parasitic barnacles). Cirripedia parasites have developed a specialised cypris larva enclosed within a bivalve shell that resembles ostracods. The female larva will attach to the crabs and penetrate the gonads. Inside the gonads it exhibits neoplastic growth. In the process, the gonads are destroyed. The feeding behaviour of the infected crab changes; it loses the ability to moult and protect the parasite as if it was its own eggs (Elumalai et al. 2014). Castration is not necessarily achieved only by internal parasites. It can also be the result of ectoparasites that consume such a large part of the host's energy that this results in reduced fecundity.

Fecundity reduction or suspension does not necessarily result in permanent castration. If hosts can outlive an infection or infestation, they might temporarily divert reproductive energy into defence to combat the infection more effectively. Even if the infection is permanent, the host can respond to only partially reduce or temporarily suspending the development of the gonads (Lafferty and Kuris 2009). Pea crabs of the genus *Calyptraeotheres* (Glassell, 1933), inhabiting the brood pouch of limpets of the genus *Crepidula* Lamarck, 1799, prevent host spawning. When these crabs are removed experimentally, the limpets resume normal spawning activities (Ocampo et al. 2013).

4.6.5.5 Parasitoidism

Combes (1995) includes the concept of duration of relationship to accommodate parasitoidism to the list of parasite associations. Parasitoidism is common amongst insects, in particular wasps. In this case the adult is free-living, and it deposits its egg or eggs on or in a larval stage of other insects. When these eggs hatch, they will consume and kill their host and from there live a free-living life. The closest marine examples which could in some way qualify to more or less fit into this category are members of the copepod family Nicothoidae, where the body shape has undergone adaptation to a life strategy mimicking embryos, resembling size and the globular body form of the eggs of their host (Boxshall and Lincoln 1983). Other members of this family are associated with a variety of crustaceans, including Decapoda, Amphipoda and Ostracoda, and species of the superorder Peracarida including amphipods, isopods, mysids, cumacean and tanaids hosts. Some parasitic amphipods (Hyperiidea) damage and kill gelatinous zooplankton (see Sect. 5.10.3 on Jelly Parasitoids).

The rhizocephalan barnacles have a highly unusual lifestyle and would not be recognised as crustaceans based on the morphology of the adults. They are parasites of brachyuran and anomuran crabs with a few species parasitising shrimps and even other barnacles. The first larval stage is, as in most crustaceans, a nauplius larva (Martin et al. 2014), which in this case metamorphoses into a cypris larva that settles on the crab host, penetrates it and metamorphoses into a complex system of rootlets (internae), eventually extending through the whole body of its host. It subsequently extends externally to form the reproductive structure (the externa) where eggs would normally be carried by the crab. At this point, a dwarf free-swimming male will penetrate the externae of the host and fertilise the parasite. The crab does not moult and will remain infected until its death.

4.6.5.6 Sponge Hotels

"Sponges are challenging subjects for ecological interaction sleuths", so commences the introduction of a review paper on ecological interactions of sponges and their symbionts (Wulff 2006). These ancient organisms are preadapted to accommodate symbionts, a fact already realised early in the twentieth century when Pearse (1934) referred to sponges as “living hotels”.

The Porifera have been around a long time, with fossils predating the Cambrian Explosion by approximately 40 to 50 million years BP (before present) (Li et al. 1998). The Arthropoda have been megadiverse from the early Cambrian, about 520 million years ago (Legg et al. 2012). With such a long evolutionary history, it is understandable that many different associations between sponges and crustaceans, other marine invertebrates and even bony fish and elasmobranchs could have evolved (Hooper and Van Soest 2002).

Sponges occur in all oceans, are abundant in tropical waters (Wulff 2006), as well as in the Antarctic shelf benthic communities, and are also found in deep-sea beds (McClintock et al. 2005). On coral reefs, they sometimes exceed corals in species richness as well as biomass (Hultgren et al. 2014). Sponges perform important ecological services to reefs and intertidal rocky shores. They are filter feeders and in the process perform nutrient recycling, primary production and bioerosion. Due to the nature of these encrusting pliable colonial organisms and goblet shapes of solitary species and the fact that they are infused with canals, they provide an ideal habitat for a variety of organisms, predominately crustaceans, to colonise (Rützler 1976).

Members of the order Spongillina occur in almost all conceivable freshwater habitats in all the biogeographic areas of the world, except the Antarctic. Freshwater sponges, as their marine cousins, also have symbiotic associations and similar to marine sponges are selective refuge microhabitats. These symbionts range from protozoans to bacteria and algae. Other freshwater invertebrate taxa recorded in sponges are hydrozoans, turbellarians, nematodes, oligochaetes, leeches, bivalves, gastropods, amphipods, copepods, ostracods, hydracarinids, bryozoans, and several families of insects (Pronzato and Manconi 2002; Manconi and Pronzato 2008).

Sponges, through their symbiotic bacteria, produce highly diversified, bioactive compounds that serve as deterrents against predation by fishes and invertebrates or rendering them unpalatable for amphipod omnivorous consumers (Pallela and Kim 2011). The pigmentation that is responsible for the brilliant colours in sponges also serves as an aposematic agent to repel predators (McClintock et al. 2005). Despite these defences, many organisms, mostly crustaceans, have established symbiotic associations with sponges, spanning the entire gamut from mutualism to parasitism (Wulff 2006).

Some of these crustaceans, whilst being sheltered inside sponges, also consume sponge tissue. Rützler (1976) summarised earlier accounts and reported on finding representative symbionts of 11 animal phyla and up to 1500 individuals per kg of sponge, in 6 species of Tunisian sponges of the order Dictyoceratida in Southeastern Brazil. More than three decades later, Thiel (1999), Poore et al. (2000), Mariani and Uriz (2001), McClintock et al. (2005), Wulff (2006) and Thomas and Klebba (2007) presented findings of a large diversity and high abundance of crustacean symbionts, of which some also parasitise the sponge hosts.

In his review, Wulff (2006) refers to amphipods, copepods, isopods and different other invertebrates which find shelter in sponges. He is also of the opinion that the variety of associations between sponges and invertebrates "synergistically improves life for both partners". Wulff (2006) concludes that sponges are preadapted to accommodate guests due to their clonal nature. Sponges consist mainly of a series of identical cells as well as some specialised cells performing different functions. This may increase the chances of an intimate association developing because of the relatively low dependence of each portion of an organism on the integrity and functioning of the other portions. Once a liaison between guests and a sponge has been consummated, the clonality of the host may be conducive for the association becoming permanent. When this has occurred, the association could become mutualistic (Wulff 1985, 2006). Of all extant animals, sponges are by far the most clonal. They can accommodate any guest of any shape and behavioural or reproductive strategy without disruption of their "mortal integrity" (Wulff 2006). General textbooks always point out that the Porifera are the most primitive of multicellular organisms, lack organs but have well-developed connective tissue in which cells perform a variety of functions (see Barnes et al. 1968, with many reprints thereafter). The same textbooks will also state that sponges are very old and are almost unchanged in anatomy from Precambrian times. If we consider sponges together with their crustacean and other symbionts, our assertion of modern sponges as simple organisms should be modified to sponges as superorganisms, which they achieved by evolving ways of collaborating with other organisms that could provide biological services whilst retaining the many advantages of not being complex organisms (Wulff 2006).

In the next section, eusocial behaviour will be discussed where sponge hotels become exclusive mansions for single species of tenants.

4.6.6 Eusociality

Free-ranging animals of the same species, including adults and immature individuals of different ages living together in groups, are common phenomenon in terrestrial and aquatic environments. Equally common in aquatic environments is the occurrence of colonial species that are usually sessile with some notable exceptions, such as free-swimming freshwater colonial rotifers (Nogrady et al. 1993). In most cases, sessile animals have free-swimming larvae (Ruppert and Barnes 1994). Social behaviour in terrestrial ecosystems is well known amongst arthropod groups and ranges from the simplest form of gregarious behaviour and extended brood care by individuals of the same generation (common amongst scorpions, spiders, mites, different families of beetles) to very complex eusocial behaviour in bees, ants and termites. The term eusociality was first coined by Batra (1966) and Michener (1969) and applies to species that live in colonies, which include overlapping generations with only one or a few females reproducing. The remaining members of the colony are mostly sterile and may be organised in casts that in some way contribute to rearing offspring. Eusocial species also live in a nest that either they construct themselves or they colonise a suitable nest or live host.

The existence of eusociality is widespread, including a range of different species, and in all cases, sterile casts are present, either as workers or soldiers, or in some cases both. These include all hymenopterans of the family Formicidae, about 12,000 species of ants, as well as a variety of bees and wasps (Hölldobler and Wilson 2009) and all the members of the insect order Isoptera, about 2600 termite species (Thorne 1997).

Spanier et al. (1993) discussed the possible reasons why there are no eusocial species amongst marine crustaceans; they even speculated that amphipods could be good candidates for this life strategy. Three years later, Duffy (1996), in a letter to *Nature*, announced the discovery of eusociality in the coral reef snapping shrimp *Synalpheus regalis* Duffy, 1996. These sponge-dwelling shrimps live in colonies of more than 300 individuals of mixed generations, with only a single female "queen" reproducing. He also observed that fully grown large individuals do not reproduce but defend the host sponges *Neopetrosia subtriangularis* (Duchassaing, 1850) and *Hyattella intestinalis* (Lamarck, 1814) against intruders. The genus *Synalpheus* Spence Bate, 1888 (Decapoda: Alpheidae) comprises more than 163 species and is a dominant component of cryptic coral reef communities worldwide. All the species of this genus are associated with specific sponges, where they spend their entire life in the canals of sponges, feeding on particles of organic matter or even mucoid secretions of the sponge. This technically then categorises them as parasites. The sponge generates currents flowing through the canals for its own feeding (Duffy 2002). The type of association with sponges varies with at least five completely eusocial species, namely, *Synalpheus regalis* Duffy, 1996; *S. rathbunae* Coutière, 1909; *S. brooksi* Coutièr, 1909 (see Fig. 4.19); *S. chacei* Duffy, 1998; and *S. filidigitus* Armstrong, 1948.

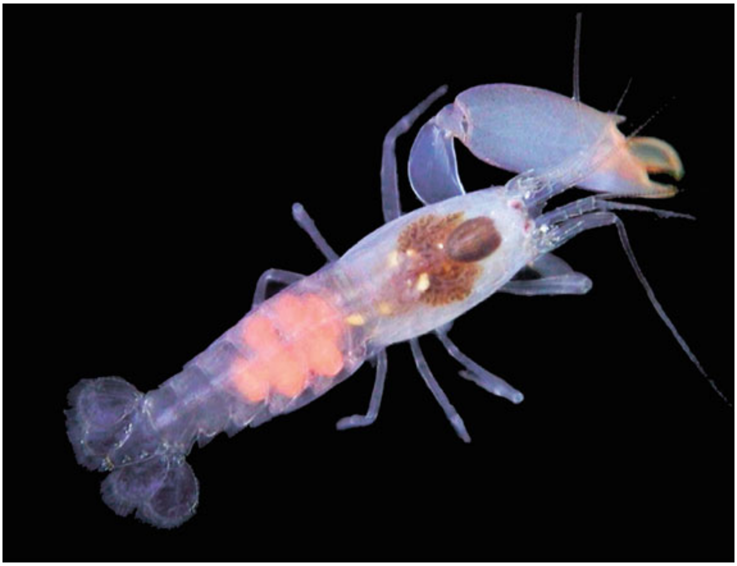

Fig. 4.19 Snapping shrimp, *Synalpheus brooksi* Coutière, 1909, live in large colonies with several reproductive females. Image © J Emmett Duffy, Virginia Institute of Marine Science

4.7 Global Distribution of the Branchiura

A fitting conclusion to a chapter on adaptations and types of crustacean symbiotic associations will be the discussion of some interesting observations on the crustacean parasites of the world, as well as emerging patterns and predictions as to what is still out there to be discovered. Present knowledge of the crustacean subclass Branchiura provides such an opportunity.

Eleven *Dolops* species are found in South America, ten of which have been recorded from freshwater fishes in Brazil. The 11th species, *Dolops reperta* (Bouvier, 1899), was described from specimens collected from an erythrinid species, *Macrodon* Schinz, 1822, in French Guiana (Gill 1903). *Dolops tasmanianus* Fryer, 1969 was found in Tasmania by Fryer (1969). A single species, i.e. *D. ranarum* occurs in Africa with a pan-African distribution south of the Sahara.

Not much is known about the South American *Dolops* species; in fact, not much is known about the fish parasites of South America in general. Eiras et al. (2011) provided a summary of the fish parasites of Brazil in English following the publication of their book on the diversity of Brazilian freshwater fish parasites written in Portuguese the previous year (Eiras et al. 2010). There are more than 4045 freshwater fish species in Brazil (Froese and Pauly 2018), one of the largest countries in the world that includes the largest river in the world, the Amazon River, as well as 6 other major rivers between 1500 and more than 3000 km long. This represents 31% of the world's fresh- and brackish water fish species as well as equals the total number of species found in the entire South American continent (Levêque et al. 2008). According to Eiras et al. (2010, 2011), the host list for the total number of 1034 nominal parasite species was collected from 451 fish species, representing only 11.1% of their total freshwater ichthyofauna. The crustacean fish parasite fauna of Brazil also includes 14 *Argulus* species from freshwater fishes and a single unidentified species from marine fish.

Avenant et al. (1989b) redescribed the African *D. ranarum* based on material collected in the Limpopo River System and Phongolo River floodplains in South Africa. This species of *Dolops* has been better studied than any of the other *Dolops* species: its distribution in South Africa, seasonality, redescription, larval development, reproductive system (Avenant and Van As 1985, 1986, 1990a, b), damage to host (Avenant-Oldewage 1994), molecular phylogeny (Møller et al. 2008) and the effect of starvation on digestive cells (Tam and Avenant-Oldewage 2009). This branchiuran has a wide host range in Africa and is found in all the major river drainage basins except the Orange-Vaal River basin and is also absent from the coastal rivers of the southern, Eastern and Western Cape. *Dolops ranarum* occurs in the Phongolo River system on the eastern coast of KwaZulu-Natal as well as in Lake Sibaya, which is known for its great fluctuation in salinity (Bruton 1979). The absence of *D. ranarum* from the southern tip of Africa, as well as South America, is probably related to its intolerance of colder conditions rather than availability of preferred host fish. It appears to indiscriminately parasitise any available hosts (see Fryer 1968; Avenant and Van As 1985; Van As and Van As 2015). In Lake Kariba, it was found associated with five species of the family Cichlidae, two species of the African endemic family Mormyridae and a single species from the families Clariidae and Mochokidae (see Douëllou and Erlwanger 1994). In the Okavango River and Delta in Botswana, *D. ranarum* was found on 12 of the 71 species of fish occurring in that part of the Okavango system. Here the main hosts for *D. ranarum* were the catfish *Clarias gariepinus* and the large cichlid species of the genera *Oreochromis* Günther 1889 and *Serranochromis* Regan, 1920. *Clarias gariepinus* is naturally distributed throughout sub-Saharan Africa, except in the southern Cape (although it has been introduced via aquaculture), whilst the assemblage of large cichlids differs in the different African river drainage basins (Van As and Van As 2015).

Dolops tasmanianus was described based on a single adult female and a few immature male specimens. The host was an unidentified species of the genus *Galaxias* Cuvier, 1816. This host according to Webb (2008) is probably *Galaxias brevipinnis* (Günter, 1866). Fryer (1968) considered two options to explain the distribution of the genus *Dolops*. One was that it could have distributed with fish hosts over the oceans. He also considered distribution through continental drift, a theory that at that time was still poorly understood.

The family Galaxiidae comprises 8 genera and 56 species (Burridge et al. 2012), of which 13 species of the genus *Galaxias* occur in Australia, 3 species in the southern part of South America and a single species in the most southern part of Africa (Skelton 2001). *Dolops* species in South America and *D. ranarum* in Africa are not found in the southern parts of the continents, thus excluding the galaxiids as possible hosts for *Dolops* there at this point in time. The disjunct distribution of the fish genus *Galaxias*, as well as that of the *Dolops* species, raises interesting questions about the age and distribution of these genera. Both the fish genus *Galaxias* and the parasite genus *Dolops* must have evolved from some ancestor before the final breakup of Gondwanaland about 25 million years ago (Torsvik and Cocks 2013). Alternatively, they must have been distributed there by some marine fish host. Considering the oceanic distribution first, galaxiids are known to be hardy fish inhabiting freshwater, brackish as well as marine habitats. The largest diversity occurs in Australia and New Zealand (Skelton 2001). Based on phylogenetic analysis of morphological and molecular evidence, it has also been found that their distribution via marine dispersal in a few cases preceded Gondwanan vicariance and that both methods of dispersal could have contributed to their distribution (Burridge et al. 2012). The fact that no *Dolops* has been found in the southern tip of Africa as well as South America, well away from the distribution of galaxiid species, makes an oceanic distribution unlikely.

4.7.1 Radiation of the Branchiura

So why did *Dolops* radiate in South America and not in Africa? Another intriguing question is why is there only a single species of *Dolops* in the Australasian and Afrotropical geographical regions, respectively, whilst at least 11 species are found in the Neotropical zoogeographical regions. So far, only 11% of the fish species of Brazil have been investigated for fish parasites. Radiation of the South American *Dolops* species must have occurred during the time when South America was isolated from all other landmasses except Antarctica, which only finally separated about 25 million years ago (Torsvik and Cocks 2013). The question is why did this not happen in Africa or in Australasia? The answer probably relates to the diversity of potential hosts available and the diversity of habitats. Brazil, with a surface area of 8.5 million km^2, has as many fish species as the rest of South America, more than 4000 (Eiras et al. 2011; Levêque et al. 2008; Froese and Pauly 2018). The whole of Brazil, and large parts of South America, are tropical. The total area of Africa is about 30.4 million km^2, i.e. more than 20% of the land surface area with less than 3000 freshwater species and only about 20% of its surface tropical, mostly the Congo basin with about 700 fish species (Froese and Pauly 2018). The Australasian zoogeographical region comprises about 260 species of freshwater fish (Levêque et al. 2008), but *Dolops* has so far only been reported from Tasmania with only 43 freshwater species presently on this continental island (Froese and Pauly 2018). This implies that conditions in South America provided more diverse hosts for the radiation of *Dolops* species to occur. In the last 25 million years, when all the landmasses of Gondwanaland were finally separated, many global climatic and geological changes occurred that could also have had an effect on the radiation of *Dolops* or even the possible extinction of *Dolops* species in Africa.

Another part of this puzzle is the branchiuran genus *Chonopeltis* that is endemic to Africa, with 12 known species. These species are much more host specific than the other branchiurans. They are incapable of swimming and only move about by sliding their relatively large sucker discs over the surface of the host fish. In *C. liversedgei*, the maxilla (Fig. 4.20a) is modified, resembling a tree-pruning cutter, and the third leg (Fig. 4.20b) is adapted, resembling a scimitar studded with strong sharp spines. The females of *C. liversedgei* have been observed to attack intruders and inflict

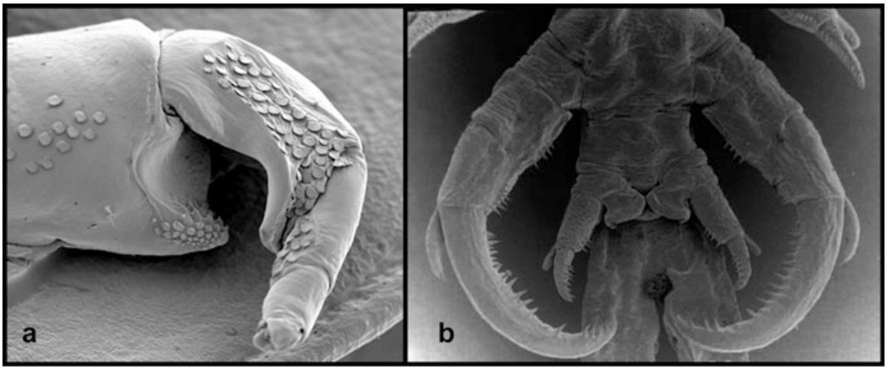

Fig. 4.20 (**a**) Maxillae of *Chonopeltis liversedgei* Van As & Van As, 1999 adapted as pincer and (**b**) third leg, specialised as scimitars

serious damage to other females (Van As and Van As 1999, 2015). Even the smallest species *Chonopeltis minutus* Fryer, 1977, has a robust prominent pincer. These adaptations and behaviourisms are unique amongst branchiurans. So far, there are no reports of the same fish infested with more than one species of branchiurans in Africa. It is not impossible that the occurrence of different *Chonopeltis* species occurring in the same rivers as *D. ranarum* could have had an influence on the radiation of the genus *Dolops* in Africa. Furthermore, it is not unlikely that *Chonopeltis* species could prevent larvae or even adults of other branchiurans from settling on their host. They certainly have the equipment to do so, and attacks between females of *C. liversedgei* have been observed and reported (Van As and Van As 2015).

It was initially proposed that each river system has only a single species of *Chonopeltis*, which is replaced by another species in the river system to the north and south (Fryer 1968). However, with more intensive surveying during the last 20 years in Southern Africa, more than one species has been recorded from the Zambezi, Okavango and Limpopo systems (Van As and Van As 2001, 2015; Piasecki and Avenant-Oldewage 2008; Van As et al. 2017). Species of *Argulus* and *Dolops* leave their hosts to deposit eggs on solid substrata (Shafir and Van As 1986). It was generally accepted that this was also the case in *Chonopeltis* as it was reported by Fryer (1961) that *C. brevis* Fryer, 1961 undergoes a host change between larvae to adults. Van Niekerk and Kok (1989) also reported this for *C. australis* Boxshall, 1976. Neethling and Avenant-Oldewage (2015) described how spermatophore transfer of *C. australis* during mating takes place on the fish host and that eggs are deposited on the glass of the aquarium whilst the female remains attached to the host. This implies that at least *C. australis* never leaves the host as adults. The authors of this chapter have so far collected and studied live specimens of *Chonopeltis australis*; *C. inermis* Thiele, 1900; *C. fryeri* Van As, 1986; *C. lisikili* Van As & Van As, 1996; and *C. liversedgei* and observed that none of them can swim when placed in a dish with water. The specimens drop to the bottom of the container, attach to the glass surface and move by sliding the two sucker discs forward, one at a time. It is therefore probably safe to infer that other *Chonopeltis* species also display similar egg-laying behaviour.

From a dispersal point of view, the distribution of species of the genus *Argulus* is far less intriguing than the other genera. About a third of the 127 *Argulus* species are found in marine and estuarine environments, and they are distributed throughout all continents, except Antarctica. At least one species, *A. japonicus*, originally described from Tokyo, Japan, has also been distributed to all continents, again except Antarctica, mostly by humans moving aquaculture species but also through the lucrative ornamental fish industry (Yamauchi and Shimizu 2013; Smit et al. 2017). Indigenous branchiurans are rare, and collecting them takes considerable effort; usually finding and describing a new species require repeated collections over extended periods (Van As and Van As 2015). As already shown above, the impact of cleaner fish on the abundance of these branchiurans cannot be excluded.

4.8 Glossary of Select Central Terms

Commensalism	Living together of two or more organisms in a bilateral relationship that is beneficial to the commensal but harmless for the other symbiont.
Directly transmitted parasites	Infect only one host individual in their lifetime, ranging from little to large pathology.
Ectoparasite	Those parasites that are found on the skin, gills and various orifices on the fish or invertebrate host.
Endoparasite	Those parasites that are found within the organs or tissues of its host's body with an escape route to the external environment.
Epibiosis	Non-symbiotic facultative, interspecific association where one organism settles on another.
Eusociality	Multigenerational family groups within a colony of adults where the vast majority exhibit cooperative brood care (caring for offspring from other individuals), often with a division of labour into reproductive and nonreproductive groups.
Inquilinism	The condition where one organism lives within another using the host (before or after death) as a place of refuge.
Mesoparasite	Parasites that live partially embedded in its host.
Micropredator	Feeds on multiple larger host individuals per generation; depending on their host specificity, these hosts may belong to one or many species.
Mutualism	A bilateral symbiotic relationship where both organisms benefit.
Parasite	The symbiotic relationship where one organism benefits by deriving nutrients at the other's expense.
Parasitic castrators	Block host reproduction and use the host's reproductive investments for their own reproduction.
Parasitoid	Grow inside a single host and kill that host as a normal and necessary part of their development.
Symbiosis	The biological interaction between different organisms living in close physical association, where at least one organism benefits.

Trophically transmitted parasite	Infect two or more host species in a given sequence and must be transmitted from an intermediate host to their definitive host, in which they mature, through predation of the former by the latter.
Vector-transmitted parasites	Infect two hosts to complete their life cycle: the first is almost always a vertebrate, and the second is a micropredator that acts as a vector between vertebrate hosts to ensure the passage of new parasite generations to new hosts.

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Chapter 5
Life Cycle and Life History Strategies of Parasitic Crustacea

Ernest H. Williams Jr and Lucy Bunkley-Williams

Abstract Different parasitic life strategies are described including four new life cycles: *complex rebrooding*, *micro-male*, *mesoparasite* and *prey-predator transfer*. Four new life cycle behaviours are named: *nursery hiding*, *mid-moult stage*, *positive precursor* (intraspecific antagonism) and *negative precursor* (ambush strategy). Further strategies discussed are *opossum attack*, *double parasitism* (doubling of the normal reproductive set), *duplex arrangement* (separated male-female pairs), *simple rebrooding*, and describing how *displaced parasites* and *superinfections* may partly elucidate life cycles. *Proportional stunting* masks life history effects of parasitism; cuckoo copepods are *true parasites* and not just associates; burrowing barnacles (acrothoracicans) are not parasites. Further findings based on life cycle information: branchiurans and pentastomes are possibly not related; firefly seed shrimp are not parasites; copepod pre-adult life cycle stages are common in the western pacific but rare in Caribbean; harpacticoids on vertebrates are not parasites; cuckoo copepods are *true parasites*; explained the importance of pennellid intermediate hosts. Crustacean parasite life cycles are largely unknown (1% of species). Most crustacean life cycles represent minor modifications from the ancestral free-living mode. Crustacean parasites have less complex and less modified life cycles than other major parasite groups. This limits their exploitation of, and effectiveness, in parasitism. However, these life cycles will be an advantage in Global Change. Most metazoan parasites will be eliminated while crustaceans (and nematodes) will inherit the new world of parasites.

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5.1 Introduction

Life cycles and life histories are arguably the most significant functional traits of all organisms (e.g. Stearns 1992; Roff 1993; McGill et al. 2006), and understanding those life cycles and life histories is essential to understanding the autecology and evolution of each organism, as well as its impact on community and ecosystem processes (e.g. Heppell et al. 2000; McGill et al. 2006).

Parasitism is the most common consumer strategy, and parasites are estimated to account for approximately half of all biodiversity (reviewed by Hatcher and Dunn 2011). Carlson et al. (2017 and references) considered that conservation of parasites is essential to maintain the diversity in major ecosystems, particularly during global climate change. Because parasites are typically small and cryptic and often infect multiple hosts and/or host species during their life cycle, unravelling the life cycles of even a small percentage of parasite species has proven to be challenging. Indeed, while life cycles and life histories have been extensively investigated for a small number of model species (mostly species that impact the health of humans and/or plants and animals of economic importance to humans), we know virtually nothing about the vast majority of species.

The phylum Arthropoda is the most diverse animal phylum, with more than 13,00,000 described species. While insects are the most diverse class within this phylum, the class Crustacea has more than 73,000 described species (Zhang 2013). The Crustacea also includes the greatest diversity of parasitic forms, with over one quarter of the described species. As with parasites generally, details of the life histories for most of these remain unknown.

The goal of this chapter is to provide an overview of the current state of knowledge regarding life cycles of parasitic Crustacea and offer insights and suggestions for future research; our suggestions and analyses are based on the authors' combined 100 years of experience working with this group.

We consider each parasite group separately in phylogenetic order, giving a brief summary of the life cycle(s) with recent discoveries and new details regarding life history strategies and concluding with some new information. We only present a brief overview of the impacts on hosts and on broader ecological aspects as these are reviewed in Chaps. 6 and 10, respectively.

General larval descriptions (unless new) have been kept to a minimum because Martin et al. (2014) presented an extensive description and collection of drawings and photographs of larval forms. The classification given in Chaps. 2 and 3 has been followed. To improve readability and referencing, an annotated glossary has been included with less familiar terms in *italics* in the text. Common names, with accompanying scientific names, are at the end (Sect. 5.17).

5.2 Branchiura: Fish Lice

This is a small group of ~158 (WoRMS 2018) species in four genera that largely ectoparasitise freshwater fishes (Poly 2008), with a few taxa on coastal marine fishes (<5; Møller 2009), and some attach to tadpoles, salamanders, and even alligators (Møller 2009). Most non-fish infections appear to be incidental or accidental, but Poly (2003) described a species from a Mexican salamander. Because of their temporary association with hosts, they may more appropriately be referred to as 'micropredators' (e.g. Lafferty and Kuris 2002); however, we feel that *serial parasites*[1]* is more appropriate. Much of the interest in this group stems from their negative effects on aquaculture and aquarium fishes (Lafferty et al. 2015) and vector fish viral diseases (Møller 2015). The Japanese fish louse, *Argulus japonicus* Thiele, 1900, is probably the most famous and has been spread around the world with cyprinids (Bunkley-Williams and Williams 1994). However, the common fish louse, *Argulus foliaceus* (Linnaeus, 1758), is also widespread, and occurs from fresh to marine waters (Møller 2015). In two cases, these parasites have infected humans. Hargis (1958) found *Argulus laticauda* Smith, 1873, in the eye orbit of a child in Virginia; and an argulid has also been observed in the orbit of a tilapia aquaculturalist in Venezuela (Williams and Bunkley-Williams, personal observation).

Life Cycle

The life cycles of only ~20 branchiuran species have been examined, mostly in *Argulus* Müller, 1785, and a few species of *Dolops* Audouin, 1837. Most males transfer sperm directly to the females using a variety of modified structures on the third and fourth thoracic legs; however, in *Dolops*, sperm are transferred in chitinous spermatophores. Sperm morphology originally linked fish lice with tongue worms (see Sect. 5.3). Molecular evidence also supports their similarities. Only the life cycle of *Argulus* is well known (Poly 2008; Neethling and Avenant-Oldewage 2016), and no life cycles of marine species are known. A mature female *Argulus* leaves its host and lays eggs in rows on a hard, submerged surface (Fig. 5.1). As many as 1200 eggs are laid at any one time and are cemented to the substrate. The eggs hatch 12–80 days later, varying by species and water temperature. Eggs hatch into (1) free-swimming metanauplius-like larvae (7 species of *Argulus*), (2) free-swimming juvenile-like larvae (4 *Argulus*, 2 *Dolops*) or (3) non-swimming larvae (6 *Chonopeltis* Thiele, 1900). The three larval stages (above) moult into second-stage juveniles, which are parasitic and repeatedly change hosts (*serial parasite*). The 8–12 stages before the adult are also parasitic and *host-hopping**. The maxillule undergoes a profound metamorphosis around the fifth stage, changing from a long limb bearing a powerful distal claw, into a short but powerful circular sucker (Martin et al. 2014). This is a remarkable transformation. Møller et al. (2007) described swimming and self-cleaning in the hatching, free-swimming stage and the subsequent juvenile stages of *Argulus foliaceus*.

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[1] An asterisk indicates our new suggested names throughout chapter.

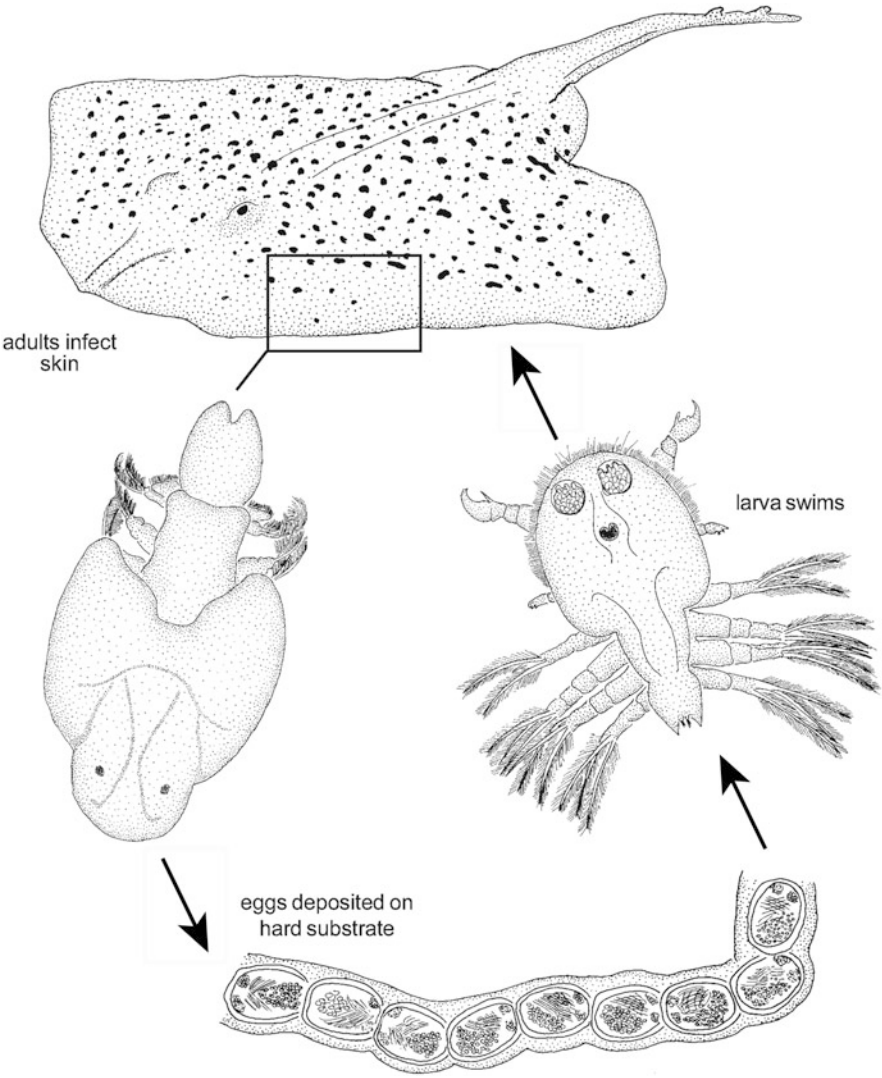

Fig. 5.1 The constructed life cycle of *Argulus megalops* Smith, 1874, an ectoparasite of the little skate, *Leucoraja erinacea* (Mitchill, 1825), based on information in Wilson (1904) and reproduced with permission from Benz and Bullard (2004). Mature adults copulate on or off the host, and gravid females will then swim and find hard inanimate objects (such as stones, walls, equipment, etc.) on which to deposit eggs. Hatching times vary according to temperatures and can take from weeks to months to occur. Once hatched, infective larvae will search for a host, attach to the suitable host, and undergo multiple moults before reaching maturation. Image modified from Benz and Bullard (2004)

Neither larvae, nor juveniles, nor adult *Chonopeltis* can swim and are therefore referred to here as ‘Non-swimming fish lice*’. Adults leave the host, mate, and deposit eggs, and how, or if, they return to a host is unknown. They have seven to eight free-living, developmental stages and are said to have intermediate hosts, but, as in other fish lice, these are really *transfer hosts**. All host infection and reinfection are through host contact with the bottom. Intermediate hosts are small, bottom-dwelling fishes, and the definitive hosts are larger, bottom-dwelling fishes (Grundlingh 1996). How they infect or attach to hosts is still unknown, possibly only floating to a new host (Fryer 1961; Piasecki and Avenant-Oldewage 2008).

Few parasite embryos have ever had mutualistic symbionts, but Banerjee et al. (2016) have found one. A rotifer, *Philodina roseola* Ehrenberg, 1832, feeds off the jelly coat of the egg strips of *Argulus bengalensis* Ramakrishna, 1951. This makes the coating thin enough for larvae to break out. If the rotifer does not feed, the larvae cannot emerge. They suggested this knowledge of the life cycle could afford parasite control. Van As and Van As (2015) found adult and larvae *Chonopeltis lisikili* Van As & Van As, 1996, on the same host specimens and suggested host-change does not occur in *C. lisikili*, as was reported for other *Chonopeltis* spp. These stages, and free-swimming adults, are attracted by bright objects, light, and motion, as Mikheev et al. (2015) demonstrated in aquarium studies. In daylight, the parasite employed *hover-and-wait* tactics with low swimming speed and an inclined position of the body. In the dark, *cruising* tactics were employed, characterised by a much higher swimming speed and a horizontal position of the body. Vision, olfaction and mechanoreception are used in daylight, whereas only the latter two are used at night. Swimming speed was 5–6 times greater at night than in the daylight. Host-induced cues increased mean swimming speed by a factor of 1.5–3. In adults starved for 1–2 days, the swimming speed was 3–4 times greater than those freshly detached from the host. A longer starvation caused a decrease in swimming activity (Mikheev et al. 2015).

Further Life History

Mikheev et al. (2015) found receptive females largely rested on hosts and attracted free-swimming males with pheromones. They also found females deposit eggs in fish spawning or nursery areas, where their offspring will have access to many fish.

Additional Information

Mikheev et al. (2015) suggested fish lice manipulate the behaviour of hosts for their benefit: (1) when one attaches to a fish, the host reaction attracts other lice; (2) injuring a host by attacking it may cause a predator-attack tightening of a school, favouring more parasite attachment. However, these effects seem too inadvertent, reactive, and temporal, to be called parasite-induced host behavioural changes. They do not help the individual parasite causing the reaction, possibly even harming it, similar to a *positive precursor*. They are certainly nothing like the host behaviour changes such as found in parasitic barnacles. Mikheev et al. (2015) also suggested microbial pathogens were changing the behaviour of hosts and fish lice to spread their infection. They found ‘sick’ fish had more fish lice and stated that the parasites vector these diseases (see Chap. 7).

Banerjee's et al. (2016) mutualistic rotifer has obviously co-evolved with *Argulus bengalensis*. We suggest that at one point, the rotifer appears to have been a *hyperparasite* (many in its genus are parasites) or predator harming the egg strip. The parasite gradually thickened the coating on its egg strip, protecting it from the rotifer. Finally, the embryos were sufficiently protected, to turn the rotifer into a mutualist, and the organisms became inexorably linked. Our suggestion is that this is first evidence of a hyperparasite evolving into a mutualist.

While fish lice metamorphosis of suckers is an interesting change from the free-living forms, they show no other major morphological developments towards parasitism. Thus, while unusual, their larvae are strange, but not necessarily modified well for parasitism.

5.3 Pentastomida: Tongue Worms

There are ~130 extant species mostly parasitising the respiratory tracks of terrestrial vertebrates (Christoffersen and De Assis 2013; Siveter et al. 2015). They are of little commercial importance even though they may be found on crocodile and alligator farms, and the eggs of ten species can infect humans with nymphs (Li et al. 2016). Their phylogenetic relationship was once mysterious because they only have reduced parasitic morphologies. Until recently, no fossil forms (~0.5 billion years ago) were known. Molecular work has suggested a relation to fish lice (e.g. Li et al. 2016 and references), although this is still debated.

Williams (1995) suggested that these parasites were important and were once parasites of dinosaurs since the remaining species parasitise many extant close relatives of dinosaurs (e.g. crocodilians and birds). Bunkley-Williams and Williams (1994) found sebekid nymphs in freshwater largemouth bass and peacock bass in Puerto Rico and speculated that spectacled caiman was the final host (Williams and Britton 1995). We now identify these nymphs as *Sebekia oxycephalum* (Diesing, 1836), and they are common in Puerto Rico (Williams and Bunkley-Williams unpublished data). Williams et al. (1996) reported nymphs in coral reef fishes in Okinawa and suggested the final hosts were sea snakes.

Life Cycle

Males fertilize females soon after they mature in the respiratory tract. Males do not live long, and often only females are found in the definitive host. Stored sperm fertilize ova released continuously from the ovaries of mature females. Fertilized eggs mature as they descend the uterus of porocephalids. Gravid females of *Armillifer* Sambon, 1922, and *Linguatula* Frölich, 1789, species may contain millions of eggs. The eggs of cephalobaenids are stored in a saccate uterus until they contain 30–50% fully mature primary larva and are infectious; then egg deposition begins. The vagina is equipped with a sieve-like mechanism only allowing mature eggs to escape. They lay eggs in the respiratory track of vertebrates, which are either coughed or sneezed out by the host or leave the host body through the digestive system. Usually, an insect or vertebrate ingests the eggs. The larva hatches into a nymph, penetrates the intestinal wall, and forms a cyst in the intermediate host's body. The nymph is rounded in form, with 4–6 short legs. The final host is infected when it eats the intermediate host, and the nymph crawls into the respiratory tract from the oesophagus or stomach. It moults several times to become a post-larval juvenile and finally an adult. A few species, mostly in birds, have direct life cycles. *Subtriquetra subtriquetra* (Diesing, 1836), in South American crocodiles, is the only tongue worm known to have a free-swimming larva. It searches for fishes as its intermediate hosts (Winch and Riley 1986).

Further Life History

They occur worldwide but mostly in the tropics and subtropics. Very few reliable taxonomic characters exist, even in adults, and these few characters change in different adult stages (supra-adults).

Additional Information

The long cherished hope of fossil forms revealing clues to relations with other groups has not been realised. Siveter et al. (2015 and references) found these forms as nearly characterless and enigmatic as the extant species.

The few fossil forms known are isolated larvae, which appear to have been free-living. Siveter et al. (2015) found adults ectoparasitic on a marine ostracod. These life cycle forms are completely different from the present-day endoparasites of terrestrial, semiterrestrial, and vertebrates. There has been either a monumental and complete change between the fossil and extant life cycles, or, which is more likely, the fossil forms are not in the same lineage as extant tongue worms. The fossils may be related to extant tongue worms, but do not represent their ancestors. Furthermore, without any interconnecting forms over half a billion years, it is difficult to try to join these fossils in a lineage with the extant tongue worms. More likely, the fossil and extant forms represent parallel evolution.

Chapter 3 does not recognise Siveter et al. (2015) fossil as a tongue worm. If correct, this leaves tongue worm fossil forms without an adult and without a host. These apparently free-swimming and unattached forms do have a modern equivalent in the larvae of *Subtriquetra subtriquetra*. Sanders and Lee (2010) suggested that these larval forms parasitised conodonts (early, eel-like organisms, famous for first teeth in the fossil record). This would agree with this only modern analogue, which parasitises fishes as intermediate hosts. However, they considered the small fossil forms adults, not larvae, with direct life cycles. Large forms with indirect life cycles only developed after the air-breathing tetropods were available ~365 million years ago. While these are interesting life strategy hypotheses, they lack any supporting evidence.

Tongue worm life cycles are like those of any other crustacean parasite. In their life evolution, they have invaded the land and colonised all four classes of terrestrial vertebrates. They are completely endoparasitic, with the exception of a free-living stage in one species. No other crustacean parasite is even similar. Their drastically different life cycles suggest they may not be crustaceans. Many other analyses agree (e.g. Christoffersen and De Assis (2013, 2015), place them in their own phylum), but most place them with the fish lice (Branchiura).

Sebekia oxycephalum is a generalist having little specificity in fish intermediate, and crocodilian and snake definitive, hosts (Silva et al. 2015). Vague reports of nymphs in lizards and reports in snakes probably represent paratenic hosts. It has the greatest range (southeastern USA to southern South America) of any tongue worm and the greatest host diversity.

5.4 Ostracoda: Seed Shrimp

Seed shrimp are a large group of largely free-living, marine species. A few are commensal on invertebrates, and extremely few are apparently parasitic on a shark, a ray, Pacific sea urchins, one polychaete, groundwater isopods, and gammaridean amphipods (Smith 2017). Many host records are based on few observations and specimens, and some relationships are unclear. Their shells in sediments and extensive fossils are very useful indicators of past conditions, climate changes, oil deposits, and crustacean sexual development. They are well known to scuba divers for their painful bites at night, for their bioluminescent glow and for their nocturnal attacks on injured fishes (Stepien and Brusca 1985).

Life Cycle

Mating typically occurs in swarms with large numbers of females swimming to join the males. However, some are partially or wholly *partheno-genetic*. All seed shrimp, except punciids (no shell), brood their eggs between the upper (dorsal) part of the body and the shell. Most ostracods shed eggs directly into the water as plankton or attach them to vegetation or the substratum. In some groups, one or two larval moults occur before the larvae are shed. Eggs hatch into nauplius larvae with a hard, bivalve shell, except punciids that have a single headshield. A nauplius stage is usually followed by 5–8 metanaupliar moults. Kretzler (1984) described the seven instars in the life cycle of *Echinophilus xiphidion* Kretzler, 1984, in Pacific sea urchins. He also found intense wave action inhibited the infection of sea urchins.

Further Life History

Males and females occur together on hosts. Most adults do not moult. Often, only a few specimens of parasitic seed shrimp are reported, although they can be very abundant. Kretzler (1984) found 5000 specimens in 218 host specimens of four species of sea urchins. He reported no damage; therefore, even heavy infections do not obviously affect hosts.

Additional Information

Bennett et al. (1997) found 17 of 28 epaulette sharks examined had *Sheina orri* Harding, 1966, ostracods attached in the gills. Light and scanning electron microscopy showed ostracods were anchored to gill tissues with their mandibular and maxillular claws. They damaged host tissues and were often located in distinct pockets, formed by local distortion of shark respiratory lamellae, strongly suggesting that they had been attached to the gills for considerable time. These details were presented because of some controversy whether *Sheina orri* was parasitic. It has also been found in the bluespotted ribbontail ray, *Skogsbergia squamosa* (Mueller, 1894), and may be a bony fish parasite (Monod 1923), but this was not clear.

Wilson (1913) found 50, 50, and 12 *Photeros parasitica* (Wilson 1913) in the gills and nasal tubes of three smooth hammerheads, one on the gills of a rock hind, and three on a blue runner in Jamaica. Williams and Bunkley-Williams (1996) hypothesised that *P. parasitica* was specific to sharks and rays and only accidental on bony fishes in the Caribbean. Cohen and Morin (2010) reported that *P. parasitica* is a luciferin bioluminescent carrion feeder, not a parasite.

Brian (1931) found *Cypridina* sp. on the gills of dolphinfish (*Coryphaena* Linnaeus, 1758) and called them parasites. However, this form is another luciferin bioluminescent seed shrimp, like *P. parasitica*, and is unlikely to be a parasite (Williams and Bunkley-Williams 2010). It is related to the famous sea firefly. Thus, 'firefly seed shrimp' do not appear to be parasites. Bioluminescent seed shrimp are sometimes reported as gill parasites because they feed on detritus, and the gills of an organism are the first part to deteriorate.

5.5 Copepoda: Copepods

Most of the ~14,000 described copepod species (WoRMS 2018) are free-living, some are commensal of invertebrates, and many parasitise invertebrates and fishes (~6500 described species, ~1700 species in fishes alone). Some parasites are little changed from the free-living form and even capable of free swimming between hosts (*serial parasites*). At the other end of the copepod, parasite spectrums are highly modified forms, which are fully embedded inside their hosts and can only be recognised as copepods by their larval forms.

Life Cycle

The basic life cycle of copepods has two phases (naupliar and copepodid) (Fig. 5.2). The egg usually hatches into a nauplius larva with a small, unsegmented body, and three pairs of functional appendages (antennules, antennae and mandibles). A maximum of six naupliar stages can occur, and all six are found in most free-living copepods and in some parasites. Nauplii may be *planktotrophic* (feed on plankton) or rely on its yolk (*lecithotrophic*). Parasitic nauplii are usually lecithotrophic, have reduced setation on the three limb pairs, and no naupliar feeding process on the coxae of the antenna. In many parasites, the naupliar phase is abbreviated or occasionally lost. The final nauplius stage moults to become the first copepodid with a segmented body, a full adult set of cephalic appendages, and the first and second swimming legs. Free-living copepods have a maximum of five copepodid stages with one body somite added at each moult. In almost all copepod parasites, copepodid I is a free-swimming stage. Only *Parachordeumium aphiurae*

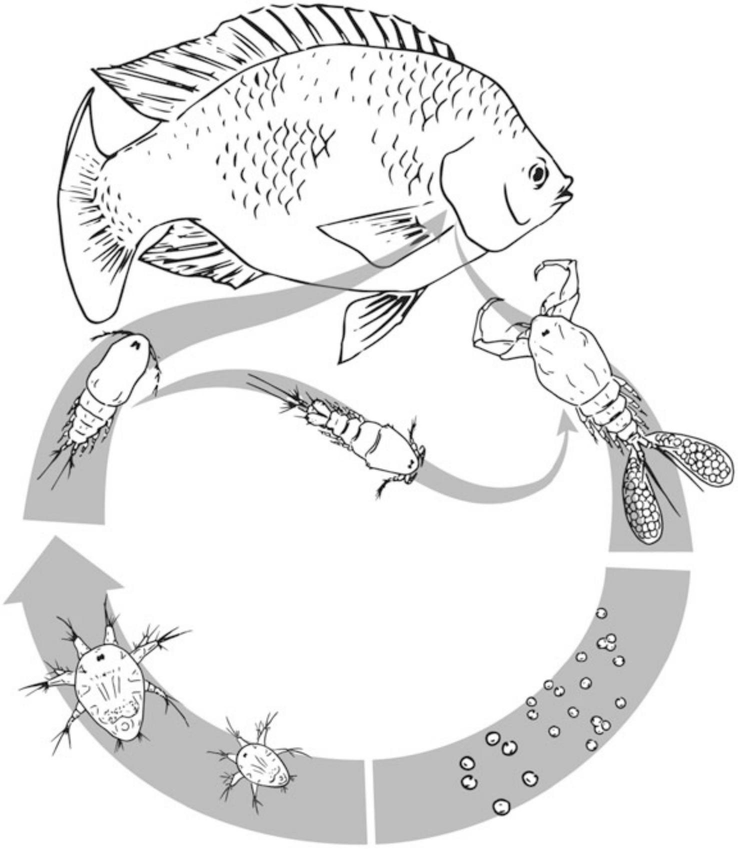

Fig. 5.2 The generalised life cycle of an *Ergasilus* von Nordmann, 1832, species showing the free-living naupliar and copepodid stages as well as the parasitic adult female. Image from Smit and Hadfield (2018)

(Hérouard, 1906) and internal sea cucumber copepods have copepodid II hatching from their eggs (Martin et al. 2014). Copepodid I is in the typical crustacean form with two pairs of biramous swimming legs, each with 1-segmented rami. It begins free-living but is usually the infective stage. The copepodid stages provide a gradual transition from the copepodid body form to adult morphology, however transformed. In the more derived families, successive copepdid stages have increasing modifications in body form and limb structures. The fifth copepodid stage moults into an adult male or female. Following this moult, the female becomes sexually receptive.

Further Life History

Adult males may conduct precopulatory mate guarding and holding pre-adult females until the final moult. Males use an array of chemosensory aesthetics on their antennules to detect pheromones produced by females. Mating takes place soon after the female becomes sexually receptive and consists of mate detection, mate recognition, and mate capture and culminates in copulation. Sperm-containing spermatophore(s) are transferred to the female and usually discharged via copulatory pores, into seminal receptacle(s) within the genital region of the female. Sperm are stored for fertilization, which occurs as egg batches are laid. Females may produce several batches of eggs during her life. Most parasitic copepods extrude their eggs into paired egg sacs or uniseriate egg strings, although some are stored internally.

Copepods have a great diversity of invertebrate and fish hosts but are remarkably limited among other vertebrate groups with a single species on whales and dolphins, none on reptiles or birds, and only a very few, almost accidentally, on amphibians. Their simple life cycles may inhibit them from colonising more diverse vertebrates since their only mammal parasite has their most complicated life cycle. The life strategies of copepods suggest the simpler the host, the easier it is to parasitise.

Additional Information

Williams et al. (1996) reported, based on decades of research, that copepodids, chalimus, and immature adult copepods were very rare on Caribbean coral reef fishes but rather common on Western Pacific coral reef fishes (a 1-year study). One possible explanation for this difference is that Caribbean, small cleaner gobies (*Elacatinus* Jordan, 1904), are much more efficient in locating and removing these small, life cycle stages than are the larger Indo-Pacific cleaner wrasses (*Labroides* Bleeker, 1851). Thus, life strategies of Caribbean and Indo-Pacific parasitic crustaceans may operate under quite different selective pressures.

Brusca (1978) found adult cymothoid isopods of the genus *Nerocila* Leach, 1818, with damaged pleotelsons and uropods and speculated these injuries might represent predation by cleaner fishes. Williams and Williams (unpublished data) have found numerous injuries and missing parts of fish lice, fish-parasitic copepods, fish isopods, and gill worms (Monogenea) on, and in the gills, or mouths of fishes, and have observed copepods on fishes scurrying away from cleaner fishes, even though they were obviously too large to be removed. Cleaners may bite and injure crustacean parasites that are too large for them to remove (*Cleaner nipping**). *Cleaner nipping* is a widespread, important, but hitherto unrecognised, life history peril for ectoparasites. Mahmoud et al. (2017) experimentally induced nipping and removal of fish parasitic isopods by portunid crabs. Cleaner shrimp similarly snip off the legs of small crustacean parasites to remove and eat them (Williams and Bunkley-Williams 1998b, unpublished data).

Copepod parasites of fish life cycles are little removed from those of their free-living ancestors. They only have a few obligate intermediate hosts (pandarids, pennellids) and facultative intermediate hosts (lernaeids). The marine anchor worm (pennellid) intermediate hosts are pelagic squid and fishes, which required little modification for their planktonic larvae. A few adult females become embedded into host tissues but only to the point of *mesoparasitism*.

Many copepod parasites of invertebrates also have direct life cycles, but some have endoparasitic larvae and free-swimming adults, mesoparasitic larvae and ectoparasitic adults, and abbreviated or no larval stages. Some endo- and mesoparasitic forms can be quite modified.

*5.5.1 Cyclopoida: Short-Antenna Copepods**

Most are small and free-living, but rarely planktonic, in marine and freshwaters. Some are commensal with invertebrates and only rarely damage their hosts (Williams and Wolfe-Walters 1990). Many parasitise molluscs, sea anemones, sea squirts, fishes, and a caridean shrimp (Conradi et al. 2012). The most well known is the anchor worm—an economically important fish pest, which was globally spread on goldfish and Asian carp and is now common worldwide. Species of the family Ergasilidae cause the most important problems in aquaculture and are distributed globally (Garcia and Williams 1985; Williams et al. 1994a, b, 1996; Thatcher and Williams 1998; Bunkley-Williams et al. 1999).

Life Cycle

Eggs are usually carried in paired or single sacs attached to first abdominal somite. However, some notodelphyids and *Pectinophilus* Nagasawa, Bresciani, & Lutzen, 1988, store eggs internally. The full life cycle occurs in many copepods parasitising invertebrates and in ergasilid fish parasites. Ergasilids are also unusual in having naupliar stages feeding on unicellular algae. Thaumatopsyllids have a life cycle similar to that of the monstrilloids with parasitic nauplii inhabiting the gut of brittle stars and nonfeeding adults living in the plankton. The copepodid phase in *Thaumatopsyllus paradoxus* Sars, 1913 comprises the full five stages preceding the adult, and the entire phase from final nauplius to adult is completed without further food intake.

Parachordeumium amphiurae (Hérouard, 1906) hatches directly as an infective copepodid II, having passed through the first within the egg. In the tunicate parasite, *Gonophysema* Bresciani & Lützen, 1960, the infective copepodid larva settles on the host and moults into an onychopodid larva, which is reduced to a simple elongate sac-like body provided with grasping antennae used for attachment. The onychopodid penetrates the skin of the tunicate and transforms into an amorphous, lobate adult (Rohde 2005).

The life cycle of anchor worms (lernaeids) has been described as direct with only one host, indirect with an intermediate host, or with a *transfer host*. The confusion lies in the apparent occurrence of all three cycles in the same species of anchor worm. The first copepodid usually attaches and develops through copepodid stages on the gills of a fish host. This may occur on the definitive host specimen, on a different specimen of the same species, or on a different species of fish. In the final copepodid stage, the female usually leaves the gills and attaches on the body of the same fish specimen (direct) or on a different one (indirect). Thus, a real intermediate host can occur, but this is not obligatory. Some of these species may be evolving towards an obligate intermediate host. This would represent a third method of

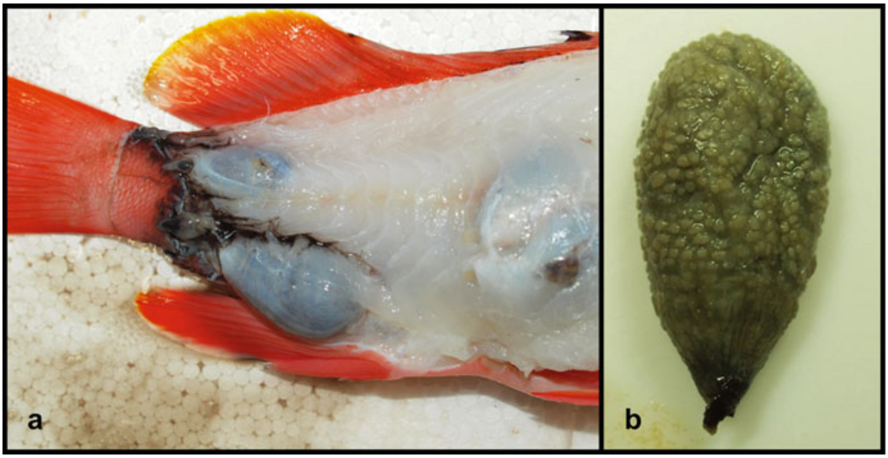

Fig. 5.3 *Sarcotaces* Olsson, 1872, from a blacktip grouper, *Epinephelus fasciatus* (Forsskal, 1775), collected in Okinawa. (**a**) embedded (skin has been removed to expose large, sack-like cysts), (**b**) removed large, sack-like cyst. Nagasawa et al. (2015) found eight cysts with females, males, naupli, and eggs in this host specimen. Images © Kazuya Nagasawa

developing, through an intermediate host, for which we propose the term *parallel incorporation**.

Deep-sea copepods have been found resting and feeding on the mucus of gelatinous plankton (Humes 1985). Gasca et al. (2007) found mating males and females and early to late copepodid stages of *Pseudolubbockia dilatata* Sars, 1909, in the subumbrella cavity of deep-sea hydromedusae. We suggest this copepod is another protelean parasite in the short-antennae copepods.

Further Life History

Recent reports and descriptions of additional copepodids or of pre-adults in short-antenna copepods were probably growth stages, not moult stages (Martin et al. 2014).

Additional Information

The free-living stages in the life cycles of ergasilids and many of the copepod species parasitising invertebrates suggest that they have more recently evolved a parasitic lifestyle.

The most modified female of any of the fish-parasitic copepods are species of *Sarcotaces* Olsson, 1872. Osman et al. (2014) described and pictured the naupli of possibly a new species of *Sarcotaces* apparently host specific to a brownspotted grouper in the Arabian Gulf. Surprisingly, they found no females in six gall cysts, even though nauplii and males were present. Eggs were attached to the inner wall of the galls. Nagasawa et al. (2015) found eight cysts with females, males, nauplii, and eggs in a blacktip grouper (Fig. 5.3a, b) in the Ryukyu Islands.

Some short-antenna copepods occur in the musculature and sinus canals of fishes. Rosim et al. (2013) reported a new genus of ergasilid in the urinary bladder of fishes and considered the process of becoming an endoparasite. The muscle parasites are mesoparasites; however, their host positions do complicate their life cycles.

*5.5.2 Harpacticoida: Wormlike Copepods**

These are a very large group of mostly benthic copepods. Very few associate with other organisms, and almost none are known to be parasitic. In the family Tisbidae, 13 species parasitise deep-sea octopuses. Red Bug, an aquarium pest, has often been called a parasite of corals and is caused by the copepod *Tegastes acroporanus* Humes, 1981. *Neoscutellidium yeatmani* (Zwerner 1967) was also said to be a parasite of fish, and other wormlike copepods were noted to be parasites of whales, sea turtles, and manatees (e.g. Aznar et al. 2010). However, others have disagreed with these statements (e.g. Suárez-Morales et al. 2010a; Domènech et al. 2017). An apparent commensal species, the ochre copepod*, *Balaenophilus manatorum* (Ortíz, Lalana & Torrez, 1992), has been observed in Caribbean manatees and sea turtles (Badillo et al. 2007; Williams and Bunkley-Williams unpublished data).

Life Cycle

Haracticoids probably follow the usual copepod life cycle of six naupliar stages and five copepodids found in their family. Dahms et al. (2000) discussed all that is known about the naupliar stages in Tisbidae. No development stages of parasitic forms had ever been found until López-González et al. (2000) described copepodids III and V. They suggested similar copepodid stages occurred internally (actually mesoparasitic) for the 12 other adult forms found in other octopuses. Therefore, their discovery completed the life cycle of these parasites (see Additional Information below). They hypothesised copepodid I was the infective stage and all these occurred internally. They did not discuss the naupliar stages, but these are expected to be the usual, six, free-swimming forms.

Further Life History

Adult males have only been found in four of the known haracticoid species. They may not live very long, not stay on the host very long, or even move to new hosts to copulate with other females.

Additional Information

The more complete life cycle suggested by López-González et al. (2000) is interesting and possibly correct. The only problem is that it is in disjunct halves. Until the external portion is matched with the internal portion in a single species, Ockham's razor would suggest these are portions of two different life cycles of tisbids on octopuses. The complete life cycle is thus still unresolved.

Ogawa et al. (1997) suggested *Balaenophilus* Aurivillius, 1879, species on sea turtles spend their entire life cycle on one host and cannot swim, like whale lice. Domènech et al. (2017) experimentally found nauplii can only crawl, but copepodids and adults can swim, albeit only for short distances.

Zwerner's (1967) discovery of *Neoscutellidium yeatmani* in the gills of Antarctic eelpout has been uncritically repeated so many times that it appears to be widely believed. However, this form has never been reported again. He found a mere seven specimens in the gills of 92 fish. These numbers are too low to sustain a viable life cycle for a parasite. This was very likely an accidental infection. This deep-water fish is known to eat molluscs, and 13 species of parasites in this family infect the gills of deep-water octopuses. These copepods could have spilled from an octopus to the fish consumed (see *Prey Predator Transfer*). More specimens with this association, with higher numbers per host, would need to be observed before this species could be confidently regarded as a fish parasite.

Many authors, even very recently (e.g. Aznar et al. 2010), have called the ochre copepod on sea turtles and manatees an ectoparasite, but it appears to be only a commensal. Suárez-Morales et al. (2010a) found that it was a harmless epibiont. This copepod formed ochre-coloured patches on the skin with no positive precursor relationship with barnacles or algae. Badillo et al. (2007) explored the possibility of parasitism of wormlike copepods on whales, sea turtles, and manatees in detail and believed that they ate keratin. They therefore claim this makes them commensals of whales, yet ectoparasites of turtles. This interpretation does not appear convincing, and we assert that they are all commensals.

Suárez-Morales et al. (2010a) also dismissed, another harpacticoid, *Harpacticus pulex* Humes, 1964, associate. It had been reported on a manatee only once, in captivity, and appears to be a non-associated predacious species.

Thus, we surmise wormlike copepods do not parasitise vertebrates or corals (Red Bugs). Some may be obligate commensals. Some may also harm vertebrates in captivity but are not parasites.

*5.5.3 Monstrilloida: Larval Parasitic Copepods**

Larval parasitic copepods are wholly parasitic and occur worldwide (tropical, temperate, polar) in marine waters and infect benthic gastropod and bivalve molluscs, polychaete worms, and sponges (Martin et al. 2014). Approximately 166 species are known in five genera in a single family. *Monstrilla* Dana, 1849 (Latin for monster) is the best-known genus. They are not abundant anywhere but more often found in coastal and coral reef areas. Their biology and ecology are poorly known. The only mortalities attributed to larval parasitic copepods was a partial die-off of cultured brown mussels (Suárez-Morales et al. 2010b) caused by copepodids, the most damaging stage.

Life Cycle

Suárez-Morales (2011) reviewed the diversity, as well as the life cycles of larval parasitic copepods. They have a protelean life history unique among metazoan parasites (Martin et al. 2014). The first naupliar stage is free-living, but the rest are endoparasitic. All the copepodid stages are parasitic. Copepodid V, called *subimago* by Suárez-Morales et al. (2014), is the emergent stage. It moults rather quickly into an adult after it leaves the host. The adults are nonfeeding, free-swimming, reproductive, and pelagic. Most copepods produce egg sacs or spawn freely in the water column, but larval parasitic copepod females attach their eggs on their long, ovigerous spines with mucous secreted by the terminal part of the oviduct. Egg masses are produced iteratively corresponding to when the ovigerous spines grow.

Eggs hatch into lecithotrophic nauplii that locate a mollusc or polychaete host and burrow into its tissues. They metamorphose into sac-like naupliar stage in the host's blood system. Two antero-ventral root-like processes absorb nourishment from the host. This stage is like no other crustacean larvae. Development continues endoparasitically until the last copepodid escapes from the host and undertakes a single moult into a reproductive adult. Suárez-Morales et al. (2014) described the first copepodids (III, IV, V) in detail, finding copepodid V to be pre-emergent and emergent.

Further Life History

Adults spend very little time in the plankton; therefore, they are rarely found and usually in low numbers. Suárez-Morales (2001) described one mass aggregation in the Caribbean Sea off Mexico.

Pelagic adults lack all cephalic appendages except antennules. The known hosts include pyramidellid and vermetid prosobranch gastropods, bivalves, and polychaete worms. Pairing the same species of free-swimming males and females morphologically has been difficult. The few morphological characters have also made taxonomic work difficult and often inconclusive, and descriptive standards have only relatively recently been upgraded (Grygier and Ohtsuka 1995). Suárez-Morales (2011) summarised the morphologies of the group to aid in identifying adults and life cycle stages.

Suárez-Morales et al. (2010b) were the first to find a monstrilloid in a commercial bivalve mollusc and to document the consequent harm and mortalities.

Additional Information

A radical placement of the larval parasitic copepods within the sea lice, based on SEM data, and antenna and caudal rami morphology, was proposed by Huys et al. (2007). The differences Suárez-Morales et al. (2014) found between these groups' copepodids suggested such a combination would be incorrect. Their life histories are also completely different in almost every respect.

A *subimago* refers to a pre-adult mayfly with wings, but no functional genitalia. It can fly, but cannot mate, and can be morphologically very similar to the adult. It moults into an adult. The copepodid V from Suárez-Morales et al. (2014) does not appear sufficiently different to warrant the use of this borrowed term. Kuris et al. (2005) suggests larval parasitic copepods are parasitoids. They do have a life cycle similar to parasitoids; however, we believe they are parasites because they do not kill their hosts.

Only 21 species (~18%) descriptions are based on both sexes, 63 on females only, and 32 on males. Molecular studies might help pair females and males of the species (Suárez-Morales 2011).

*5.5.4 Siphonostomatoida: Siphon-Mouth Copepods**

Siphon-mouth copepods have siphon-like mandibles and a frontal filament that attaches to the hosts. These attributes have contributed to their great diversity

Fig. 5.4 Cuckoo copepods (nicothoids) parasitise the eggs of lobsters and spider crabs in Asia and Brazil. They mimic the eggs of their host and are not removed from the host's eggs, which they eat. The copepod (arrow) has egg strings. See life cycle in Otake et al. (2016). Image © Kaori Wakabayashi

(~2233 species in 39 families) and success. Sea lice (caligoids) are well known fish copepods and are very damaging to fishes in cage culture, salmon being particularly damaged by the salmon louse. Cuckoo copepods*, or nicothoids (Fig. 5.4), are the most famous of this group of parasites of invertebrates that harm commercially important lobsters and spider crabs.

This order holds 75% of the known copepod parasites of fishes (1544 species in 17 families). Most species are marine, but a few are freshwater (Garcia and Williams 1985; Williams et al. 1994a, b, 1996; Williams and Bunkley-Williams 1996; Bunkley-Williams et al. 1999).

Life Cycle

The full copepod life cycle occurs in many families of siphon-mouth copepods, especially those utilising invertebrates as hosts, such as asterocherids and cancerillids. In parasitic copepods, the infective larva is, with rare exceptions, the first copepodid, and life cycles are direct, involving only a single host. In fish parasites, the nauplius phase is reduced to two lecithotrophic stages and has uniseriate egg strings in which disc-shaped eggs are closely packed into one row extending the length of the string; and most nauplii have a single pair of modified caudal setae known as balancers (function unknown). Related families with multiseriate egg strings, such as lernaeopodids, sphyriids, and two genera of hatschekiids, have nauplii lacking balancers. In some lernaeopodids (*Allela* Leigh-Sharpe, 1925; *Clavella* Oken, 1815; and *Nectobranchia* Hesse, 1863), the nauplius phase is reduced to one stage. In other lernaeopodids and some pennellids (*Salmincola* Wilson, 1915; *Cardiodectes* Wilson, 1917; and *Peroderma* Heller, 1865), it is lost completely, and eggs hatch directly into the infective first copepodid. Life cycle abbreviation also occurs in some parasites of invertebrates. The Herpyllobiidae and the genus *Trochicola* Dollfus, 1914, have only two naupliar stages, and only one nauplius is known for *Gonophysema* Bresciani & Lützen, 1960, and for some genera of nicothoids. In other genera of nicothoids, some chordeumiids, and cucumaricolids, there is no nauplius stage. Izawa (2010) experimentally showed that there could be five naupliar stages in *Gangliopus pyriformis* Gerstaecker, 1854. In most fish parasites, the first copepodid secrets a chitinous frontal filament from an anteriorly located gland, soon after it settles on the host. This filament anchors the developing chalimus larva securely to its host (Rohde 2005).

The life cycles of sea lice have been the topic of much research and debate of late. This attention is due to the damage that they cause cage cultured fishes, particularly of salmonids (Lafferty et al. 2015). Knowing the correct life cycle is critical in determining when to treat for the damaging stages. Caligid sea lice were thought to have four chalimus stages and one or two pre-adult stages. Several recent papers have challenged this scenario (e.g. Hamre et al. 2013; Venmathi Maran et al. 2013). They found that the typical caligid life cycle comprised eight stages: two naupliar, one copepodid, and four chalimus stages preceding the adult in *Caligus* Müller, 1778, but with the four chalimus stages represented by two chalimus and two pre-adult stages in *Lepeophtheirus* Heegaard, 1943. This is a profound change with significant implications for the aquaculture industry. As the typical caligid life cycle may not exist, it may be necessary to determine the life cycle of every species of damaging sea louse. Again, only 3.8% (17) of life cycles are known for 450 caligid species (Venmathi Maran et al. 2013).

The new Stingray Laser Gun has only been used to shoot adult sea lice (Bevanger 2016). Considering the flexibility and accuracy described for the gun, it could probably be used to shoot multiple life cycle stages.

Pre-adults also secrete a frontal filament during moulting but soon detach and become motile. Frontal filaments and chalimus larvae occur in most fish parasites for which the larvae are known, but none occur in the lernanthropids. Nicothoids use a similar filament to attach their developing larva to the exoskeleton of a crustacean host. The basic copepodid stages, as primitively retained in *Cancerilla* Dalyel, 1851, comprise five stages plus the adult. One pre-adult stage in *Caligus clemensi* Parker & Margolis, 1964, or two pre-adult stages in sea lice, as true moult stages, have been added to the basic life cycle. The general trend in parasites is to simplify or reduce ancestral free-living life cycles. These additions are quite unusual and have only been found in this order.

Pennellids (marine anchor worms*) differ from all other copepods by needing (obligate) intermediate hosts (fish, squid, pelagic gastropod) in order to develop. The copepodid larva becomes a chalimus larva stage on the intermediate host. Some male and female chalimus individuals mate on this host. Others leave the host and mate in the water column. Males soon die; females have a short planktonic period, find a final host, and metamorphose into an adult (Poulin 2011a). Brooker et al. (2007) reviewed the literature and thoroughly described the life cycle and life history of the famous pennellid copepod *Lernaeocera branchialis* (Linnaeus, 1767).

Not all marine anchor worms have intermediate hosts. Okawachi et al. (2012) suggest *Peniculus minuticaudae* Shiino, 1956, has a direct life cycle, unlike most pennellids, because copepodids, chalimi, adult males, premetamorphic adult females, and post-metamorphic adult females of the parasite were all found on a single fish. They also describe adult male, copepodid I, and late chalimus stages and redescribe post-metamorphic and premetamorphic adult females.

Ismail et al. (2013) described a complete, direct life cycle of a pennellid, *Peniculus minuticaudae* Shiino, 1956. The hatching stage was an infective copepodid followed by four chalimi and adult instars. Males associated with various pre-adult females, but copulation only occurred between adults. Fertilised premetamorphic adult females carrying spermatophores may detach from the host and settle again before undergoing massive differential growth into the post-metamorphic adult female. Many marine anchor worms (pennellids) have intermediate hosts. This is the first life cycle of the group in which the female remains in the same position on the same host specimen (Ismail et al. 2013).

Otake et al. (2016) had named a new cucukoo copepod* in 2013 and described its abbreviated nicothoid life cycle of free-living nauplius I (NI) observed hatching from female egg sac, copepodid I (CI) found on body of host, and copepodid II+ (CII+) and adults found on host eggs. They surmised NI develops into infective CI in the water column, CI settles on the body of host, and CI moults to CII, migrates to host egg masses, and develops into CII+ and then adults. Adults mate on host egg masses.

Brazenor and Hutson (2013) examined the effects of temperature and salinity on the life cycle of *Lernanthropus latis* Yamaguti, 1954, on the euryhaline barramundi in Australia. Nauplii hatched best at 30–32 °C and 35‰. None hatched in freshwater and only a few in brackish water. *Lernanthropus latis* is euryhaline, but freshwater can be used to break its life cycle.

Økland et al. (2014) described two new rhabdovirid viruses, which occurred in all life cycle stages of the salmon sea louse in Norway. The viruses caused tissue necrosis in adult copepods but did not infect fish. They speculate the copepod injects the virus in the fish to confuse its immune system as part of its purposeful life cycle strategy. We find their suggestion interesting but rather astonishing. Copepods do not purposely use viruses; theirs was not the first report of copepod viruses but the fifth; many other fish-parasitic *viral vector mutualists** exist to the benefit of crustacean infective stages; and we designated the first *viral crustacean mutualists**.

Further Life History

Sea lice are notorious for causing problems in marine aquaculture, particularly of salmonids (e.g. González and Carvajal 2003; Lafferty et al. 2015). The contamination of the environment by salmon sea lice from fish farms is a politically and economically important question that has received recent attention. Serra-Llinares et al. (2016) found that farms increase the infection of local, wild salmonids. They also noted Thorstad et al. (2015), and others strongly suggested the transmission of lice from farm salmon to wild salmonids in systems where the fish occur in close vicinity. These adult caligids can freely swim between hosts (*host hop**) and build up in fish cages. Few parasitic copepods have this life-history advantage (*serial parasites*). The filtering effect of cages tends to concentrate sea lice. Adult male and female caligids are frequently found in plankton samples (Venmathi Maran and Ohtsuka 2008). They must spend considerable periods free-swimming off hosts. Some species have even been described only from the plankton, and their hosts remain unknown.

Ohtsuka et al. (2011) previously described a dajid isopod and a nicothoid copepod parasitising the marsupial lumen of a mysid in Japan. The adults eat mycid eggs and drastically reduce the population of mysids. Infective stages of the copepod penetrate host body tissues, feed, and grow. Infective isopods penetrate the space between the carapace and the dorsal tergites. Remarkably, isopods and copepods rarely occur together, but alternately, albeit continuously, parasitised the same host at different times of the year. This life history association is unique in parasitology. We will call it *alternate host sharing**. This allows both parasite species to use all available resources of the host.

Additional Information

Three species of copepods are known to fully encyst in intermediate host fish tissues. Only one has been named. Lewis (1964) found the first pandarids to encyst in the fins of bony (teleost) fishes in Hawai'i. Lewis only found male copepodids and immature males, which he tentatively identified as *Nesippus* cf. *costatus* Wilson, 1924.

Amaterasia amanoiwatoi Izawa, 2008, was described from female copepodids I, III, IV, and V and a female escaping from a copepodid V. Izawa found 5, 13, 16, and 41 copepodids in fin galls on a single striped triggerfish from the Eastern Pacific (Izawa 2008). A new species of *Amaterasia* Izawa, 2008, was found in individual cysts, as Lewis (1964) had found, not galls, on the body and dorsal fin of 14 species of fishes in Puerto Rico (Williams and Bunkley-Williams unpublished data).

Tang et al. (2012) found that Lewis' (1964) younger early encysted stage was a copepodid IV, the older early encysted stage was a copepodid V, and the late-encysted and recently excysted stage was an immature adult male. Izawa (2008) and Tang et al. (2012) speculated about the life cycle of their species but made no descriptions. Tang et al. (2012) suggested encystment could be protection from coral reef cleaners.

We propose a new life cycle for these encysted copepods*: there are five planktonic nauplii (Izawa 2010) and a first copepodid stage. The CI is infective (found in galls; Izawa 2008) and settles from the plankton onto a host and forms a cyst or gall under the skin on the fins or body of a variety of different bony, coral reef fishes. Lewis (1964) found surgeonfishes (acanthurids) were preferred in Hawai'i. However, parrotfishes were preferred in Puerto Rico (Williams and Bunkley-Williams unpublished data). The cysts are open posteriorly for respiration (mesoparasite). After feeding, developing, and moulting through CI–CIV, the fifth copepodid emerges from the cyst leaving a moulted exoskeleton behind. Lewis (1964) found these forms were soft and pliant, which he interpreted to be of value in leaving their cysts. It was actually because they had recently moulted. The CV then swims out and searches for a shark definitive host. There could be some *predator transfer* involved since the copepodids are in hosts preyed upon by sharks. The encysted copepod life cycle* is the only mesoparasitic life cycle known in parasitology and only the second obligate intermediate host life cycle discovered in copepod parasites of fishes. Many tapeworm (cestode) shark parasites have bony fish intermediate hosts, but this is the first crustacean one ever discovered.

The evolutionary usefulness or necessity of pennellid intermediate hosts has never been explained (Poulin 2011a; Martin et al. 2014). We can discern at least seven, nonmutually exclusive explanations:

1. *Easier to Find*—the open sea is a vast 'desert' with very few final hosts, but intermediate hosts are far more common (Williams and Bunkley-Williams 1996).
2. *Easier to Infect*—intermediate hosts are generally smaller, slower, and have better attachment sites.
3. *Longer Survival*—feeding and resting on the immediate host extends the parasite life cycle and replenishes their energy.
4. *Bigger is Better*—adult females are stronger and attach better than larval forms.
5. *Ride to Final Host*—intermediate hosts are often food for, or associated with, the final hosts. Even when eaten, prey-predator transfer can occur (Williams and Bunkley-Williams 1996).
6. *Faster Attachment*—when the female settles on the final host, water currents, host movements, and sometimes host cleaning or cleaner organisms make her stay perilous (loose on the host). Nutrients from the intermediate host can be used to permanently attach without waiting to feed on the final host and digest.
7. *Widen Host Range*—the only crustacean parasite to infect mammals cannot do so without an intermediate host.

Kik et al. (2011) found *Lepeophtheirus acutus* Heegaard, 1943, was a potentially dangerous sea louse of elasmobranchs in captivity. Not only did it damage sharks and rays but could complete its life cycle in an aquarium.

Muñoz et al. (2015) found early and late copepodids of two species of *Caligus*, two of *Trifur* Wilson, 1917, and two of unknown families, on juvenile fishes. They examined thousands of nearshore, planktonic fishes, found 3% infected, and 1% infected by multiple species. They thus opened a completely new dimension into parasitic life strategies, which we have termed *planktonic juvenile fish infection**. Juveniles of a single host species have sometimes been examined for parasites (e.g. Nielson et al. 1987; Herrera 1990), but masses of juveniles have seldom been studied (e.g. Herrera 1984; Felley et al. 1987; Cribb et al. 2000). Muñoz et al. (2015) concluded these juvenile fishes were intermediate hosts for these copepods. However, caligids are not known to have intermediate hosts, and pennellid intermediate hosts are adult fish or squids. They had also concluded the copepods would mature too soon to develop with the host fishes. However, we believe the hosts and the parasites will grow up together in these cases. Alternatively, these may be *small predators** feeding on juvenile fishes as a part of their life cycles (Table 5.1). Whichever is the case, this

Table 5.1 Crustacean life cycles with predation phases

Name	Predator/host	Examples
Micropredator	$<1/1000$	No crustaceans, microbial organisms
Minipredator	$>1/1000 < 1/100$	Fish gnats, serial parasites, jelly parasitoids
Smaller predator	$>1/100 < 1/10$	Copepodids, fish gnats, fish isopods, fish lice
True predator	$>1/10$	Some fish isopod juveniles

extends and prolongs life cycles further than we had imagined. Interestingly, only copepods are taking advantage of this resource, not only among crustacean parasites but also among all parasites. Muñoz et al. (2015) also searched for internal parasites and found none.

Venmathi Maran et al. (2013) clarifications of sea lice life cycles are important for timing the treatment of these damaging parasites in cage culture. As noted above, of the 450 species of caligids, only 17 complete life cycles are known in three genera (*Caligus*, *Lepeophtheirus*, *Pseudocaligus* [=*Caligus*]) (Venmathi Maran et al. 2013). Thus, and similar to many other parasitic Crustacea, we know very little about them.

Cuckoo copepods are named after the nest-parasitic birds by that name (Cuculidae). These copepods parasitise the eggs of lobsters and spider crabs in Asia and Brazil. They mimic the eggs of their host (Fig. 5.4) and are thus not removed by the host, as they resemble the real eggs, which they eat. Otake et al. (2016) called these copepods ‘associates’. Kuris et al. (2005) calls them ‘symbiotic egg predators’. However, we consider them to be true parasites, damaging and feeding off their hosts, with adults that never leave the host.

Flyingfishes are food for many large offshore predators, which host *Pennella* spp. Flyingfishes were probably a downward incorporated intermediate host for a *Pennella* spp. at one point. Eventually, a former intermediate host speciated into *Pennella exocoeti* (Holten, 1802) on flyingfishes.

5.6 Cirripedia: Barnacles

Høeg et al. (2009) found that cypris larva morphologies of the barnacles reinforced the concept that this larva was a prerequisite to the tremendous success of that taxon. The evolution of parasitism, obligatory in three major taxa, was the result of convergent evolution. Thecostraca was distinct from Tantulocarida (Sect. 5.10) because they differed in the life cycle stages that penetrated their hosts (Høeg et al. 2009).

5.6.1 *Acrothoracica: Burrowing Barnacles**

Burrowing barnacles (burrowing crustaceans of Kolbasov 2009) have 70 species in 12 genera, 4 families, and 2 orders, but many species have probably not been discovered. They have been called parasites of molluscs, echinoderms, and corals (anthozoan cnidarians) by many authors (e.g. Williams et al. 2011) but are not.

Life Cycle

These very small, naked barnacles bore into calcareous material such as animal shells and inanimate hardgrounds. Burrowing barnacles produce a slit-like hole in the surface known by the trace fossil name *Rogerella* Saint-Seine, 1951. They feed on plankton (Kolbasov 2009). They do not feed on their associates. Burrowing barnacles are only found in their hosts' shells and never touch their flesh, except possibly in the case of corals. They are not obligates, perfectly happy living on inanimate hard ground, and do not harm their hosts. We do not understand how they can be called parasites?

Additional Information

Williams et al. (2011) called a burrowing barnacle a parasite and showed that it fed on its host hermit crab's eggs. However, this was predation, not parasitism. Murphy and Williams (2013) suggested burrowing barnacles in hermit crab shells were 'transient parasites' because they somehow consumed hermit crab eggs and preferred female hermit crab shells. In our opinion, burrowing barnacles are not parasites, as least when considering the current available information.

5.6.2 *Rhizocephala: Parasitic Barnacles**

The parasitic barnacle is the 'poster child' for gross modification of parasitic forms. Adults are unrecognisable as crustaceans, let alone barnacles. Only their larval forms resemble those of normal barnacles (see Sect. 5.6.3). They are also famous for controlling the behaviour and morphology of their hosts. They damage commercially important crustaceans. About 288 species are known, about a quarter of all barnacle species. They infect crustaceans, mostly true crabs (brachyuran) and anomuran crabs (hermit crabs, squat lobsters, etc.). A few parasitise caridean shrimp, mantis shrimp, peracarids, and even other barnacles. We worked on the button-crab parasite* on the blue crab in the Gulf of Mexico but have not found such obvious parasitic barnacles in the Caribbean.

Life Cycle

Unlike most barnacles, parasitic barnacles have separate sexes. Adults are sessile, with females consisting of a sac attached to the crab host (externa) (Fig. 5.5) with rootlets of tissue flowing cancer-like through the host's body (interna) and dwarf males inside the female. Some females sequentially only produce male larvae from large eggs, female larvae from small eggs or mixed sexes. They have the usual

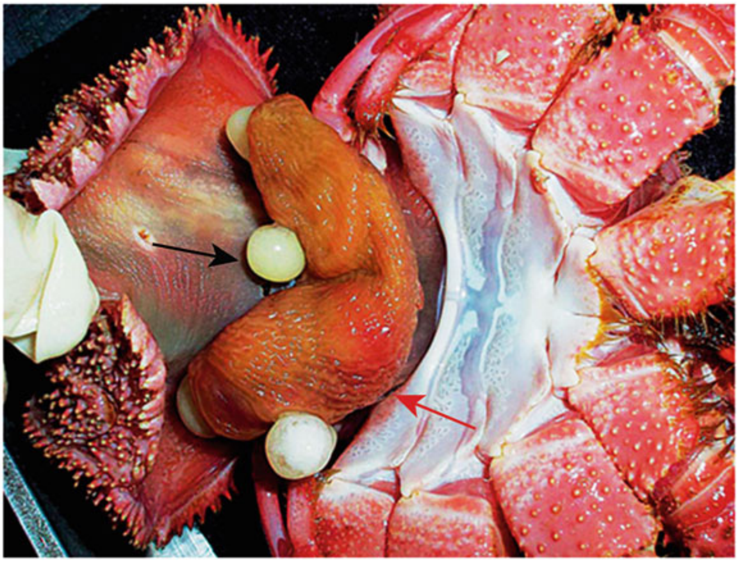

Fig. 5.5 Ventral surface of the false king crab, *Paralomis granulosa* (Hombron & Jacquinot, 1846), parasitised and sterilised by *Briarosaccus callosus* Boschma, 1930 (*"greater than" symbol-shaped mass—red arrow*), externa of this rizocephalan parasitic barnacle, which, in turn, was hyperparasitised and rendered sterile by four *Liriopsis pygmaea* (Rathke, 1843) (*pearl shapes—black arrow*) epicarid parasitic isopods (Cryptoniscidae). A different black-and-white photograph of these associations was in Lovrich et al. (2004). Associates in this present colour photograph have been misidentified in several popular sites online. Image © Gustavo A. Lovrich

naupliar instars and infective cyprid; however, in some species, embryos develop directly into cypris larvae before adult females release them. The nauplii are smaller than those found in other barnacles, which may be necessary to produce them in much greater numbers. The larvae are lecithotrophic. The cypris are usually at least 2 days old before they settle on a host. In kentrogonids, male cyprids are larger than female ones. Some have a naupliar eye, and others have compound eyes. Injection of the vermigon (the migratory internal stage) happens within 1–3 days after settlement. When many male larvae exist, only the fastest and strongest will succeed. When there are few males, the female remains receptive longer. When a virgin is found, the male cyrid must settle close to the orifice, enter the brood chamber, and inject a trichogon stage. The trichogon looks like a verogon, except with a spiny collar. It becomes a dwarf male and reaches one of two male receptacles. Once established, the dwarf male undergoes spermatogenesis and is nourished by the female parasite for the duration of its life (*cryptogonochorism*). The male cypris of akentrogonids penetrate the host or the virgin female with their antennules and without a kentrogon or trichogon. A single male can fertilise all the broods of the female. A female externa produces several batches of larvae and drops off the host just before the host moults. A new, young externa is produced from the interna and emerges from the host body (Waiho et al. 2017).

Further Life History

The externa takes the place of the crab egg sac. The host's behaviour is chemically altered causing sterilisation and only moults when the aged externa drops off. The host treats the externa as if it were its egg sac. Male crabs, which would never have carried eggs, care for the externa. They are even more affected since their tail shape changes to the female configuration to better protect the externa (*feminization*). An externa may last for several years.

Additional Information

These life cycles show parasitic barnacles are the most parasitic of the crustaceans. They totally penetrate all the tissues of their host, control the behaviour of the host, and are drastically modified for the parasitic existence.

Glenner and Hebsgaard (2006) made a comprehensive phylogenetic analysis of the evolution of life history strategies in parasitic barnacles. They found they were monophyletic with a filter-feeding barnacle-like ancestor. The host-infective kentrogon larva, inserted in the life cycle of Kentrogonida, was ancestral, and a homologue of the juvenile thoracican barnacle. The host inoculation in Akentrogonida (last pelagic larval stage directly injects into haemolymph) is derived and has evolved only once within the parasitic barnacles. The ancestral host is anomuran (hermit crabs, squat lobsters, etc.).

Alverez et al. (2010) described the externae of the button-crab parasite in detail. Unlike most parasitic barnacles, they found only a single male receptacle but two implanted males. They questioned what sorts of male-male competition occurs when they are not separated.

Glenner et al. (2010) used light and SEM microscopy of cypris larvae to supplement molecular data showing that parasitic barnacles, thought to be the most primitive, were actually the most advanced, along with many evolutionary extrapolations.

These parasitic barnacles are sometimes hyperparasitised by cryptic isopods (Fig. 5.5). Just as the barnacle sterilises its crab host, the hyperparasite sterilises its fellow parasite. There are some indications that swimming decapods, which must remove epibionts, are more resistant to the attachment of settling crustacean parasites; however, no experimental evidence exists (Boyko and Williams 2009). In the reverse, Li et al. (2015) found a species of crab parasitised by a rhizocephalan had many more barnacles, and other epibionts, than those not parasitised. This is an example of our *positive precursor**.

Several authors have recently suggested parasitic barnacles could be host-specific control agents for nonindigenous crabs, such as the problematic green crab. However, parasites seldom make effective controls, and well-intended introductions have often been disastrous.

*5.6.3 Thoracica: Normal Barnacles**

This group containing the normal acorn and gooseneck barnacles has four parasitic species in three families and three genera. The shark barnacle* is little modified for parasitic existence except for the loss of its shell and adding a tough tegument. Polychaete barnacles* are moderately modified. The jellyfish barnacle* is the least modified with small, thin plates. The cirri (feeding legs) are still used for obtaining food. These free-living-to-parasitic transitionals are, of course, of great scientific interest (Rees et al. 2014). The shark barnacle is famous for promoting Charles Darwin's interest in barnacles.

Life Cycle

They are hermaphroditic with all individuals possessing a penis, and no dwarf males are known in shark barnacles and polychaete barnacles. Adults are receptive as females for fertilisation after moulting. They use their penis to copulate with an adjacent individual as other hermaphroditic free-living barnacles. Barnacles have the longest penises, relative to body size, in the Animal Kingdom. Oddly, dwarf males have been found attached to larger hermaphrodites in some species (*androdioecy*; Sawada et al. 2015).

The fertilised egg hatches into a standard, barnacle nauplius, a one-eyed, pear-shaped larva with a head, a naupliar eye, a pair of horns, and a telson. Nauplii are usually brooded by the parent and released after the first moult swimming freely with setae. Towards the end of the sixth instar, they begin to develop compound eyes and a globular shape. They undergo 6 months of growth, passing through five instars, before transforming into the cyprid stage, which has a carapace, is torpedo-shaped and is the stage before adulthood. It does not feed and only searches for a host. This may last for a period of days to weeks. It explores potential hosts with modified sensory antennules. Once it finds a host, it undergoes metamorphosis into a juvenile barnacle. Shark barnacles are usually found in pairs near the dorsal fin of their shark host; therefore, the cypris larvae must not only find a host but also a partner (see *founder pair**).

Further Life History

Shark barnacles breed through the year and live on their host for at least a year. Both genera feed on the host by roots formed from their peduncles. They mostly infect small specimens of sharks (10%), and incidence is reduced (2%) in large ones. Gonads of infected sharks never develop (*nutritional sterilisation**).

Additional Information

Williams et al. (2010) reported a prey-predator transferred isopod in a lantern shark but found no barnacles. Some epiphytic normal barnacles attach to hosts or parasites (e.g. Williams 1978; Williams and Williams 1986b; Mignucci-Giannoni et al. 1998), and the sea turtle barnacle has been found on the carapace of a speckled crab at Dauphin Island, Alabama (Williams and Bunkley-Williams unpublished data).

Shark barnacles parasitise at least seven deep-sea lantern sharks and dogfish (Ommundsen et al. 2016). Furthermore, two species of polychaete barnacles and a jellyfish barnacle are known (Yusa et al. 2015). The jellyfish barnacle is an obligate associate of jellyfishes, and Pagès (2000) found it attached in an area with few nematocysts near the gonads of the jellyfish host. We believe the lack of stinging cells may have originally attracted the barnacle infective stage to this area, and the gonads became a convenient food source later. A simple development of parasitism is still in progress.

5.7 Facetotecta: Y-Parasites*

The 11 species in the larval genus *Hansenocaris* Îto, 1985 of y-parasites remain a mystery in parasitology. Y-larvae have been known for 129 years, but their assumed parasite adult forms and hosts have never been found. These parasites are both everywhere and nowhere. They must be both parasitologically and ecologically very important, but how remains a mystery.

Life Cycle

Y-nauplii are egg-shaped, with a faceted cephalic shield and carapace (reticulated cuticular ridges, forming plates), from which the group derives its name, and a relatively long, ornamented abdomen. They have a characteristic bobbing motion when swimming that makes them easy to distinguish in plankton samples. The function and homology of the naupliar horn pores and dorsocaudal organs have been much debated but remain uncertain. They are either *planktotrophic* or *lecithotrophic*. Only lecithotrophic nauplii have been raised through all five instars. Planktotrophic nauplii have food visible in their stomachs. Unlike barnacle larvae, the y-cyprid is constantly swimming. This larva is distinctively the costracan. The y-cyprid has a univalved carapace that only partially covers the larval body and resembles an inverted boat but with elongated sharp posterior ends (Fig. 5.6). Paired compound eyes lie anteriorly in the body with antennules, labrum, paraocular processes, postocular filamentary tufts, and two pairs of rudiments of antennae and mandibles underneath (ventrally). The antennules have four segments. All larval stages are free-living and semitransparent. The cyprid does not feed. A number of species have been described based only on a y-cyprid ($N = 7$) or even a y-nauplii ($N = 4$). As with barnacles, the cyprid seeks a host to infect. It has compound eyes, is ambulatory with its antennae, and can produce an adhesive glue. Recently, possible juvenile forms have been produced by treating y-cyprid with the hormone 20-hydroxyecdysone to stimulate ecdysis and the transition to the next life cycle phase. The resulting slug-like, unsegmented, and limbless form was called 'ypsigon' (Fig. 5.6). It is formed in the cypris and escapes from its body (Glenner et al. 2008). This may be a juvenile. See Høeg et al. (2014) for more detailed descriptions, illustrations, and photographs.

Further Life History

Molecular studies support the present phylogeny of the y-parasites (Høeg et al. 2014). They remain mysterious parasites with unknown adults and hosts.

Additional Information

Glenner et al. (2008) suggest the ypsigon is the 'vermigon of the y-parasites'. Just like the barnacle vermigon, it is the injected form that will become the parasitic adult. This may be true, but just because formless structures are produced by similar

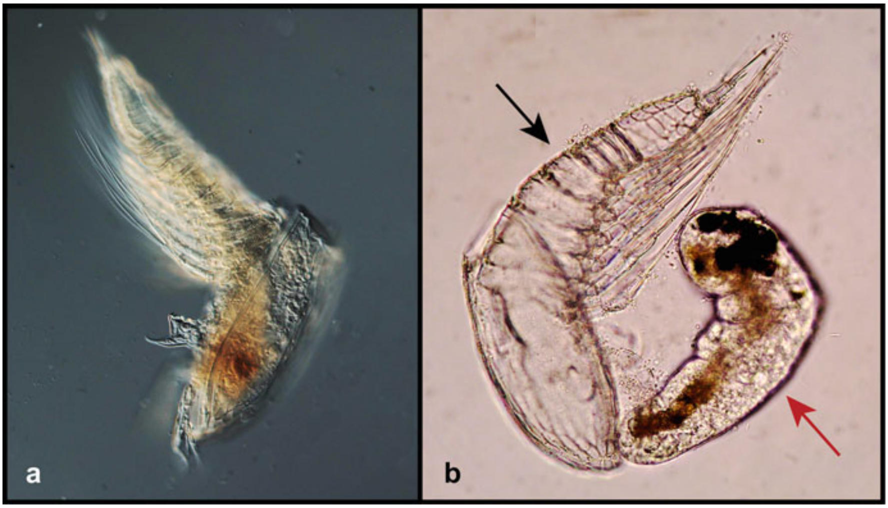

Fig. 5.6 Facetotecta (y-parasites). (**a**) Free swimming y cyprid: showing the carapace, the thorax with six pairs of natatory legs and the segmented abdomen, (**b**) an ypsigon (red arrow) within minutes of leaving the empty cuticle of the spent y-cyprid (black arrow). The cuticles of the carapace, thorax, appendages and abdomen are clearly visible, but no tissues remain in the spent y-cyprid. The worm-shaped ypsigon exits by amoeboid bending and peristalsis movement of the body and is believed to be the initial parasitic stage that enters into the tissue or body cavities of a still unknown host. Details in Glenner et al. (2008). Images © JT Hoeg, M Grygier, Y Fujita, H Glenner, J Olesen

methods and appear similar does not make them the same. Their notion is courageous, albeit premature.

Glenner et al. (2008) found that 40+ morphological types of y-larvae occurred very abundantly around Sesoko Island in Okinawa. This unusual situation may indicate a centre of origin or, possibly, a diversity *hot spot*. Yet, the adults remain unknown. The ‘phantom’ adults are neither too rare to discover, nor in some obscure unexamined hosts, nor in some restricted localities. The larvae are just too abundant, widespread, and diverse for such restrictions. This is an adult that parasitologists may be encountering all the time but just cannot recognise. The adult y-parasites may be morphologically similar to another parasite, with which they are confused, or so morphologically indistinct as to be unrecognisable as a parasite. Glenner et al. (2008) came to a similar ‘highly simplified structure’ conclusion.

5.8 Ascothoracida: Copebarnacles*

These are uncommon parasites that cause little damage and infect non-commercially important hosts. Copebarnacles are a small group of ~107 species in 23 genera, 6 families, and 2 orders, which are ecto-, meso-, and endoparasites. They occur from the intertidal to the deep sea around the world.

*5.8.1 Laurida: Coral Copebarnacles**

Coral copebarnacles are ecto-, meso-, and endoparasites of corals (Scleractinia, Zoantharia, Antipatharia and Alcyonacea) and ectoparasites of crinoids (Waginella). The suggested common name is based on their bodies that are similar to copepods but are related to barnacles.

*5.8.2 Dendrogastrida: Echinoderm Copebarnacles**

Echinoderm copebarnacles are meso- and endoparasites of echinoderms (Asteroidea, Echinoidea and Ophiuroidea).

Life Cycle

Sexes are separate except for the hermaphroditic petrarcids. Sex determination is genetic, and some male and female larvae differ in the armature of chemosensory aesthetascs (as in most parasitic barnacles). A-nauplii have an oval, bowl-shaped head shield, which is broader anteriorly, and setiform frontal filaments. A-cypris have a bivalve carapace and antennules with hooked claws. Echinoderm copebarnacles brood their larvae and only release a-cypris, while coral copebarnacles release nauplii. Usually, six naupliar instars (sometimes two brooded) are followed by one to two cypris-like stages (a-cypris, ascothoracid larvae) (similar to the cirripede single cypris and the y-cypris of y-parasites). Many are lecithotrophic, but some species are planktotrophic. Coral copebarnacles a-cypris occur in the plankton. The a-cypris (ascothoracid-larva) attaches by grasping antennules rather than by glandular secretions as in cirripede cyprids. When two a-cyprid instars occur, the second is the settlement stage. Many species have an abbreviated ontogeny, and the entire naupliar phase is sometimes brooded or embryonised. No complete life cycle is known for any copebarnacle. Neither host infection, nor copulation has ever been observed. Most females have seminal receptacles on their legs, but not in dendrogastrids. Some male a-cyprids have testes with mature sperm and possibly fertilise the females through the pore in the host. Some dwarf males sit close to the aperture, and others live in the mantle cavity of the female. The transition from a bivalved stage to a sac-like carapace is suspected to occur in one moult, but this remains unresolved. A ‘post-larval’ stage of females and males has been discovered, and second-stage a-cyprids, ready to moult to the male stage, have been observed. The cypris for the modified, enlarged female, and dwarf males of Gorgonian copebarnacles (*Gorgonolaureus* Utinomi, 1962) are not known. The complete life cycle is equally not known (Kolbasov et al. 2015). Three-five naupliar instars occur. *Gorgonolaureus muzikae* Grygier, 1981 has been noted to be frequently infected by hyperparasitic cryptoniscoid isopods (Kolbasov et al. 2015).

Further Life History
Some ectoparasitic males and females can swim from host to host. Others are semi-permanently glued in place. Some are endoparasites in galls in corals and sea stars. Others even start as an endoparasite but eventually create an opening to the outside and become mesoparasitic. Parasites of cnidarians occupy individual polyps or nodules formed from several polyps. Many of those in echinoderms sterilize their hosts. Feeding methods are uncertain. Many have piercing-sucking mouthparts, and the cuticle of at least one species seems capable of absorptive feeding (as in parasitic barnacles). Hyperparasitism of ascothoracidans by cryptoniscid isopods is not uncommon, occurring in four of the six families. Some sterilise their copebarnacle hosts. In a spectacular case, a copebarnacle, which had sterilised its host, was, in turn sterilised by an isopod. Their body is enclosed by a bivalve carapace often modified and enlarged for brooding and possibly food absorption in females.

5.9 Subclass Tantulocarida: Minute-Crustacean Parasites*

Minute-crustacean parasites are a highly specialised, small (36 species in 23 genera and 5 families) group of minute (<0.3 mm) ectoparasites on small benthic crustaceans (copepods, isopods, tanaids, amphipods and ostracods). They occur from the subtidal to the abyssal, widespread in the southern and northern hemispheres, and in both cold and warm waters. They claim the fame of the world’s smallest arthropod (76 μm).

Life Cycle
Minute-crustacean parasites have asexual and sexual life cycles. The first is when a parthenogenetic female develops from a tantulus larva and remains permanently attached to its larva, and the host, as sort of a ‘Frankenstein’ female. It feeds off the host and produces numerous eggs. This adult female has a large, sac-like trunk attached by the larval head. The larval trunk is sloughed leaving a scar, but no complete moult occurs. Eggs develop within the trunk sac and hatch directly into the infective tantulus larval stage.

The second life cycle occurs when a free-living *semelparous* female is produced by an attached tantulus larva, escapes from the larva, and swims away to copulate with a similarly produced free-swimming male. These minute-crustacean parasite life cycles are unique. Instead of the standard moulting cycle of all other crustaceans, the mature adults develop in the attached parasitic tantulus larva. The extreme brevity of early ontogeny seems to be an adaptation to parasitism in situations where a high dispersal ability is not advantageous.

Further Life History

Minute-crustacean parasites have a dramatic reduction in body form compared to other crustaceans, with an unsegmented sac-like thorax and a much reduced abdomen. The attached larvae and *parthenogenetic* females are permanently attached to their host by the oral disc with an adhesive. In the centre of the disc, they make a minute puncture, through the host integument, with their cephalic stylet. This is their only access to the body fluids of the host.

The free-swimming, nonfeeding adults lack cephalic appendages but possess two clusters of aesthetascs on its anterior margin. They are free swimming and have six pairs of large thoracopods without endites. The first two thoracic somites are incorporated into the cephalothorax. The male abdomen bears a posteriorly directed, median stylet and intermittent organ. It originates on the first abdominal somite. The parthenogenetic females live longer than their sexual doppelganger and are responsible for the majority of the reproduction of their species.

Additional Information

Knudsen et al. (2009) described tantulus larvae, developing males, parthenogenetic females, and only the third developing sexual female ever found. They noted that the taxonomy of the group is based mainly on the tantulus larvae, which is quite an unusual role for a larval life cycle stage. Some suggest these minute crustacean parasites, with no larval stages, are the adults of the orphan mysterious y-parasites (facetotectans), which have no known adults, only larvae. There are myriad reasons why these life cycles are, unfortunately, unlikely to fit together.

5.10 Amphipoda: Scuds

Scuds are a minor group of known parasites, but they have many species commensal on ascidian, bryozoan, cnidarian, echinoderm, mollusc, sponge, and crab hosts. Many of these may be parasitic or at least well on their way to parasitism. They are called commensals because we just do not know enough about most of them to make a proper categorisation. Whale lice and jelly parasitoids are known to be parasitic, and we believe a bivalve scud is also an unrecognised parasite.

5.10.1 Cyamidae: Whale Lice

There are 32 species in 6 genera and one family (Cyamidae) of whale lice. They have no carapace, and their bodies are dorsoventrally flattened instead of laterally compressed as in other amphipods. They are one of the few aquatic crustaceans that cannot swim in any part of their life history. Molecular studies of whale lice have determined the evolution of their host whales (Kaliszewska et al. 2005). Infections can be heavy on whales and other marine mammals (Mignucci-Giannoni et al. 1998;

Colón-Llavina et al. 2009), and superinfections can harm whales. Whale lice will also attach to humans handling whales.

Life Cycle
There is an easily discernible life cycle. Eggs are held in the marsupium of the female. Females produce more eggs in each brood as they age. A quarter to half of the eggs die in the marsupium. The eggs hatch directly into a juvenile form with no larval stages, similar to fish isopods and all Peracarida. They have clawed pereopods and immediately attach to the cetacean skin. Sexual maturity is usually reached after six moults. Some eat their *exuvia* (exoskeleton remains) after moulting. The complete life cycle may take 8 or 9 months.

Further Life History
Whale lice parasitise cetaceans (whales, dolphins, porpoises). Since whale lice cannot swim, they can only be spread by direct contact among hosts such as during mating, nursing or care giving. They feed on dead cetacean skin and algae and are attracted to wounds on hosts but more for attachment than actual feeding. They may even clean up wounds and so speed up healing. Whale lice also like creases, crevices, and barnacles for attachment. By eating algae, they control its growth on their host. In general, slow swimming whales have more whale lice, than fast swimming whales. Some suggest that host jumping or breaching is done in order to knock off whale lice. Some online videos show human divers easily brushing whale lice off whales with only their fingers. Heavy infections reportedly harm humpback and gray whales. We found a heavy infection on a sperm whale that may have contributed to its death (Mignucci-Giannoni et al. 1998).

*5.10.2 Melitidae: Bivalve Scuds**

Melita anmyeonensis Shin, Coleman, & Kim, 2013, is found between the gills and mantle cavity of the broad angel wing bivalve, *Barnea dilatata* (Soulelet, 1843), in South Korea. Scuds in six families associate with bivalve mollusc hosts but never in high numbers of adults. Shin et al. (2013) found no damage to the host. Kretzler (1984) could not detect obvious physical damage to sea urchins even by very heavy infections of scuds. They could not determine if the association was obligate. They called it commensalism. We feel the high prevalence (100%) and intensity [1–169 (av. 28.8)] in the broad angel wing, and the lack of free-living collections suggests that it is an obligate parasite. This bivalve is no stranger to crustacean parasitism having two species of parasitic copepods. Shin et al. (2013) noted *host abandonment** of *M. anmyeonensis* from damaged and captured broad angel wings. Host abandonment is a frequent strategy of crustacean parasites for finding another host.

*5.10.3 Hyperiidea: Jelly Parasitoids**

They are often called parasites or parasitoids (Lafferty and Kuris 2002; Kuris et al. 2005) but are not exactly parasites either. We term them *serial parasitoids**. In various parts of their life histories, they may be free-living, *kleptoparasites*, *minipredators**, *parasitoids*, *serial parasitoids*, or a mix. They have an obligatory association with jellies (salps and jellyfishes) as a nursery for their young (*parasitoidism*), often rest on jellies (*phoresis*), but spend most all of their lives as minipredators (see Table 5.1). Jelly parasitoids have ~283 species in 22 families.

They damage and kill some gelatinous zooplankton but have no known ecological or commercial importance. Now that jellyfish are held and reared in major aquaria, jelly parasitoids have become a problem. Effective chemical treatments have been developed (e.g. Boonstra et al. 2015).

Life Cycle

Mating occurs on a host jelly, males depart, and ovigerous females remain on the host while brooding the eggs. Brood sizes range from 50 to several hundred eggs. The eggs are relatively small for amphipods. Larval stages are in the female marsupium. The first stage is the *pantochelis* larva with four cheliform pereopods and unsegmented and limbless metasoma and urosome. The pantochelis stage metamorphoses into a ‘protopleon’ larva (often divided into three sub-stages), having a segmented metasome and imperfect pleopods. In many species, there is no pantochelis stage, and the egg hatches directly into a first protopleon stage. The last (or only) protopleon stage gives rise to the first juvenile stage (a miniature adult) and marks the *demarsupiation* or the deposition by the female of the larvae (in rare cases the juveniles) into a host. During demarsupiation, the gravid female swims out to find a host and deposits one or a few larvae upon the host specimen (depending on host size and capacity). She continues infecting one host after another. Some females penetrate a host, split a gonad with its mouthparts, and inserts the larvae deeply into the organ. As they grow, the juveniles leave the gonad and start feeding on the prey trapped by the host. Some females deposit pantochelis larvae on the surface of salps with their specialised seventh pereopods. When the larvae moult a few hours later, the ensuing protopleon larvae enter the branchial cavity and eat its wall or feeds on the collected suspended matter. Once the host can no longer support the young as they mature, they leave it for another salp in the chain. Species of phronimids excavate solitary salps or pyrosomes into ‘barrels’ open at both ends and in which they hide and use as a nursery. The larvae are *demarsupiated* into the barrel where they soon bunch together into a tight cluster that slowly moves around on the inner barrel wall. The female stays with the barrel and prevents the young from passing to the outer surface. At intervals, she makes short excursions into the water and returns with prey to feed her brood. The pereopods are used to maintain the position of the animal within the barrel, and beating of the pleopods propels the combined barrel-jelly parasitoids through the water (bio-jet ski).

Further Life History

Some adults feed on small plankton, at least part of the time; others steal small plankton out of jellies; and some eat jelly tissues as minipredators. They certainly use jellies as places to rest. Jelly parasitoids seem immune to the stings of medusa. Males are better swimmers than females.

Additional Information

Gasca and Browne (2017) found ten hyperiid amphipods, a copepod, and a pycnogonid in jelatinous plankton in the Gulf of California. They also named a new species, *Megalanceoloides aequanime* Gasca, 2017, based on a redescription of *M. remipes* (Barnard 1932) in Gasca and Haddock (2016), distributions, sizes, and a few morphological differences. We name *Megalanceoloides gascae* n. sp. based on the descriptions by Vinogradov (1964) and Vinogradov et al. (1996) of '*M. remipes*'. We also distinguish *M. gascae* from *M. remipes* on the basis of geographical distributions in the northern Indian Ocean (Vinogradov 1964) vs southwest Atlantic (Barnard 1932; USNM 301871, 1090231), south-east Pacific (USNM 1090233, 1090237), and Antarctic Ocean (USNM 1090236). The former three records represent two new locality records. The two species are further distinguished based on the sizes of females, 19 mm female (Vinogradov 1964) vs 40 mm male (Barnard 1932), and morphological differences discussed by Gasca and Haddock (2016). The holotype is the specimen collected by Vinogradov (1964: 114–117, by monotypy ICZN 1999: Art 73.1.2) and also in illustrated ions by Vinogradov (1964: Figs. 4, 5) and Vinogradov et al. (1996: Fig. 26) (ICZN 1999: Art 72.5.6, 73.1.4). The new species is the third in the *Megalanceoloides remipes* species complex and in genus *Megalanceoloides* Zeidler, 2009.

5.11 Isopoda: Isopods

*5.11.1 Anuropidea: Jelly Isopods**

Jelly isopods are giant, blind isopods that occur in all oceans except the Indian Ocean (to date) and parasitise large scyphozoans in the deep sea of the Eastern Pacific and Japan (Ohtsuka et al. 2009). Ten species in one genus, *Anuropus* Beddard, 1886, are known, but only two have been associated with scyphozoans. They live in and feed on their host, but very little else is known (Ohtsuka et al. 2009). Our lack of knowledge may be an artefact of destructive net collections (Gasca and Browne 2017).

*5.11.2 Cymothooidea: Fish-Associated Isopods**

Fish-associated isopods are relatively large as adult parasites, in comparison with most other parasitic Crustacea, and are often seen by divers on the outside of marine-reef fishes (Figs. 5.7 and 5.8) and by fishermen in the mouths and gill chambers. Fish gnats*

Fig. 5.7 Yellow angelfish, *Centropyge heraldi* Woods & Schultz, 1953, with female *Renocila kohnoi* Bunkley-Williams & Williams, 1987, attached to the caudal peduncle from Ishigaki Island, Japan. Image © Lucy Bunkley-Williams

Fig. 5.8 The most spectacular Caribbean *Anilocra* Leach, 1818, is this black female *Anilocra holacanthi* Williams & Williams, 1981, on the yellow face of the rock beauty, *Holacanthus tricolor* (Bloch, 1795). There are two micro-males just anterior to the female. Image © Lucy Bunkley-Williams (taken at the insular shelf edge off La Parguera, Puerto Rico)

(see below) are much smaller (1–3 mm) and highly mobile ectoparasites on marine and estuarine fishes (Smit and Davies 2004; Tanaka 2007). Fish gnats are not true parasites but serial parasites. Four other families have been variously stated to have parasitic species. No cirolanids are parasites, some corallanids may be parasites (Gentil-Vasconcelos and Tavares-Dias 2015), and, very likely, some salve bugs (Aegidae) and nasal isopods* (Tridentellidae) are parasites (e.g. Bruce and Wong 2015).

The life cycles of fish-associated isopods and fish gnats are so completely different that their sharing a superfamily seems incongruous. Fish-associated isopods are permanently parasitic as adults and fish gnats only as juveniles. Fish-associated isopods hold their eggs in a marsupium and fish gnats in pouches in the female body. Fish-associated isopods attach with their pereopods and fish gnats by their mouthparts.

5.11.2.1 Corallanidae: Serial Fish Isopods*

We have collected these isopods on fishes but have not considered them to be *true parasites*, because so little is known about their associations. Some species do feed on fish blood.

Gentil-Vasconcelos and Tavares-Dias (2015) considered *Excorallana berbicensis* Boone, 1919, to be a parasite of South America freshwater fishes and *E. tricornis* (Hansen, 1890) a facultative parasite of many marine fishes. They may be correct about *E. berbicensis*, but we are not ready to accept *E. tricornis* as a true parasite (Bunkley-Williams and Williams 1998a). We would call it a serial parasite. Very little is known about any life cycles of *Excorallana* Stebbing, 1904.

5.11.2.2 Cymothoidae: Fish Isopods*

The most famous cymothoid is the so-called tongue-replacement isopod (Brusca and Gilligan 1983), which was also featured as the monsters in the horror movie 'The Bay' (2012).

Fish isopods may cause some problems in aquaculture (Williams 1974; Woo 2006). They drastically affected fisheries in a large lake in Egypt (Mahmoud et al. 2017). Juveniles may kill juvenile fishes, and adults may seriously stunt and slow the growth of hosts (Bunkley-Williams and Williams 1998a; Mladineo 2003). Fish isopods have also been shown to increase swimming drag and metabolic demand of their hosts (Östlund-Nilsson et al. 2005).

More than 369 species of fish isopods exist in 43 genera (see Chap. 3). They occur in and on fishes around the world, but mostly in the tropics and subtropics, in coastal waters, with some in freshwaters largely in South America with a few species in Africa and Asia (Bunkley-Williams and Williams 1998a; Smit et al. 2014), and even the deep ocean (Quattrini and Demopoulos 2016; Williams and Bunkley-Williams 2003). Some almost complete life cycles are known (e.g. Williams and Bunkley-Williams 1994; Aneesh et al. 2015).

Klompmaker and Boxshall (2015) listed many fossil fish parasitic isopods but dismissed all due to insufficient evidence. Nagler et al. (2017) claimed the oldest fossil parasitic isopod based on sucking mouthparts and legs suited for attachment, but these could be just as indicative of a *minipredator*. We are also in the process of describing a parasitic fossil isopod (Williams and Bunkley-Williams 2008, unpublished data), which may prove equally disputable.

Life Cycle

Fish isopods may go through four parasitological life cycle stages: free-living, *smaller**, serial parasite, and true parasite (see Table 5.1). Brood pouch development may include egg, oblong embryo *predator*, curled embryo with enlarged cephalic end and tapered posterior, uneyed embryo, eyed embryo, pre-manca, and manca juvenile (Williams and Williams 1985a, b). Embryology is often neglected in species descriptions and even in life cycle studies. Embryos in brood pouches number from 37 to 1600 (Adlard and Lester 1995) but are usually in the low to mid-hundreds. Larger and older supra-females have more offspring. Although some brood mortality is expected, Bakenhaster et al. (2006) found none in *Glossobius hemiramphi* Williams & Williams, 1985.

Pre-manca in the marsupium of some species are larvae. Mancae in, and escaping from, the marsupium are juveniles. To avoid confusion, we here refer to this as a *manca juvenile**. Once the manca juvenile begins to form the seventh pair of legs in 1–4 moults, we consider these instars juveniles. The few juvenile stages that we know spend the daytime in the surface plankton. They descend at night, finding transfer or definitive hosts. The first to settle on a definitive host develops through the male stage and directly into a female. The second becomes a male. This was the traditional infective assumption based on little data. However, they may actually be infected by *founder pairs*.

Mladineo and Valic (2002) and Mladineo (2003) found only two *Ceratothoa oestroides* (Risso, 1816) *manca* infected each annular sea bream even when more mancae were available. They attached to the fish body and migrated under the operculum, rather than being swallowed as previously suspected (e.g. Bunkley-Williams and Williams 1998a).

Supposedly, a few complete life cycles of fish isopod are known, but none are complete. First, a natural release of mancae has only been closely observed once (Williams and Williams 1985c). A female on a brown chromis in a coral reef reared her posterior from the surface of the host and released a juvenile from the rear of her marsupium, slowly lowered back down, and reared up again to release another. This process was slowly and methodically repeated, although the complete release was not observed. Adlard and Lester (1995) found it took 1–3 h in the lab. The juveniles swam upwards towards the surface. Some authors have mistaken our *burst release* (Williams and Williams 1985c) with the normal release process. Burst release occurs when a host is caught or struck. All juveniles are released at once even if they are not quite mature (pre-manca and manca; Williams and Williams 1985c). Adlard and Lester (1995) caused this response in the lab with pressure on the dorsal surface of a female and found it took 1–2 min.

The second problem with most 'complete' life cycles is they do not include the free-swimming juvenile stages. We have found up to six stages (Williams and Bunkley-Williams 1994; and see below). The fish isopod manca juvenile has six pairs of legs. Most manca juveniles are much more setose than later juvenile stages. The final juvenile has seven pairs of legs. Intermediate juveniles may have 6.25-, 6.5-, and/or 6.75-leg pairs. Some suggest escaping mancae require a free-swimming period before they can attach to hosts; however, Thatcher (2000) found they were ready to attach to fishes as soon as they left the brood pouch, and Williams and Williams (1985c) reported that *Anilocra chromis* Williams & Williams, 1981, and *Cymothoa oestrum* (Linnaeus, 1758) could attach immediately. Large samples of all post-manca juvenile stages (*C. oestrum*) have only been examined by Williams and Bunkley-Williams (1994). Juveniles are positively phototaxic and can be captured in light traps at night. They swim to the surface light when released from the female. They can also be captured with surface plankton nets during the day. They thus appear to avoid the diurnal planktivores on the reef. Adlard and Lester (1995) found they rested at the surface of the water with their hooks (dactyls) through the day, but this was demonstrated in aquaria and not in the field. They descend back to the reef at night and can be caught near the bottom with diver-towed plankton nets. Some have suggested juveniles must feed within 1–2 days to survive (Lester 2005). However, manca juveniles, unfed, for more than a week, are still capable of infecting hosts. Adlard and Lester (1995) reported that only half of the mancae were infective after 8 days. Juveniles of *Glossobius hemiramphi* and *Livoneca ovalis* (Say, 1818) use resting hosts before locating their final hosts. Cook and Munguia (2015) found mancae of *Cymothoa excisa* Perty, 1833 had a window of 7 days to infect hosts. Juveniles of *L. ovalis* are micro-males since an adult male has never been found. Resting hosts are commonly used by many species (Thatcher 2000) and may be a part of the normal life cycle. This predisposes them to becoming micro-males.

Thatcher (2000) described an interesting life cycle strategy. A manca juvenile swimming right-side up (dorsal up), stops swimming, falls to the bottom landing up-side-down (ventral up), and does not move. When a small fish comes near to investigate or eat it, the manca springs to life and attaches to the hapless fish. The isopod now has either a resting host to feed on or a final host on which to mature. This 'dead bug' or 'playing opossum' behaviour, we will call the *opossum attack**. Thatcher (2000) found mancae could feed on and kill up to four small fishes in 24 h. This behaviour was in freshwater isopods.

Mancae attach all over the body of the host and move to the normal attachment site (Adlard and Lester 1995) as we have seen (Williams and Bunkley-Williams unpublished data). Legrand (1952) suggested mancae of *Anilocra physoides* (Linnaeus, 1758) were attracted to the motion of fish fins. Some mancae fall off when they attempt to move to the normal attachment site (Williams and Bunkley-Williams unpublished data). Cook and Munguia (2015) found that manca of *Cymothoa excisa* located hosts by visual and chemical clues.

The number of juvenile moults have not been determined for most species; however, Williams and Bunkley-Williams (1994) reported finding six post-manca juveniles in *Cymothoa oestrum* (Fig. 5.9). A juvenile attaches to a host and begins to

Fig. 5.9 Superinfection of juvenile *Cymothoa oestrum* (Linnaeus, 1758) on a Crevalle Jack, *Caranx hippos* (Linnaeus, 1766), incapacitated in a fish trap on Mona Island, Puerto Rico. Image © Lucy Bunkley-Williams

develop through a series of instars: juvenile-male transitional, immature male, male, male-female transitional, immature female, virgin female (no oostegites), and ovigerous female. The second juvenile that arrives will cease developing and remain as a male, with development hormonally controlled by the female. If the female dies, the associated male resumes developing into a female. *Anilocra* Leach, 1818, juveniles replace solitary dead females. Williams and Bunkley-Williams (unpublished data) have often seen a juvenile attached in the attachment scar where a female was formerly located. Micro-males may be attracted to dying females and begin to develop into females protected underneath the 'cougar' (old female). Williams and Bunkley-Williams (unpublished data) have reared juvenile *Anilocra haemuli* Williams and Williams, 1981, to females and *A. chromis* to male-female transitionals, on their natural hosts, in the lab.

Adlard and Lester (1995) found *Anilocra pomacentri* Bruce, 1987, recruited from July to December, with a peak in September to October, at Heron Island, Great Barrier Reef. They never saw males with females despite intense efforts in the field and laboratory. One of their hypothetical scenarios is essentially our micro-male life cycle.

Aneesh et al. (2015) gave the 'complete' life cycle for *Cymothoa frontalis* Milne Edwards, 1840. However, they have the same problems discussed above: (1) omitting how the manca are naturally released (*demarsupiation*) and (2) omitting the number of free-swimming juvenile stages. They did recognise six female stages.

However, their stages Fs-1 to Fs-3 appear to be within the first female instar, which is confusing. Furthermore, size alone does not determine supra-stages or instars (see *size* discussion below). Their Fs-4 would be our *vegetative* supra-female* (Sf-2). Their Fs-5 to Fs-6 would be the second marsupial stage (Sf-3). Overall, this does agree with our assertation that females have more than one brood with feeding vegetative stages in between. However, we think most fish isopods have more than two broods.

When all brown chromis hosts with *Anilocra chromis* on seven 100 m segments of a linear coral reef were eliminated, and recovery followed for a year, the hosts recruited evenly from the plankton, but the isopod recruitment was significantly higher on the ends of the linear reef adjacent to areas still populated with isopods. The same result was obtained in a subsequent year (Williams and Bunkley-Williams unpublished data). Thus, the swimming juvenile stages only appear to disperse over very short distances.

Further Life History

Several studies on cymothoid-host associations have examined impacts of *Anilocra* on components of host fitness (reviewed in Chap. 10). Adlard and Lester (1995) found that *Anilocra pomacentri* reproductively compromised its female host. Fogelman et al. (2009) found *A. apogonae* sterilised its female host. Other studies have shown an apparent effect of cymothoid infection on drag associated with swimming (Östlund-Nilsson et al. 2005), and oxygen consumption (e.g. Binning et al. 2013), and on host movement and migration (Meadows and Meadows 2002; Welicky and Sikkel 2015). Brown chromis males infected with *Anilocra chromis* appear unable to maintain a spawning site (Williams and Bunkley-Williams unpublished data). Contrastingly, Meadows and Meadows (2002) and Robinson (2005) found little to no effect on host mating success or fecundity.

A tenet in the strategy of fish isopod infection has always been that the first manca juvenile to arrive becomes a female and the second remains a male (*epigametic sex determination*). Mladineo and Valic (2002) and Mladineo (2003) found a pair of *Ceratothoa oestroides* manca juveniles became established simultaneously together in the mouth of a host and excluded all other mancae. Aneesh et al. (2015) found something similar with *Cymothoa frontalis*. Possibly almost all fish isopod juveniles infect hosts in juvenile pairs, which we will call *founder pairs**. This may change all cymothoid infection methods.

Life strategies sometimes consistently 'deposit' the male and the female of a pair on different sides of a host. Williams and Williams (1982) have described these *duplex arrangements* for males and females in opposite gill chambers and on different sides of a fish caudal peduncle (Williams and Williams 1987). This allows space for larger females and larger brood pouches, allows smaller fishes to be parasitised (Williams and Williams 1982), prevents *double parasitism*, and separates areas of isopod feeding and damage. Female hormonal fixing of their male appears to remain intact over these distances. Thatcher (2000) found this arrangement with *Anphira xinguensis* Thatcher, 1995, in the gill chambers of the beaked pacu.

Occasionally, site-specific isopods are found in a different location on their hosts, and they do not migrate to their normal site. When these parasites are kept from their site because of preoccupation, we call them *displaced parasites**; when their normal sites are available, we say they are *accidental attachments**. For example, we have seen normally under-eye *Anilocra* attach above the eye or on top of the head when both of their normal sites were occupied. These are the normal attachment sites for other species of isopods and may help to explain how utilisation of different sites evolved. We found 13 longsnout bullhead sculpins*, most with female *Elthusa* sp. isopods in their gill chambers and males underneath the females. However, we also found three males, of the same size and species, attached in two of the same hosts on the body near the opercular openings (Fig. 5.10). The evolution of gill-dwelling isopods into external attaching isopods has been previously hypothesised (Brusca 1981) but never demonstrated. These normal female-male gill-chamber-dwelling isopods with externally attaching cohorts represent the first ever observation of an example of this event (Fig. 5.10).

When two reproductive sets of the same species occupy the same host, when normally only a single set occurs, we call it *double parasitism*. This often occurs with the micro-male life cycle. It is common in *Anilocra chaetodontis* Williams & Williams, 1981, but less so in other *Anilocra* spp. We found it was detrimental with *A. brillae* Welicky, Hadfield, Sikkel & Smit, 2017 on red hinds and coneys, and with *Livoneca redmanii* Leach, 1818 in Cero (Williams and Bunkley-Williams unpublished data). It is rare in gill-chamber isopods, and, of course cannot occur in oral cavity ones. The *duplex arrangement* also prevents this situation.

As is typical of isopods generally, adult females continue to grow and moult on the host. Older, larger females can be quite different morphologically from males and immature females (supra-*females*, Bunkley-Williams and Williams 2003). These differences have caused many taxonomic problems. Adult females moult on the host in two parts. This is probably necessary to have some hardening of the pereopods to maintain attachment on the host. We have seen this many times on *Anilocra* spp. where the posterior part is shed usually posterior to the 3rd pereon,

Fig. 5.10 Normally gill-dwelling *Elthusa* Schioedte & Meinert, 1884, attached externally under pectoral fin and near the gill openings on longsnout bullhead sculpins, *Ereunias grallator* Jordan & Snyder, 1901, in Japan. Image © Lucy Bunkley-Williams

sometimes the 4th. There must be a considerable delay between moult halves, or we would have never seen so many. We call these *mid-moult stages*. The delay allows the new hooks (dactyls) to harden before the last anterior segments are shed. We have seen mid-moult stages with a large posterior body and a much smaller anterior body (Williams and Bunkley-Williams unpublished data). We have also seen mid-moult stages in four wild *Cymothoa oestrum* juveniles (Williams and Bunkley-Williams 1994).

Discerning the different juvenile stages of cymothoids is most difficult. Mid-moult specimens clearly mark the lower size range of each juvenile stage. When enough specimens exist to find mid-moults, the complete juvenile life cycle can be discerned. Four mid-moults in *C. oestrum* allowed us to discern six post-manca juvenile stages (Williams and Bunkley-Williams 1994; Williams and Bunkley-Williams unpublished data). As far as we are aware, this is first time all juvenile stages have been identified in the wild.

Post-juvenile mid-moults allow the elucidation of what changed in the moult and to positively identify instars. Some supra-females regain their marsupium in one moult. Spectacular, mid-moult stage half-female/half-male forms have been observed (Williams and Bunkley-Williams unpublished data), as have supra-females with half formed marsupiums, indicating two moults are needed to form a marsupium (Williams and Bunkley-Williams unpublished data). As noted above, isopod effects on hosts often cannot be measured with fish condition factors. We studied 120 specimens (85 infected) of doctorfish with 0–8 specimens of two species of adult isopods and noted there was no difference in condition factors (Williams and Bunkley-Williams unpublished data). The isopods cause the host to grow more slowly, but they remain proportional (*proportional stunting*). Östlund-Nilsson et al. (2005) also found no conditional factor difference and summarised the literature on this topic. A male-female pair of *Livoneca redmanii* in each gill chamber of mackerel will cause a decline in condition factor and often kills the host (Williams and Bunkley-Williams 1996). Lanzing and O’Connor (1975) also found host condition was only reduced in multiple isopod infections. However, Robinson (2005) found a reduced condition in bicolor damselfish infected with single *Anilocra partiti* Williams & Williams, 1981 females, and Sala-Bonzano et al. (2012) found no condition factor effect of *Ceratothoa italica* Schioedte & Meinert, 1883, on sand steenbras in a protected area, but severe effects in a similar overfished (unprotected) area. The prevalence of infection was also different (30 vs 47%, respectively). Obviously, the life cycle success rate was improved by stresses on the host, particularly when the lower abundance of host specimens should have had the opposite effect.

The sizes of gill- and mouth-dwelling cymothoids are closely correlated with their host size due to space constraints; externally attaching ones are slightly less coordinated. However, isopod and host sizes are related suggesting they grow simultaneously. This also suggests most hosts are infected young, by young parasites, and the host and parasite grow up together.

Some have suggested that females only have one brood and others that they have one brood immediately after another. In many cases, the so-called virgin female (no oostegites) was the largest of the female specimens collected (Williams and

Williams 1982, 1986a). Obviously, these females are in a feeding (*vegetative*) stage between broods. The number of adult moults and their morphological stages are not known for any cymothoid. However, Aneesh et al. (2015) found six adult female stages corresponding to two of our supra-females, including a vegetative one (see above).

Adlard and Lester (1995) found spent (*demarsupiated*) females could moult, feed, rejuvenate, and lay new eggs, all in one instar. No intervening vegetative instar was necessary. Evidence exists to support two life cycle portions in these fish isopods: simple and complex rebrooding. *Simple rebrooding** with relatively small brood sizes, where the female internal organs are only flattened by the marsupium, not atrophied, and no vegetative moult is necessary to re-establish feeding. *Complex rebrooding** with large brood sizes, where female internal organs are atrophied, a moult to a vegetative supra-female is necessary to re-establish feeding, and a second moult is necessary to re-establish a supra-female with a marsupium. Simple rebrooding is more economical and faster but limited numerically in offspring. Complex rebrooding is slower and uses more resources but produces many more offspring. Adlard and Lester (1995) found simple rebrooding in an external-attaching isopod. Williams and Williams (1982) found complex rebrooding in a gill chamber-dwelling isopod, Williams and Williams (1986a) in an externally attaching isopod, and Aneesh et al. (2015) in a buccal cavity-dwelling isopod. Isopods producing larger broods may require the energy resources afforded by vegetative supra-female instars. Of course, many other, undiscovered, reproduction scenarios probably exist.

External isopods do not live as long as their hosts, as evidenced by empty attachment scars. Additionally, some isopods become covered with encrusting organisms. These are likely old isopods which have ceased moulting and are about to die.

Bakenhaster et al. (2006) found that *Glossobius hemiramphi* live for a year in south Florida (USA). Adlard and Lester (1995) found *Anilocra pomacentri* lived for a maximum of 13.5 months. Bakenhaster et al. (2006) found monthly 4.6–18.2% (ave. 10.1%) prevalence throughout a year, in 2928 ballyhoo with the highest prevalences in the summer, with small, young-of-the-year hosts. With larger hosts, the prevalence exponentially declined.

Adlard and Lester (1995) found *Anilocra pomacentri* changed the behaviour of the Great Barrier Reef chromis making them not migrate with uninfected cohorts. We (Williams and Bunkley-Williams unpublished data) observed a similar phenomenon in brown chromis infected with *Anilocra chromis*. The infected adults stay under coral heads with the juvenile brown chromis, while the uninfected adults go out above the reef slope to feed on plankton. Meadows and Meadows (2002) similarly found foureye butterflyfish infected with *Anilocra chaetodontis* stayed in low-energy areas where their offspring were more available to young potential hosts. The diel migratory reef fish, French grunt, usually migrates from reef to seagrass habitat at dusk. Those infected with *Anilocra haemuli* were less likely to migrate than their uninfected schoolmates (Welicky and Sikkel 2015).

Adlard and Lester (1995) interpreted this as a depression of the host reproductive response to move to spawning areas on the reef slope. We interpret the observed behaviour of brown chromis to be because the infected adults cannot feed and survive in open waters (Williams and Bunkley-Williams unpublished data). Meadows and Meadows (2002) suspected this was also a host behavioural change caused by the isopod. Welicky and Sikkel (2015) were not certain if infected fish had less energy to migrate or if uninfected cohorts harassed them. However, all four behaviour modifications, caused by the isopods, accomplished the same availability of manca juveniles to infect juvenile and young fishes. We will call this effect *nursery hiding*. These are newly recognised life cycle innovations caused by parasite modification of its host behaviour.

New Life Cycle: Micro-male Life Cycle

Among the nine species of *Anilocra* described by Williams and Williams (1981) and two from Japan (Williams and Williams 1986a), no males have been reported. After juveniles were found in apparent copula with females, we assumed that juveniles were functioning as males. To test this assumption, individual juveniles were raised on their host, periodically preserved, sectioned, and stained. The infective, 6-leg juvenile was a functional male as were all intermediates up to and including the 7-leg juvenile. However, as soon as a juvenile began to obtain an adult shape (juvenile-male transitional), it began to lose its male characters. Only juveniles were reproductive males. This resolved the 'mystery of missing males'. We refer to this reproductive juvenile as a *micro-male*. Juveniles with full male characters have been found in several species, but these have never been suspected to be sexually active. Many species are known to use paratenic hosts (Thatcher 2000; Bakenhaster et al. 2006), which may predispose them to becoming micro-males.

Six-legged manca juveniles are released from the marsupium (Williams and Williams 1985c), swim to the surface in the daytime, and descend near the bottom at night. They find small hosts, which do not go to cleaner fish or shrimp (blennies, gobies, cardinalfishes), attach, feed, and moult once, or several times, into 7-legged juveniles. In off-reef areas in Venezuela, these juveniles were found on adult glasseye (Bunkley-Williams et al. 2006). They may sense the pheromones of receptive females, leave this *micro-male host*, swim to the female, crawl under her, and mate belly-to-belly. We have observed them in copula and found a semen string when they were separated. They may hide under the female either before or after copulation, return to their *micro-male host*, or find another small host. They may eventually locate a juvenile of their definitive host and develop into a female as their host develops. No adult male stage exists. Juveniles develop directly into juvenile-female transitionals, immature females, and females.

We sometimes found juveniles under females or very close to females on the final host, but usually we found them on cardinalfishes, gobies, and other small fishes (Williams and Bunkley-Williams unpublished data). Adlard and Lester (1995) found *Anilocra pomacentri* juveniles on the final host, blennies, and cardinalfishes. They apparently spend most of their time attached and feeding on resting hosts and only visit the female to mate.

This life cycle is unique, not just among isopods, but in parasites in general. We are not aware of anything similar. It is a modification of juveniles on resting hosts probably driven by cleaner pressure. It seems to be widespread and highly successful.

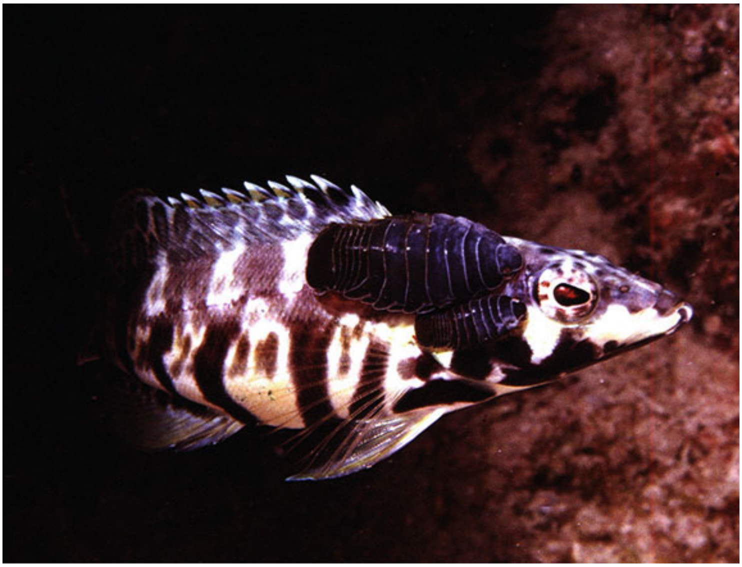

Fig. 5.11 Female-male pair of *Renocila bowmani* Williams & Bunkley-Williams, 1980, on harlequin bass, *Serranus tigrinus* (Bloch, 1790), in the Dominican Republic. Image © Lucy Bunkley-Williams

While we have not seen males associated with many other *Anilocra*, some *Anilocra* do have associated males. Possibly, this life cycle and other host specificity differences will place the micro-male *Anilocra* in a different genus. We are exploring this possibility. Other cymothoids share this life cycle, e.g. *Livoneca ovalis* (Williams and Bunkley-Williams unpublished data), *Anilocra apogonae* (see Fogelman and Grutter 2008), and *A. pomacentri* (see Adlard and Lester 1995).

The advantages of this live cycle have allowed *Anilocra* spp. to be the only large, external cymothoid isopod of larger Caribbean coral reef fishes (Fig. 5.8). *Nerocila* spp. occur around but are unable to penetrate any distance into the Caribbean (Bunkley-Williams et al. 1998; Bunkley-Williams and Williams 1999); and *Renocila* spp. only infect a few small species (Fig. 5.11; Williams and Williams 1980). The apparent advantages of this life cycle include the following:

1. It allows the female to grow larger on the host because no resources are used by a male partner (Fig. 5.8).
2. Two females may be supported by a host, instead of a male-female pair (Fig. 5.11).
3. Larger females produce more offspring and two females twice as many.
4. It protects vulnerable juveniles from cleaners.
5. It produces greater genetic diversity as many micro-males are available at different times to fertilise each female, instead of one permanent male partner.

6. The abundance and close proximity of numerous micro-males solve the problem of finding a mate.
7. Micro-males form a quick reserve available for developing new females.
8. Micro-males become sexually mature quicker than true males.
9. The energy necessary for a female to hormonally control a male partner is unnecessary.
10. Larger-growing females quickly become too large for cleaner organisms to threaten.
11. Micro-males can parasitise smaller hosts that do not seek out cleaner organisms.
12. Micro-males can easily change host specimens and/or species and are thus more flexible and resilient.
13. Micro-males could potentially use up the resources of one host and just move to another with little effort or danger.
14. The lack of host specificity in micro-males allows them to exploit a broader and more available food supply and to be more flexible and resilient.
15. The time a planktonic reproductive form has to locate a final host is almost infinitely extended by being able to exploit a broad range of more available smaller fishes.
16. Copulation while on the outside of a fish host is easier and safer with a tiny micro-male than with a larger and more bulky ‘true’ male.
17. This life cycle also resolves the classic question of the expense of sexual reproduction, since all adults produce eggs.
18. It maintains, or even multiplies, the advantage of diversity in sexual reproduction while not sacrificing the productivity advantage of asexual reproduction.

New Life Cycle: Prey-Predator Transfer Life Cycle*

Many intriguing questions regarding the cymothoid life cycle still exist. These include the following: how can little, slow, juvenile fish isopods (cymothoids) possibly chase and infect fast-swimming pelagic fishes? Why do juvenile isopods infect and develop into non-swimming forms in the mouths of fishes too small for them to develop into adults? Juvenile isopods may not chase large, fast hosts, but rather rest and wait for small, slow ones. Are little hosts dead-ends or ‘bait’?

Apparent prey-to-predator transfer has been observed in king mackerel (Williams and Bunkley-Williams 1994), shortfin smooth lanternshark (Williams et al. 2010), and red lionfish (Aguilar-Perera et al. 2018). Connors et al. (2008, 2011) experimentally showed sea lice would abandon their host, when it was attacked by a predator (~70% of the time), and reattach to the predator.

Juvenile isopods infect the mouths of common, small, easily infected, ‘bait’ fishes. They feed and pass through moults from the 6-leg juvenile to a post-juvenile, non-swimming stage on this transfer host. At any point during this development, if the host is eaten by a predator, they flee their (prey) host and attach in the mouth of the predator host (final host). The first isopod to arrive becomes the female and the second a male, as was once thought to happen in all other cymothoids (Mladineo and Valic 2002; Mladineo 2003; Aneesh et al. 2015).

Isopods in trap, net, and trawl fisheries are well documented to frequently abandon their host and sometimes enter a different fish host. Three cases of natural prey-to-predator isopod transfers have been described (Williams and Bunkley-Williams 1994; Williams et al. 2010; Aguilar-Perera et al. 2018), and adult and juvenile isopods have successfully, experimentally, been transferred between the same and different host species (e.g. Williams et al. 1982). The attack of a predator or its feeding action may dislodge an isopod from a transfer host or the isopod may abandon the host. Swallowing a single prey fish may be too fast for a transfer, but with a mouthful of prey fishes, adequate time may exist for a transfer. All transfers need not be successful, just enough.

Cymothoa spp. are quite common (~5%) in the two most abundant bait fishes in the Caribbean and in five small species of cardinalfishes in Okinawa. Can all these juveniles be 'wasted' in dead-end hosts? They cannot develop into adults in these small fishes, and they can no longer swim. We have collected these juveniles from the plankton and found they attach to any available fish in aquarium experiments. Is this a desperate survival mechanism or something more? We have described *burst release* (Williams and Williams 1985c), which is female isopods reacting to predator attack by dumping, and thus saving all her juveniles in her marsupium. These juveniles immediately attach to anything including humans. If juveniles react this way to attack, and adults are known to switch hosts, why would juveniles in a prey host not transfer to a predator?

In field experiments, we found juvenile isopods first attached all over host fishes and then crawled to their adult positions. Transferring juveniles could attach anywhere in the mouth or throat of predators and then crawl to their adult position. In contrast, adult transfers attach wherever they can and do not migrate (Williams and Bunkley-Williams 1994; Williams et al. 2010; Aguilar-Perera et al. 2018).

Infecting small, slow-swimming, schooling, abundant fishes seems rather easy as evidenced by ~5% success rate. Infecting fast-swimming, pelagic fishes seems almost impossible. We have observed many diverse cases where the isopods appeared to slow down their hosts and make them more susceptible to predation. In this case, it is a benefit for the completion of the parasitic life cycle and another form of a parasite modifying the behaviour of its host.

The proposed life cycle occurs in *Cymothoa* spp. and *Livoneca ovalis* and may also occur in others. It may also occur as a supplemental life cycle to isopods that also have normal life cycles and could explain some of their unusual hosts. Isopods of most predacious fishes infect juvenile hosts and mature with them. Only a few older host specimens are infected. These could have been parasitised by prey-predator transfer.

This life cycle is unique, not just among isopods, but in parasites in general. We are not aware of anything similar, although Pascual et al. (2002) reported an accidental prey-predator transfer in decapod isopods. The transfers may have begun as accidents and then gradually evolved into an important pathway. This allowed isopods to infect a variety of hosts that they could not have possibly otherwise reached.

5.11.2.3 Gnathiidae: Fish Gnats*

Fish gnats are small (1–3 mm) ectoparasites on marine and estuarine fishes (Smit and Davies 2004; Tanaka 2007). As protelean parasites, they are only parasitic as juveniles and, due to their typically brief associations with hosts, may best be termed 'micropredators' (e.g. Lafferty and Kuris 2002). Fish gnats are perhaps best known as the main food of cleaner fishes on coral reefs (Grutter 1997).

Approximately 226 species of fish gnats (most in *Gnathia* Leach, 184) in 12 genera and a single family are known around the world from the marine shallows to the deep sea. They occur at all latitudes but are more diverse and abundant in the tropics. The study of fish gnats has had a 'split personality' until recently, with benthic ecologists studying the adults and parasitologists the juveniles. Only recently has the morphology of juveniles been included in the taxonomy (Hadfield et al. 2008; Farquharson et al. 2012). However, the life cycles of six species are known (Smit et al. 2003; Tanaka 2007; Hadfield et al. 2009; Hispano et al. 2014).

Life Cycle

Even the most basic life cycle of fish gnats has only very recently been discovered (Fig. 5.12; Smit and Davies 2004). Zuphea are the first juvenile stage of fish gnats that leave the female, find a host, gorge and swell up with blood, and become the second stage called 'praniza'. The praniza eventually drops off the host and finds a secluded place on the bottom to develop into the next zuphea (Z2). Z2 swims up, finds a host, and repeats the cycle (P2). Zuphea feeding times vary from a few hours to a few days with Z3s taking the longest. They can be as short as an hour on coral reef fishes. Zuphea may attack, feed off (snack*), and kill larval or juvenile fishes as *smaller predators**. Eventually, P3 moults into an adult (Fig. 5.12). In some species, in genera *Elaphognathia* Monod, 1926, *Gnathia*, and *Paragnathia* Omer-Cooper & Omer-Cooper, 1916, this occurs in one moult. In one species in genus *Caecognathia* Dollfus, 1901, the first moult results in a pre-adult, which later moults into an adult. We call these feeding and metamorphing units *serial parasites*, which is somewhat similar to the life cycle found in ticks (arachnids). Praniza may only stay on bony fishes for a few hours but on sharks and rays for weeks. Complete life cycles vary from short to lengthy, directly in relation to seawater temperature: polar (~4–5 years), temperate (~2 years males, ~1 year females), and tropical (~2 months) (Smit et al. 2003). Life cycle fluctuations appear to be seasonal in most species but could be dependent on host availability in some. Adults are benthic, nonfeeding, and *semelparous*.

Global warming could make them more successful and more damaging (Hispano et al. 2014). Some Z1 have mouthparts too small to swallow blood cells and must feed on lymph. At Z2, they can feed on blood (Hispano et al. 2014).

Ota et al. (2012) appear to have solved the mystery of why P3 (praniza III) were only found on elasmobranchs. They collected hundreds of praniza I and II of *Gnathia trimaculata* Coetzee, Smit, Grutter, & Davies, 2009 on bony fishes (teleosts) and hundreds of praniza III only on sharks. This host switch seems to be the life

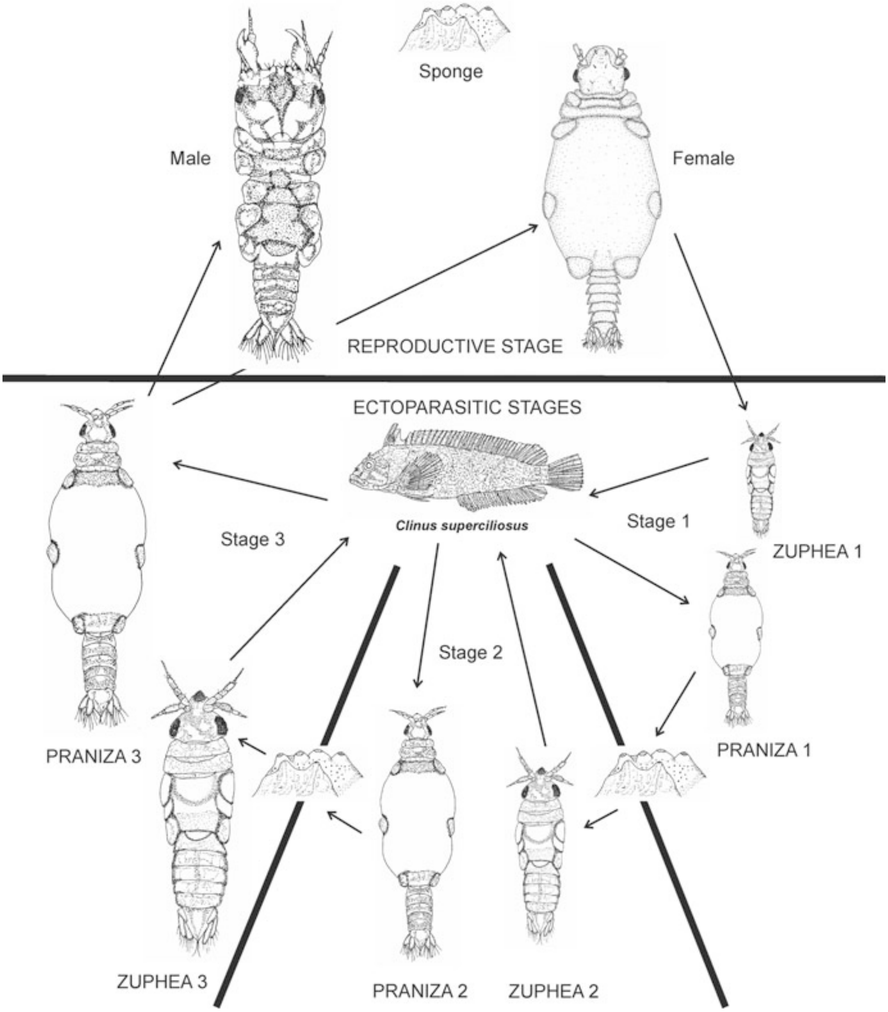

Fig. 5.12 Schematic representation of the life cycle and life stages of *Gnathia africana* Barnard, 1914 on its host fish, *Clinus superciliosus* (Linnaeus, 1758). Image from Smit et al. (2003)

strategy of all fish gnats so far found on sharks and rays. Praniza III takes the most time to feed. Attaching to an elasmobranch protects this stage from cleaners.

Several recent studies on Australian and Caribbean recently settled, larval, coral reef fishes found gnathiid micropredation [= our *smaller predator*] damaged and/or killed them (Artim et al. 2015, and references therein). This can have great importance in fish recruitment (Artim et al. 2015). Sikkel et al. (2017) suggested gnathiids are *micropredators* [= our *minipredators**] but act like parasites by not leaving the host during each larval life cycle instar (*protelean*).

Fish gnats are also implicated in the spread of a parasitic protozoa such as *Haemogregarina bigemina* Laveran & Mesnil, 1901, between hosts (Smit and Davies 2004). Juvenile fish gnats on fishes often cannot be identified morphologically as the taxonomy is based on adult males, although this is beginning to change in recent studies (Jones et al. 2008). Fish gnats on coral reefs appear most active at night (Sikkel et al. 2006), although this may not be the case in other environments. At least in the eastern Caribbean, diel activity appears to be related to both life history stage and sex (Sikkel et al. 2006). Fish gnats appear to be generalists. They are known to parasitise 61 families in 18 orders of fishes; however, some fishes are infected more often and more heavily (Tanaka 2007; Coile et al. 2014). This could be attributable to some combination of preference, host susceptibility, and/or host behaviour. Fish gnats may even appear on pelagic fishes (Williams and Bunkley-Williams 1996). For example, amberjack (Carangidae), which fed near the bottom, have been infected with fish gnats, and fish species which did not feed near the bottom were free of gnathiids (Williams and Bunkley-Williams unpublished data). Coile et al. (2014) found fish gnats, which fed on more susceptible hosts, produced larger, presumably more successful offspring.

Fish gnats can attach all over the body of fishes. Smit et al. (2003) suggested where they first attach is where they stay. Some studies suggested site preferences, but whether this is by selective settlement or migration is unknown. Fish gnats are repelled from the skin of toxic gobies by their poison glands but do attach to their fins. It seems likely that they also avoid the toxic skin of trunkfishes (ostraciids, fishkill toxin) and also puffers (tetraodontids, fugu toxin).

Further Life History

Adult fish gnats do not feed. Males attract females, usually young females with pheromones, and there are some reports of males defending or acquiring harems of females (Smit and Davies 2004). In reality, of the few relationships known, in only two species have males been reported with many females. Males do appear to fight with the big, impressive, giant mandibles, at least not under lab conditions. Brood sizes vary from a few to almost 200 and may vary by female size and environmental conditions (Coile et al. 2014 and citations).

Additional Information

We suggested that another reason mudskippers leave the water during low tides was because fish gnats are concentrated in the remaining, small, tide pools (Williams et al. 2007). The small Atlantic cleaner gobies, with small mouths, swallow fish gnats whole. In contrast, the bigger, Indo-Pacific cleaner wrasses, with larger mouths, appear to bite them into pieces (Williams et al. 1996). Some of these cleaners selectively feed on larger gnathiids (Grutter 1997). With implications for our understanding of cleaning symbioses, cleaner fishes often do not eat the fish gnats that are not gorged with blood. Is this because the blood-swollen ones are more easily found? Or is this due to preference by cleaners for fish blood rather than gnats without blood?

*5.11.3 Epicaridea: Crustacean Isopods**

The category 'epicardeans' was formerly considered a suborder but is now an infraorder placed in suborder Cymothoida. It contains 704 described species of crab isopods and cryptic isopods. Crustacean isopods are almost unique in using crustaceans as their intermediate and final hosts, with the exception of a few corallanids and a cirolanid (Bruce pers. comm.).

Williams and Boyko (2012) call them *partial castrators* because reproduction is often not completely blocked. This is nutritional sterilisation, not hormonal sterilisation. Boyko and Williams (2016) reviewed the methods to find, collect, and preserve crustacean isopods.

5.11.3.1 Cryptoniscoidea: Cryptic Isopods*

Cryptic isopods are poorly studied, but interesting, with most of their species hyperparasitic on other isopods in their own order, or in parasitic barnacles (Fig. 5.5). They also parasitise a variety of free-living crustaceans. There are 146 species in 51 genera and nine families. They are of little commercial interest, except as potential hyperparasitic controls for other crustacean parasites.

Life Cycle

Adult female cryptic isopods usually have neither pereopods nor oostegites. Their epicaridian larvae must develop within the female since there is no marsupium. Her body ruptures to free the larvae. They find and attach to copepods, and their life cycle is the same as in decapod isopods, except the males stay in the cryptoniscus larval form.

Further Life History

Cryptic Isopoda are ecto-, meso-, or endoparasitic. Liriopsids are hyperparasites of parasitic barnacles and parasites of other symbiotic crustaceans. Lovrich et al. (2004) found *Liriopsis pygmaea* (Rathke, 1843) (Fig. 5.5) infected 36.5% of the externa on the parasitic barnacle, *Briarosaccus callosus* Boschma, 1930, parasitising false king crabs in Argentina. These were mostly (208 of 238) cryptonicus larva. This suggests to us that most of the infective larvae, even finding a correct host, fail to infect the host. Larvae were highly aggregated with 92.7% inside empty externae, suggesting these sites attracted cryptonici. Only a few early subadult females, late subadult, and one late subadult were found along with 18 adult females. Parasitic barnacles recovered from hyperparasitic sterilisation once the cryptic isopods died.

Cabiropsids, with 34 species, are parasitic on free-living isopods and hyperparasitic on other crustacean isopods. The family may also include a few parasites of cumaceans. Hemioniscids (barnacle isopods*), with eight species, are parasites of barnacles. Dajids (backpack isopods*), with 56 species, are external parasites of krill (euphausiids and mysids) and midwater shrimp; however, Ohtsuka et al. (2011) found an endoparasitic species alternate host sharing with a copepod (see copepod section above). The parasites look like backpacks on their hosts and are often mistaken as fleshy growths or tumours. A few occur in the gills. Cyproniscids, with 30 species, are hyperparasitic on parasitic barnacles (some formerly liriopsids), occasionally directly parasitic on decapod hosts, and parasites (hypersymbiotic) on symbiotic crustaceans. Podasconids (amphipod isopods*), with four species are parasites of amphipods. Asconiscids only have a single species parasitic on a mysid. Crinoniscids, with three species, also only have one species on a cirripede barnacle. They are parasitic on sessile and pedunculate thoracican barnacles. Entophilids, with two species, are endoparasitic in callianassid shrimp and munidid squat lobsters.

Other cryptic isopods, besides the one we found (Williams and Williams 1987), hyperparasitically infect the brood pouches of isopods. Stone and Heard (1989) found a new cryptic isopod in the serial fish isopod* *Excorallana delaneyi* Stone & Heard, 1989. Many species of cryptic isopods remain undescribed.

5.11.3.2 Bopyridae: Decapod Ectoparasitic Isopods*

There are more than 651 species of decapod isopods (Bopyroidea). Members of families Bopyridae and Ionidae cause a noticeable swelling of the gill chamber or carapace (Boyko and Williams 2016). The bulges they cause in the carapace of decapods make them among the most impressive and distinctive crustacean parasites. The deformities named *Kanthyloma crusta* Klompmaker, Artal, Van Bakel, Fraaije, & Jagt, 2014 (ichnotaxa—trace fossil evidence), date these parasites in the fossil record back to the lower Jurassic (182.7–174.1 million years ago; Klompmaker et al. 2014), and they have been found in ~92 species of fossil decapods (Klompmaker and Boxshall 2015). They slow the growth and *nutritionally sterilize* some commercially important crabs and can cause the collapse of a population but have also been used as bioindicators (Williams and Boyko 2012).

Life Cycle

Eggs develop into free-swimming larvae within a ventral brood pouch (marsupium) formed of lamellar outgrowths of the female pereopodal coxae (oostegites). Larvae of a single brood mature synchronously and are released simultaneously as microniscan larva (epicaridium, microniscus or microniscid). The microniscan attaches externally to a pelagc calanoid copepod, pierces its cuticle to feed on its blood, and undergoes six moults and becomes a cryptoniscan (cryptoniscus and cryptoniscid). When it drops off its copepod host, it seeks a crab or shrimp definitive host in the earliest post-larval stage. On the host, it develops into a juvenile (bopyridium) and then into a female. The first cryptoniscan arriving at a host becomes a female and the second, a male (epigametic sex determination). The female attracts a male with pheromones and hormonally controls it to remain a male similar to cymothoids. The female grows large, while the male remains a dwarf attached to the female.

Further Life History

They are ectoparasites. Females look nothing like isopods, except for some vague segmentation. Males look more like isopods. They attach in the branchial chamber of their hosts. Some adults do not moult to grow. Partial or complete sterilisation of hosts is due to energy loss from parasitic feeding, not hormonal control as in parasitic barnacles. It is temporary and reversible once the parasite is gone.

Williams and Boyko (2012) summarise the papers following the introduction of a nonindigenous decapod isopod, a drastic population decline of a mud shrimp, and possible collapse of a north-west Pacific ecosystem. Williams and Boyko (2016) found double parasitism of two species in the gills and abdomen of a specimen of hermit crab in Indonesia.

5.11.3.3 Ionidae: Ghost Shrimp Isopods

Only eight species are known and are ectoparasitic on the gills or under the abdomen of ghost shrimp. Similar to bopyrids, they cause a noticeable swelling of the gill cavities. In most respects, they are like the decapod ectoparasitic isopods (above).

5.11.3.4 Entoniscidae: Crab Mesoparasitic Isopods*

There are 40 species of crab mesoparasitic isopods. They are mesoparasites in the haemocoel of brachyuran and anomuran crabs. They make a small, chiselled hole through the host's exoskeleton to communicate with the environment.

Life Cycle

They release larvae, through an exit pore near the base of the fourth pereopods of the host, which follow the typical bopyrid life cycle. Apparently, this also involves a copepod intermediate host, and they presumably settle as cryptoniscid larvae in the branchial chamber and then penetrate their hosts. They first become endoparasitic and later mesoparasitic. However, their life cycle is poorly and incompletely known (Williams and Boyko 2012).

Further Life History

Females produce a posterior stalk that extends to the external environment of the host through the branchial region or eyestalks. As in bopyrids, females look nothing like isopods, except for some vague segmentation. Males look more typical. Some adults do not moult to grow. Partial or complete sterilisation of hosts is due to energy loss from parasitic feeding, not hormonal control as in parasitic barnacles.

Additional Information

They have been suggested as biological control agents for introduced crabs (Williams and Boyko 2012). Kuris et al. (2005) suggested *Portunion maenadis* (Giard, 1866) could be used as a biological control of the green crab.

Squid are intermediate hosts for marine anchor worms and have been reported to attract many forms of crustacean parasites accidentally. Pascual et al. (2002) surmised a prey-predator transfer of larval isopods when patagonian squid ate the intermediate host copepods. Their cryptoniscus larvae successfully penetrated and colonised the squid. They were entirely embedded in the oral bulb at the beginning of the oesophagus of two female squid. They suspected this was only accidental parasitism; however, this could represent a strategy for host switching, new resting host, or even eventual speciation. A shift of phyla in hosts is always of interest.

5.12 Tanaidacea: Tunnelling Tanaids*

Tanaids are a large, free-living group with only one species, *Exspina typica* Lang, 1968, often found in the intestine and body cavity of deep-sea holothurians, assumed to be a parasite (e.g., Kudinova-Pasternak 1987). Alvaro et al. (2011) confirmed it was a parasite. Many species associate with invertebrates and *Hexapleomera robusta* Moore, 1894, even with sea turtles and the Caribbean manatee from which we have collected it.

Life Cycle
Most are similar to fish cymothoid isopods with a free-swimming manca leaving from the marsupium. Two manca life cycle stages of one species were found in the gut of a deep-sea polychaete in the Florida Straits (Suárez-Morales et al. 2011). These stages are probably endoparasitic.

Further Life History
The adults show few modifications to a parasitic life. However, the full reduction of maxillule setation only occurs in *E. typica*, and the bifurcated and sharply tipped dactyli in the pereopods is probably a parasitic adaptation for anchoring the crustacean in the soft tissue of the host (Alvaro et al. 2011).

Additional Information
The unmodified life cycles would suggest a parasitic mode of life is in the early developmental stages. Many tanaidacean species make sand tunnels. This behaviour could have predisposed them to making tunnels in the body wall of holothurians.

5.13 Decapoda

Several families of shrimp are well known as associates of other invertebrates, notably sponges and corals, also bivalve molluscs and echinoderms. These species are generally categorised as *commensal* and not considered parasites as such. A review of these taxa is beyond the scope of the present work.

*5.13.1 Palaemonidae, Alpheidae, and Atyidae: Sponge Shrimps**

Shrimp that inhabit sponges are usually referred to as commensals largely because very little is known about their habits. Only a few parasitic species have been determined from two superfamilies; however, many more species are parasitic and probably not just in sponges.

Life Cycle

Small, *eusocial Synalpheus* Spence Bate, 1888, carry one to a few dozen large eggs that hatch directly into benthic juveniles (Duffy and Macdonald 1999). Large, male-paired *Synalpheus* sp. females release several hundred small, planktonically dispersing nauplii from a clutch (Duffy and Macdonald 1999). Eggs hatch into nauplii, which are feed on yolk reserves (*lecithotrophic* larvae), and metamorphose into zoeae. Zoeae feed on algae (*planktotrophic* larvae) and metamorphose into myses, which look like tiny adults, and feed on algae and zooplankton. The final instar is post-larvae.

Typton carneus Holthuis, 1951, form heterosexual pairs and exclude conspecifics and other shrimp (*negative precursor*). Duffy et al. (2000) found *Synalpheus regalis* Duffy, 1996, excluded heterospecific shrimp. He also demonstrated this species had a colony hierarchy with only one reproductive female and hundreds of helpers. This was the first case of *eusociality* noted in a marine animal. Six more, probably parasitic, species in the same genus have been found to practice eusociality. We suggest these are the first known *eusocial parasites**.

Hyperparasites

Williams and Boyko (2012: Fig. 1a) illustrated a crab isopod, probably *Bopyrella harmopleon* Bowman, 1956, on a sponge shrimp, *Synalpheus fritzmuelleri* Coutière, 1909, from Panama. This may be a *hyperparasite*, but we cannot be certain. We do not know if the shrimp was collected from a sponge and this shrimp species is not an obligate parasite. Anker (2016) published a photograph of a decapod isopod on *Synalpheus brevicarpus* (Herrick, 1891), which is definitely a hyperparasite. Several other species of sponge shrimp have hyperparasitic decapod isopods.

Additional Information

Duffy et al. (2000) showed that shrimp of the *Synalpheus gambarelloides* group, and *S. regalis*, in particular, were sponge parasites. Ďuriš et al. (2011) studied *Typton carneus* in Caribbean fire sponges in Belize and found it was parasitic. They also examined two other species of *Typton* Costa, 1844, and three species in three other genera of palaemonids (Pontoniinae) from the western and eastern Atlantic and Indo-Pacific and one alpheid from the Indo-Pacific and found them to be parasites. Their results suggested parasitism by sponge shrimp was widespread.

Zitzler and Cai (2006) reported the first obligate sponge shrimp*, *Caridina spongicola* Zitzler & Cai, 2006, in freshwater. This spectacularly coloured, now popular aquarium, shrimp infects an undescribed spongillinid sponge in an ancient lake in Indonesia. We believe it is also the first obligate parasitic sponge shrimp reported from freshwater. Zitzler and Cai (2006) only found diatoms in six shrimp stomachs and called them commensal. However, they have a life cycle like *eusocial* sponge shrimp [a few (12–18) black eggs directly develop and are released as immature adults with no planktonic phase]. Have numbers (up to 137/host) like eusocialists. We doubt diatoms alone would support any shrimp, much less this many. All marine obligate sponge shrimp, studied thus far, are parasitic.

5.13.2 Brachyura: True Crabs

True crabs do not make very good parasites. We would call them *semi-parasites* or *kleptoparasites*, at best. We believe this is because their basic adult structure is so very unsuited for parasitic adaption and modification. Coral gall and pea crab parasites have a long fossil record but remain low in diversity. Their life cycles also show no adaption for parasitism. They mostly steal their host's food, may slow host growth, but do little, if any, physical damage to the host. Many reside at the uneasy border between parasitism and commensalism.

We have seen indicators of the potential for the development of 'better' parasitism, for example, a superinfection of crab zoea living in the gills of a gray angelfish at Mona Island, Puerto Rico, and adult burrowing crabs living in the gill chambers and feeding on the gill filaments of two gray snappers in Colombia (Williams and Bunkley-Williams 1994). However, these examples were rare, in incapacitated hosts, and proved impossible to duplicate.

5.13.3 Cancroidea: Jelly Crabs

Jelly crabs benefit by their life cycles associating with gelatinous plankton through protection, transportation, food, and development faster in warmer waters and saving energy (Towanda and Thuesen 2006). Their relationships with their hosts are more complicated. Ohtsuka et al. (2009) summarised the symbionts of gelatinous plankton. They found crab larvae were only associates, not parasites. However, at least four jelly crabs feed on their hosts, and they spend their entire life cycles on one host. This seems to us to be protelean parasitism. They also steal the food of their hosts, which seems to us *kleptoparasitism*. We know too little about most jelly crabs to determine their kind of symbiosis. Towanda and Thuesen (2006) closely studied one species, graceful rock crab, but did not diagnose their type of symbiosis.

Life Cycle

Not much is known. Adults are benthic and planktonic zoea search for and attach to jellyfish. The megalopae and juveniles develop on the host. Eventually, the cypris drops off the host and develops into adults. Sometimes hundreds of megalopae occur on the host. Fewer juveniles are seem, which might suggest some cannabilism occurs (Towanda and Thuesen 2006).

Further Life History
Jelly crabs steal food and eat tissues of their hosts; however, they eat jelly parasitoids, which greatly benefit their hosts. Is parasitism rated as a proportion of good vs evil? We do not think so. This is mutualistic parasitism*.

5.13.4 Cryptochiroidea: Coral Enveloped Crabs

Klompmaker et al. (2016) objected to the existing common name 'Gall Crab' because so few actually form real galls. Whether these crab are parasites or commensals, if they damage corals, and even what they eat remains unknown (Vehof et al. 2016). There are 53 species in 21 genera and a single family, which form galls in shallow reef corals and in some deep-water corals (Castro 2015). We have seen these crabs on coral reefs all over the world.

Life Cycle
They have separate sexes, different internal fertilization, and mate belly-to-belly. Mating takes place just after the female has moulted and is still soft. Females only mate once and store the sperm to fertilise all their batches of eggs. The eggs are released onto the female's abdomen, below the tail flap, secured with a sticky material, and protected there during embryonic development. Females with eggs are called 'berried' (as are all egg-carrying decapods) because the eggs resemble round berries. When development is complete, the female releases the newly hatched larvae into the gall; they pass out into the water and become part of the plankton. Zoea have a tall dorsal spine and may have additional spines for predator deterrence. The zoea of most species must find food (planktonic), but some crabs provide enough yolk in the eggs that the larval stages can live off the yolk (lecithotrophic). Larval development is scarcely known for coral enveloped crabs but is thought to consist of at least five, and possibly seven, planktonic larval stages (Van Der Meij 2014). Different species may have various numbers of zoeal stages, separated by moults, before they change into a megalopa stage. This last larval stage resembles an adult crab, except for having the abdomen (tail) sticking out behind. Megalopae settle in hole, cracks, or creases in living corals. After one more moult, the crab is a juvenile. The coral grows around the crab, and somehow the crab forms a gall to its particular specifications. Females become sexually mature after the 4th instar in the gall but continue to enlarge until the 7th instar. They somehow manage to enlarge the gall. They produce multiple broods of eggs fertilised by the first mating.

Further Life History
Many feed on mucus secreted by the corals, inadvertently a little coral tissue, and detritus. Some filter feed. Males are smaller than females. Females cannot leave their gall, but males can. Sometimes pairs live together in one gall, in adjacent galls, or

even in interconnected galls. They cause no real harm to corals. These crabs form their gall to their own size and design. Related crab species form similar galls; therefore, the galls have phylogenic importance (Wei et al. 2013). Some galls are too closed to be accessible to males. These females copulate before the gall closes, store sperm, and produce up to eight broods over the next 10 months (Vehof et al. 2016). They found evidence of recent mating of females in more open galls.

Additional Information
Castro (2015) discussed all the publications concerning the food habits of gall crabs. They were largely based on supposition, and Castro concluded, like Vehof et al. (2016), that we still do not know what they eat. He also found the question of their types of symbiosis unresolved. Badaro et al. (2012) observed mucus feeding in the laboratory and suggested all enveloped crabs fed this way and that they are not parasites. We disagree with Badaro et al. (2012) because corals are their obligate hosts and they feed off coral-produced products, if not tissues, which the corals need. That they cause little harm to corals may be true but is not relevant to their type of symbiosis.

5.13.5 Pinnotheridae: Bivalve Pea Crabs

The most famous species in this group is the oyster pea crab. They are cosmopolitan, but more common in the tropics and subtropics, and speciose with 322 species in 57 genera and 2 families. They are tiny soft-bodied crabs that live parasitically largely in the mantle of bivalve molluscs and in a few large gastropods, sometimes inside sand dollars and sea urchins, in the rectum of sea cucumbers, tubes of parchment worms, burrows of mud shrimp, and gills of sea squirts (Castro 2015). Some have been reported commensally in, on, or in tubes or burrows of various invertebrates. Many of these relationships are not well studied, and some may be parasitic. They retard the growth of some commercial molluscs by 30% causing serious problems and millions of dollars in losses in aquaculture (Trottier and Jeffs 2015).

Life Cycle
Many males venture out of their hosts to visit females in other hosts, mostly at night. This is because hosts are more active and sensitive during the day and can squash males. Trottier and Jeffs (2015) observed males being crushed. Additionally, they are subject to predation less in the dark, than in the light of day. However, we documented the first record of predation on a male, and probably at night, since it was by a cardinalfish, on a coral reef in Okinawa (Williams and Williams 1986c). Pea crabs find females by their pheromones. Male crabs sometimes must rub, or tickle, bivalve mollusc hosts for hours to make them open up (Trottier and Jeffs 2015). Once in the host, they copulate with the female, who never leaves the host. Thus, females can become relatively larger (still only pea-size) to produce eggs, while the polygamous males are smaller and flatter to sneak in and out of hosts. In hosts with more roomy

accommodations, males may reside with females. Females carry egg masses attached to the pleopods, where they develop until they hatch into zoeae.

Usually, there are five zoeal stages, but some only have one. The zoeal and one megalopal stages are usually separated by only a few days. Hernández et al. (2012) found extended parental care and the suppression of the free-living megalopa in a species associated with western Atlantic ascidians. They undergo a complex metamorphosis during the post planktonic development. The male passes through two forms after the invasive stage, the pre-hard stage with a soft bare, carapace, and no swimming setae on the pereopods and the hard-stage with a hairy, hard carapace and natatory setae on some legs. The female goes through two very similar stages, only differing in the number of abdominal appendages, and five more feminine stages.

Further Life History

Population biology of few species has been studied, those in tropical and subtropical regions reproduced year round and in temperate regions seasonally during the summer. Reproduction and the presence of juveniles were not related to water temperature or salinity. The greatest abundance of juveniles (pleopods poorly developed) occurred just after the peaks of abundance in gravid females. Very few recruits (megalopal I) were found (Peiró and Mantelatto 2011); therefore, they must pass through this stage quickly. The female-juvenile correlation also suggests they do not disperse very far.

De Bruyn et al. (2011) examined *Dissodactylus primitivus* Bouvier, 1917, ectoparasitic on two spatangoid echinoid (heart urchins) hosts, *Meoma ventricosa* (Lamark, 1816) and *Plagiobrissus grandis* (Gmelin, 1791), which have the entire life cycle on *M. ventricosa* and only adults on *P. grandis*, but with more fecundity. Crabs detected hosts by olfactory cues. Crabs from *P. grandis* were more attracted by this host (where the entire life cycle can be fulfilled, possible imprinting). Crabs from *M. ventricosa* are equally attracted to either host. *Host switching* may explain asymmetrical infection rates and specialisation on *P. grandis* may be in progress.

Jossart et al. (2014) characterised pea crabs ectoparasitic on sea urchins at Discovery Bay, Jamaica, in which both sexes changed hosts, searched for sexual partners, and had a polygamous mating system. Most mate by polygynandry between large females and wandering small males, although some by monogamy, or temporary monogamy between adults of similar sizes, and a few by swarming of males (Castro 2015).

Ambrosio and Baeza (2016) found the pea crab, *Tunicotheres moseri* (Rathbun, 1918), did not attempt to infect previously, conspecific infected ascidian hosts, *Styela plicata* (Lesueur, 1823), to avoid conflict, even though this host was scarce and defence of the host was minimal. This is another variety of *negative precursor*. We wonder if defence of the host was once fiercer, incited this avoidance, and then faded with non-use.

Additional Information

Castro (2015) listed many damages attributed to pea crabs. The most common was slowed growth, and the most harmful, sterilization and sex reversal. He concluded that most associations were parasitic and only some more loosely associate forms in tube- or burrow-dwelling hosts might be commensal.

The California bay pea crab has the distinction of being one of only two marine crustaceans on the IUCN Red List (Wikipedia), and it is the only possible parasite on this list.

5.14 Concluding Remarks

The life strategies of most parasitic crustaceans are not very modified from their free-living ancestors. With a few notable exceptions, their life cycles suggest they just do not make very good parasites. Most would seem to have recently evolved into parasitism, yet fossil evidence shows otherwise. The most grossly modified females still metamorphose from simple life cycles. Even the most successful group, the copepods, is still hindered in exploiting different classes of hosts by the simplicity of their life cycles.

The rigidity of their life cycles seems a major limitation of crustacean parasites. Part of this apparent situation may be a result of our lack of knowledge and understanding. Here we described four new and innovative life cycles, *complex rebrooding*, *mesoparasite*, *micro-male*, and *prey-predator transfer*; four instances of a new life cycle host behaviour modification, *nursery hiding**; a common, but undescribed, life cycle form, *mid-moult stage**; two instances of parasite intraspecies facilitation, *positive precursor**; parasite intraspecies antagonism, *negative precursor**; an ambush life cycle strategy, *opossum attack**; doubling of the normal reproductive set on a host, *double parasitism**; and separated male-female pairs, *duplex arrangement**. We also named and redescribed a known life cycle, *simple rebrooding**. Possibly, many more life cycles and modifications remain to be discovered. However, these still represent rather minor modifications. Crustacean parasites lag far behind the other major parasite groups in both complexity and modification of their life cycles.

*Mid-moult** individuals are an important new means to identify juvenile life cycle instars. They are also very useful in determining exactly what changes occur in a moult and can also be used to distinguish between *supra-female* instars. Our term *displaced parasites** refers to life cycle forms which matured in the wrong locations on their host due to their normal sites being occupied. This is also linked to *superinfections**, which are mass infections of many parasites on or in a host (often resulting in the death of the host and the parasites). These occurrences strain the fabric of normal parasite relations, and life cycles, often revealing unimagined changes and trends (Williams and Bunkley-Williams 1994; Madinabeitia and Nagasawa 2011; Ismail et al. 2013).

We used the term *proportional stunting** to describe the slowing of growth in fishes caused by fish isopods (cymothoids). This cannot be evaluated by host condition factors, which have confused many into believing these parasites do little harm. Actually, they are quite detrimental and cause major economic loses to aquaculture and commercial fisheries.

The hypothesis of the first crustacean cymothoid being external attaching and then forms moving into the gills or mouth has not been supported by molecular phylogeny. The gill chamber appears to be a much more inviting and less hostile habitat for initial colonisation, as we have seen in two cases of unusual crustacean infections (Williams and Bunkley-Williams 1994). Our displacement cases seem to also suggest this scenario.

Schmid Hempel (2011) did not find well-adapted parasites became harmless but rather more efficient at countering the defences of their host. Many recent authors have suggested parasite evolution favours virulence. However, we report the first hyperparasite ever known to evolve into a mutualist and explain the pathway. Poulin (2011a) thought that parasites with few adaptions could revert to a free-living existence but cited few examples. He found no *parasite reversals** to mutualism.

Predation has only recently been shown to occur within parasitic crustacean life cycles and cause damage and death of hosts. Parasitism and predation are difficult enough to distinguish when isolated, much more so within a life cycle. As we learn more details of life cycles, predation may become important phases. We attempt to define the types involved (Table 5.1 and Annotated Glossary (Sect. 5.15) below).

Cleaners feeding on fish gnats (gnathiids) may be *accessory vampires*. They may more easily find and/or select larger, swollen fish gnats filled with blood. Eckes et al. (2015) suggested cleaners benefited more from consuming fish mucus than fish gnats. We certainly believe they benefit more from eating blood-filled gnathiids, than ones without fish blood.

We found copepod pre-adult life cycle stages were common on Western Pacific fishes but very rare on Caribbean ones. This indicates that smaller cleaner gobies may be more efficient than larger cleaner wrasses and a factor in parasites completing life cycles.

Contrary to the literature, we find the wormlike copepod on sea turtles, manatees, and whales are not parasites. We described how *Pennella exocoeti* may have speciated. Flying fishes are food for many offshore large predators, which host *Pennella* species. Flying fishes were probably a *downward incorporated* intermediate host for *Pennella* spp. at one point. Eventually, a form became isolated and speciated into *Pennella exocoeti* on flying fishes.

Fish isopods (cymothoids) seem on the verge of evolving a real intermediate host. Fish gnats (gnathiids) may also be exploring intermediate hosts through micropredation. A new ergasilid copepod seems to be becoming an endoparasite.

Tongueworms are completely parasitic with no free-living stages, endoparasitic in an intermediate and a final host, and so modified to parasitism we cannot even equate their life cycle stages to free-living ones. All other parasitic crustaceans are incompletely parasitic in one way or another. Therefore, these life cycles suggest tongue worms are not crustaceans. They further suggest tongue worms are not even related to crustaceans, and this needs further investigation.

Fish lice and tongue worms have long been suspected to be related on the basis of their sperm morphology. Recent molecular work also finds them similar. Their life cycles are the same in having no free-living larval stages but are otherwise worlds apart. Fish lice are not even good ectoparasites, flitting around from host-to-host as juveniles and adults with females free-living off hosts. Tongue worms are good endoparasites every step of their way. The life cycles of fish lice and tongue worms suggest they have no phylogenetic relationship.

The few fossil 'tongue worms' only recently discovered are larval parasites of marine invertebrates. Equating these with tongue worms of present terrestrial vertebrates with no larval stages is impossible. These fossil tongue worms may be related to extant tongue worms, but they are not their ancestors. A parallel, and completely separate, evolution is more likely.

Octopus copepods (Harpacticoida) and tunnelling tanaidaceans (Tanaidacea) have similar life histories tunnelling through the tissues of octopuses and sea cucumbers, respectively. They also represent the rare parasitic forms in their largely free-living orders. Both also have commensal species on sea turtles and manatees. However, their life cycles are quite different (López-González et al. 2000; Alvaro et al. 2011), and they reside in different classes of crustaceans. Their modes of living and feeding must represent parallel evolution.

Anchor worms (lernaeids) and marine anchor worms (Pennellidae) are an astonishing example of parallel evolution. So much so that they were originally classified together in *Lernaea* Linnaeus, 1758. They are also the only copepods to make major host group switches: Amphibia and Reptilia by the anchor worm and Mammalia by the marine anchor worm. Even their life cycles are similar with intermediate hosts, except that it is not an obligate intermediate in the anchor worm. Furthermore, the anchor worm is freshwater, and marine anchor worms are marine, and they are classified in different orders.

Lafferty and Kuris (2002) recognised four life cycle strategies (a bit too simple) and ten trophic strategies. Poulin (2011b) arranged all parasites into six major life strategies (see Table 5.2). All categories, except vector transmission, apply to crustaceans. Poulin and Randhawa (2015) further defined and defended the categories but made little more use of them. Half were named for transmission methods and half for effects on the hosts, which seems confusing as they are not, necessarily, mutually exclusive. In order to standardise his terms, we rephrase *parasitoid* to 'adult injection transmitted', *parasitic castrator* to 'larval penetration/injection transmitted', and

Table 5.2 The original six major life strategies from Poulin (2011b) and our seven proposed transmission strategies

	Original category name	New transmission-standardised names
1	Parasitoid	Adult injection transmitted*
2	Parasitic castrator	Larval penetration/injection transmitted*
3	Directly transmitted parasite	Direct life cycle transmitted parasite
4	Trophically transmitted parasite	Prey-predator transmitted parasite
5	Vector-transmitted parasite	Vector-transmitted parasite
6	Micropredator	Minipredator transmitted*
7	–	Inanimate transmitted*

micropredator to 'micropredator transmitted' (see Table 5.2). We also add a seventh strategy. Most microbial parasites have no animate transmission agent. They contaminate potential hosts in incidentally shed host products or by long-lived free-living stages. Some symbionts on sea turtles and manatees spend their entire life histories on their hosts, never leaving, never transmitted. Poulin and Randhawa (2015) call their categories 'dead ends', but we do not believe *micropredator* is necessarily a parasitological dead end.

If we use the seven new transmission-standardised names to categorise crustacean parasites:

1. *Adult injection transmitted*—larval parasitic copepods (Sect. 5.5.3) have a life cycle similar to parasitoids but do not kill the host, and jelly parasitoids (Sect. 5.10.3) are almost parasitoids.
2. *Larval penetration/injection transmitted*—some parasitic barnacles (Sect. 5.6.2), some echinoderm copebarnacles (Sect. 5.8.2), and some crab barnacles sterilise their hosts. Sterilisation is not one strategy but two. *Hormonal sterilisation* is a permanent, parasite chemical control of a host. *Nutritional sterilisation* is a temporary parasite use of the host resources to the extent that host reproduction cannot occur.
3. *Directly transmitted parasite*—represents almost all of the crustacean parasites. Poulin and Randhawa (2015) found these forms were the simplest and least parasitically evolved of the parasites, which agrees with our analysis.
4. *Trophically transmitted parasite*—is only found in tongue worms (Sect. 5.3, which are probably not crustaceans). Marine anchor worms (pennellids) have this strategy, except the intermediate host is not eaten by the trophically higher predator. Our prey-predator life cycle follows this strategy, except the parasite juvenile only moults to an adult in a paratenic (not intermediate) host, before it is eaten.
5. *Vector-transmitted parasite*—does not occur in crustacean parasites.
6. *Micropredator transmitted parasite*—occurs in fish lice (Sect. 5.2), sea lice (Sect. 5.5.4, caligids), jelly parasitoids (Sect. 5.10.3) and some juvenile fish isopods (Sect. 5.11.2) that are micropredators.
7. *Inanimate transmitted parasite*—occurs in non-swimming fish lice (Sect. 5.2) and whale lice (Sect. 5.10.1).

Williams and Bunkley-Williams (1996) made the first, large-scale comparison of Caribbean and Western Pacific parasites of coral reef fishes using the same collection and examination techniques. In terms of crustacean parasites, they found less aegid associates and more tongue worms in the Pacific. Cymothoids, fish gnats, copepods, and barnacle associates were approximately equal. In contrast, non-crustacean parasites were less diverse and abundant in the Pacific than the Caribbean.

Fish lice, tongue worms, larval parasitic copepods, isopods, and whale lice lack larval dispersal stages. Fish lice and isopods have free-swimming juveniles to make up for this limitation, somewhat. Larval parasitic copepods, fish lice, and sea lice have free-swimming adults.

Many recent authors seem to equate, or even confuse, the complexity of parasitism with its severity. Sometimes these do go hand-in-hand, but they are different.

Complexity makes parasites more resilient, adaptable, and in the case of marine anchor worms more able to switch major host groups. Severity is how voraciously and efficiently parasites use host resources to successfully reproduce the most. Some of the most severely parasitic crustaceans actually have rather simple life cycles (e.g. parasitic barnacles and *Sarcotaces*). The elaborate modification of adults is also sometimes equated to severity. Again, these may co-exist but are different.

Many crustacean parasites, in general, seem to infect young hosts and 'grow up' with them. This has been shown in many parasites where the younger hosts, even planktonic juveniles, are much more often parasitized than the larger, older ones. In addition, host tissues growing around their parasites indicate long-term association. Younger hosts are easier to find and infect often occurring in inshore schools. Our prey-predator transfer may be one of the only ways older host can be infected.

To evolve towards greater parasitism, the life cycle stages of crustaceans must be less and more. They must be less like the free-living crustacean stages (e.g. fish lice and fish isopods) and/or must add more parasitic stages in real intermediate hosts (e.g. tongue worms). They can either convert their free-living stages to parasitism or metamorphose new parasitic stages. Those few that have developed parasitic larval or juvenile parasitic stages are progressing. However, the free-living adults many retain must become parasitic. Adults must also become more modified and adapted to a parasitic existence. Crab barnacles have done a pretty good job of this, and a few copepod adults are well modified, but in general, crustaceans have done a terrible job of adapting to and exploiting parasitism.

Currently, we know only a minute fraction of the crustacean life cycles. Additional studies may turn what we think we know on its head, upside down, or throw it out the window. We are fooling ourselves that the little we know is typical. We expect most known group life cycles are not only unknown but probably false. Not only do we know few life cycles, but we also know few of the species in most groups, and these may have even different life cycles. Also, major groups are still springing into existence. Life cycle study is a field where magic is still awaiting discovery.

5.15 The Future of Parasitology

Crustacean and nematode parasites will soon dominate metazoan parasitology. We call the present dominating parasites (flatworms, tapeworms, thorny-head worms, etc.) as "Climax Parasites". They are ancient, stable, and perfect to take maximum advantage of the current conditions. Unfortunately, they are also practically unchangeable in having no free-living forms to become parasitic, no adults in invertebrates, major parasitic modifications, and low species abundance. We call crustaceans and nematodes (ecdysozoans) as "Transitional Parasites". They would eventually evolve into Climax Parasites but now possess just the opposite of the climax characters stated above. The Climax Parasites have traded flexibility and the ability to innovate for stability and the maximum parasite experience. They are rigid and vulnerable with exposed multiple hosts and complex life cycles, unable to make major host group shifts, life cycle reductions or additions, and too involved in, and dependant on, stability. Major global changes will leave them behind, at worse in extinction or, at best, in remnant triviality. Crustaceans and nematodes will inherit the new world of parasites.

5.16 Annotated Glossary

An astonishing number and variety of recent authors misapply and misuse common life cycle terms. This inaccuracy creates misunderstanding and undermines scientific precision. We here precisely define these terms.

Abandon host—when parasites evacuate a host that has been captured, injured, incapacitated, or poisoned.

Accidental attachment—(a) a host-specific parasite rarely attaching to an *accidental host* or (b) a site-specific parasite rarely attaching in a different position.

Accidental (incidental) host—(a) a host on which the parasite cannot complete its life cycle; (b) also used for very rarely infected hosts on which the life cycle can be completed.

Aegathoa—a juvenile genus used for Cymothoidae juveniles that could not be identified to genus and as such is a form genus. This should no longer be used, but inexplicably, recent uses exist.

Aesthetascs—chemosensory organs on the antennae and other structures of larval crustaceans used to locate appropriate hosts, virgin females, etc.

Aggregation—(a) usually refers to the distribution of parasites within hosts. Often, these are not uniformly distributed among host but aggregated in a few hosts; (b) can also refer to a group of hosts or to a cloud of parasite infective stages.

Alternate host sharing—a life history strategy where two different species of parasites infect the same host, but not at the same time.

Ambushing—a manner of searching for hosts used by larvae and free-swimming adults, generally, resting still in the water column arched upwards at a 45° body angle and then suddenly attacking an unaware host. Used in the daytime by some forms. *Opossum attack* is a form of ambushing. See *cruising* and *hover and wait*.

Androdioecy—having dwarf males and larger hermaphrodites. The small male is usually attached on or near a larger hermaphrodite.

Antennae—the second pair of antennae, usually longer than the first.

Antennulae—the first pair of antennae, which are usually shorter than the second.

Biological control—an agent killing or sterilising unwanted organisms.

Biphasic moult—a moult occurring in two posterior (first) and anterior (second) parts. This occurs in all Peracarida. See *moult*, *mid-moult stage*.

Body—is in three sections: the head (cephalon), thorax (pereon), and abdomen (pleon). See *metasome* and *protosome*.

Bopyridium (juvenile)—the third life cycle stage of epicaridian crustacean isopods.

Brood mortality—loss of some individuals in developmental stages in the marsupium. This has only been measured indirectly with counts of different stages from different females.

Burst release—when a predator attacks a host and its parasite dumps out all its juveniles at once.

Capsule—a layer produced by a host to isolate a parasite. See *cyst.*

Castration—refers to removing male testicles. It has been classically misused in parasitology for sterilization. We change it to the correct term 'sterilization'. See *hormonal sterilization*, *nutritional sterilization*, *partial sterilization,* and sterilization.

Casual parasite—see *periodic parasite*, *accidental host.*

Cephalon—the head of the crustacean. See *body*.

Cephalothorax—the joined head and pereonal first somite (the maxillpedal somite). See *body*.

Chalimus—the third larval stages in sucker-mouth copepods (siphonostomatoids) between the infective copepodid stage and the adult. It is attached to the host by a filament and develops in a series of moults to the adult.

Cleaner nipping—a cleaner attacking a parasite, which is too large for it to remove, by biting or tearing off a piece or appendage.

Climax parasite (perfect parasite, advanced parasite)—one that has evolved to a 'perfect state' to take advantage of existing conditions and hosts to maximise its existence.

Clutch size—the number of eggs produced in one spawning event. See *fecundity.*

Commensalism—means living with, and benefiting from, a different species. Distinguishing commensalism from parasitism can be difficult. The trophic nature of many crustacean symbiotic relationships remains uncertain.

Complex life cycle (indirect life cycle)—one with two or more hosts.

Complex rebrooding—a series of marsupial reproductions with vegetative instars between marsupial stages. When a female is reproductive, the marsupium contents occupy all the body space with a large number of offspring. Her other organs atrophy, and she does not feed. See *vegetative stage* and *simple rebrooding*.

Copepodid—the second larval stage in copepods, between naupliar stages and adult. The first copepodid is free swimming. The others are on the host. See *recently encysted* and *later encysted*.

Cruising—a manner of searching for hosts used by larvae and free-swimming adults. Generally, it means swimming in the water column with an even keel.

Cryptogonochorism—a degenerative male form, attached and parasitic on a female, fertilising her eggs. Found in parasitic barnacles (rhizocephalans).

Cryptoniscan (cryptoniscus and cryptoniscid)—the second larval stage of epicaridian crustacean isopods.

Cypris stage (cyprid) (plural: cyprii, cyprids)—the second larval form in many crustaceans. There are usually one or two instars, and it is the infective stage.

Cyst—a parasite forming a protective coating or layer around itself generally inside a host, under its skin, etc. When the host forms a layer to isolate the parasite, this is called a *capsule*. In some cases, both contain a parasite. Some life cycle forms are *encysted* and/or *encapsulated*. See *gall*.

Definitive host (final host, primary host)—the usual, or normal, host of the parasite and the one on which it can complete its life cycle.

Demarsupiation—the releasing of the swimming or infective or reproducing stage from the marsupium (brood pouch).

Direct life cycle—involves a single host.

Direct develop larvae (crawl-away larvae)—larval stages that have very low dispersal potential and usually appear like the adult form of the animal. Fish lice (branchiurans) are crustacean examples. Non-swimming larvae of *Chonopeltis* are definitely crawl-away larvae.

Dispersal stage—free-living larval or adult stages that swim around, or are carried in water currents, to new areas.

Displaced parasites—when all the normal attachment sites are occupied forcing additional parasites to attach in unusual positions.

Double parasitism—when two reproductive sets of the same species occupy the same host, when normally only a single set occurs. See also *multiple parasitism*.

Downward incorporation—adding a new host after the original host with the new host becoming an intermediate host. Moving down the food chain. See *parallel incorporation* and *upward incorporation*.

Duplex arrangement—the separation of the male and female of a pair on opposite sides of a host.

Dwarf male—small male usually attached on or near a larger hermaphrodite (e.g. normal barnacles, Thoracica) or inside the female (parasitic barnacles, Rhizocephala). See *androdioecy*.

Ecdysis (moult)—the moulting of the cuticle and the transition to the next stage of development.

Ectoparasite—parasites that attach to the outside of their host. However, there is some disagreement about what is outside. We consider the brood chamber, eye orbit, gill chamber, mouth, nares, and open sinus cavities as external as their surface is ectoderm. See *endoparasite*.

Encapsulated—see *cyst* and *capsule*.

Encysted—see *cyst* and *capsule*.

Endoparasite—completely within the host. It has no opening to the environment as in a *mesoparasite*. We consider closed sinus cavities, lacunar canals, rectum, intestine and urinary bladder internal. See *ectoparasite*.

Epicaridium larva—see *microniscan larva*.

Epigametic sex determination—first infective life cycle stage arriving at a host becomes a female and the second, a male, e.g. decapod isopods (bopyrids) and fish isopods (cymothoids). See *founder pair*.

Epiparasite—see *hyperparasite*.

Eusociality—a colony system where only the queen is reproductive and is served and protected by relatives. Life cycles are direct lacking a planktonic stage. Sponge shrimp (carids) are the first known eusocial parasites.

Exoskeleton—(a) the outer covering of crustaceans; (b) the old shell left after moulting or the *exuviae*.

Externa (plural: externae)—the outside, egg-, larvae-holding, sac of a female of parasitic barnacles (rhizocephalans).

Exuviae (formerly only plural, but exuvia is coming into use)—see *exoskeleton*.

Facultative intermediate host—infecting the host is not necessary to complete the life cycle.

Facultative parasite—may parasitise a host, but the host is not necessary to complete its life cycle.

Feeding stage—see *vegetative stage*.

Feminisation—parasitic barnacles (rhizocephalans) change the pleon configuration of male crabs they infcct into the female configuration to better protect their externa. Cryptic isopods (cryptoniscoids) residing in the marsupium of other isopods may control their host to retain this brood pouch.

Final host—see *definitive host*.

Founder pair—two infective stages attaching to a host together, excluding other cohorts, and successfully developing into a male and female pair (e.g. cymothoids).

Fugu toxin—tetrodotoxin (TTX) in puffers, which repels gnathiids from the skin of puffers, and we believe some other crustacean parasites.

Gall—a plant term. It is sometimes misused for large, parasitic cysts. Usually galls contain more than one parasite, often both sexes and life cycle stages. See *cyst*.

Good parasite—see *true parasite* and *strict parasite*.

Growth stage—a distinctly different morphological form not resulting from a moult. Some pre-adults may qualify. Many crustaceans have different growth stages as adults age or grow in size. See *Supra-female*.

Hover and wait—a form of ambush host seeking employed by fish lice (branchiurans) during the day. See *ambushing*.

Hormonal sterilisation—a permanent, parasitic chemical control of a host. See *nutritional castration* and *partial sterilisation*.

Host hopping—is adults, and/or larval life cycle stages, leaving one host and finding the same, or another, within a life cycle stage.

Host switching—can be (a) a long-term evolutionary change usually to quite a different kind of host; (b) part of the prey-predator transfer life cycle sequence; (c) casual parasite survival (e.g. Connors et al. 2008, 2011); or (d) even within a life cycle (Ota et al. 2012).

Hyperparasite (epiparasite)—a parasite parasitising another parasite.

Hypersymbiotic (episymbiotic)—a symbiont, usually a parasite, associating with/infecting another symbiont, usually a commensal.

Immature—a young individual and another name for post-larva or juvenile.

Indirect life cycle—see *complex life cycle*.

Infective stage—the larval stage, which attaches to or injects infective material into a host. In many forms a cypris.

Infection—(a) parasitologically, a parasite or microbe invading a host (formerly referred only to endoparasites; see *infestation*); (b) medically, invasion of endoparasites; and (c) microbiologically, invasion of an organism that multiplies within the host (e.g. bacteria, fungi, protozoans, viruses).

Infestation—(a) parasitologically, ectoparasite on host can still be refer to parasites in the environment; (b) invasion of any parasite; (c) medically, sometimes used for ectoparasites; (d) medically, sometimes refers to the initial stage of parasite invasion followed by infection; and (d) common usage, aggregations of pests (e.g. mosquitoes, rats).

Inquiline—an animal living in another species of animal's nest, burrow, den, or resting place.

Instar—a larval stage between moults. For example, there are usually five naupliar instars.

Intermediate host—a host that a larval stage infects, feeds on, and undergoes at least one moult upon. See *micro-male host*, *resting host*, and *transfer host*.

Interna (plural: internae)—the internal and anastomosing part of a female parasitic barnacle (rhizocephalans).

Iteroparous—females have multiple broods, e.g. cymothoids.

Juvenile (immature, immature adult, post-larva)—a miniature adult. In cymothoids, the juvenile escaping the female marsupium has six pairs of legs (six-legged juvenile). See *larva* and *manca*.

Juvenile-like larvae—look like adults with four pairs of active thoracopods, but no suction disks. They are larvae of fish lice (branchiurans).

Kentrogon—an infective stage, metamorphosed from a crypis, of parasitic barnacles (rhizocephalans). The kentrogon injects a vermigon.

Kleptoparasites—steal the food or food stores of its host.

Larva (plural: larvae)—an immature greatly differing from the adult form, which must go through a metamorphosis to be an adult. Some authors use the terms juvenile and larvae interchangeably; however, these are different and distinct stages, which should not be confused.

Lecithotrophic larva—do not feed but use their yolk for nourishment.

Leg—see *pereopod*.

Lice (singular: louse)—technically phthirapteran insects; fish lice are branchiurans; and sea lice are either micro stinging jellyfish (since 1949), bird schistosomes (since 1928), or caligid copepods (since ~1975); and whale lice are cyamid amphipods. *Tongue-eating louse* is an incorrect name for the famous *tongue-replacing isopod*.

Life cycle—development from conception until the organism produces its own offspring. Its study often emphasises stages of development. See *life history*.

Life cycle abbreviation—the brooding or elimination of normally free-living larval stages.

Life cycle truncation—the elimination of parasitic larval life stages.

Life history—reproductive strategies and traits plus other key events in the life of an organism. See *life cycle*.

Lifestyle—the mode of life. Habit (behaviour) and habitus (form). Mobility, feeding, nutrition, habitat, activity period, etc.

Major host group switch—parasitising a new class of host.

Manca juvenile (plural: mancae) (*Aegathoa*, manca, micro-male, pullus II)—the post-larval juvenile of many pericardians (not amphipods), which leaves the brood pouch. See *Aegathoa*.

Marsupium (brood pouch)—formed of lamellar outgrowths of the female pereopodal coxae (oostegites). This pouch is under the ventral body surface of the female. See *complex rebrooding* and *simple rebrooding*.

Marsupium stages—various egg, embryo, and larva stages. This embryology is seldom considered in life cycle studies.

Megalopa—a post-larval crab. Extreme transformations occur in this stage.

Mesoparasite—(a) inside their host but retains a pore or hole connecting to the outside; (b) half-in-and-half-out as anchor worms (*Lernaea*); and, quite confusingly, (c) also used for parasites that enter host orifices (ear, nares, etc.). The latter might be less confusingly called *Orifice Parasites*.

Metanauplus (pleural: metanauplii)—see *nauplius*.

Metanauplus-like larvae—are similar to crustacean nauplii, but not metanauplii because of post-mandibular appendages and differentiated first thoracopods. They are larvae of fish lice (branchiurans).

Metasome (tail)—the posterior part of the protosome.

Micro-male—a 6-, 6.25-, 6.5-, 6.75-, 7-leg juvenile functional male of *Anilocra* spp., *Livoneca ovalis*, and possibly other cymothoids.

Micro-male host—a resting host for some juvenile fish isopods (cymothoids) on which moults from the 6-leg to 7-leg micro-male stage can occur. This is not an intermediate host because no larval stages are involved. The micro-male leaves this host to fertilise a female on the final host. It may return to this host specimen or another micro-male host.

Microniscan larva (epicaridium, microniscus or microniscid)—the first larval stage of epicaridian crustacean isopods.

Micropredator—like a mosquito; a small predator feeding on a big host and not spending much time with its macroprey. Predator less than 1000 times size of prey. See *minipredator*, *smaller predator*, and Table 5.1.

Mid-moult stages—a form of half delayed moulting found in some parasitic forms that must stay firmly attached to a host. The first half moults as usual, but the second half moult is delayed until the first half hardens.

Minipredator—a small predator that may, or may not, kill its prey and spends little time with it (feeds and leaves) but is greater than 1/1000 of its host's size, but less than 1/100 (e.g. gnathiids, cirolanids, some corallanids, some leeches). See *micropredator*, *smaller predator*, and Table 5.1.

Molt (apolysis, ecdysis)—the splitting of the outer covering (cuticle carapace, etc.) in order for a larger and/or different form to emerge in the life cycle. Outside the USA, the preferred British spelling is *moult*.

Multiple parasitism—when one host is infected with two, or more, different species of parasites representing, three or more reproductive sets. See *double parasitism*.

Mutualistic parasitism—when the symbiont is both harmful and helpful. Similar to sickle cell anaemia and malaria.

Mutualistic symbolism—when both host and associate benefit from the other.

Natural history—the interactions of an organism with its environment that influence behaviour, forms, function, and abundance. See *life history*, *life cycle*, and *lifestyle*.

Nauplius stage (plural: nauplii)—is characterised by the use of the appendages of the head (antennae) for swimming. This first series of larvae has been shared by almost all crustaceans for the last half billion years.

Negative precursor—when one species of parasite or commensal infects a host first and causes a second species of parasite to be less successful in infecting the same host. See *positive precursor*.

Non-swimming larvae—the odd larvae of *Chonopletis*, a fish louse (branchiurans).

Nursery hiding—infected adult hosts staying with juveniles or young of the same species instead of migrating elsewhere with non-infected adults.

Nutritional sterilisation—is a temporary parasite use of the host resources to the extent that host reproduction cannot occur. See *hormonal castration* and *partial castration*.

Nymphs—are small 4–6-legged, larval forms of tongue worms (pentastomids).

Obligate parasite—is a species that must infect a particular host to complete its life cycle.

Onychopodid larva—replaces the on-host copepodid larva in *Gonophysema gullmarensis* Bresciani & Lützen, 1960, a copepod parasite of a tunicate.

Oostegites (marsupium coverlets)—see *marsupium*.

Opossum attack—when a manca juvenile swimming dorsal side up, stops swimming, falls to the bottom, lands dorsal side down, and does not move. When a small fish comes near, the manca springs to life and attaches. See *ambushing*.

Orifice parasite—a term we prefer in place of *mesoparasite* for parasites living in natural orifices or openings in hosts.

Orthonauplius—a nauplius but has a shorter head, antennula, and two additional pairs of limbs.

Ova—eggs.

Overdispersed (aggregated, clumped)—in parasitology is a distribution with a higher variance than expected (e.g. when most hosts have a few parasites, but a few have many).

Pantochelis larva—the first larva of jelly parasitoids (hyperiideans) with four cheliform legs (pereopods) and an unsegmented and limbless metasome and urosome. It metamorphoses into a protopleon larva.

Parallel incorporation—adding a new host after the original host with the new host becoming an intermediate host. Begins with a resting host or transfer host becoming an intermediate host and eventually an obligate intermediate host. Moving sideways on the food chain. See *downward incorporation* and *upward incorporation*.

Parasite—takes benefits from the host it harms but very rarely kills it. True parasites or good parasites stay on their final host specimen never leaving.

Parasite Increased Trophic Transmission (PITT)—a parasite changing the behaviour of its intermediate host making the prey more likely to be eaten by the predator definite host.

Parasite reversal—a parasite becoming free-living.

Parasitoid—an insect infecting another species of insect with its larvae. The larvae feed off the host and eventually kill it and escape as adults. Larval parasitic copepods (monstrilloids) have a similar life cycle, but do not kill their host.

Paratenic host (transfer host, transport host)—like an intermediate host, except the parasite does not go through any life cycle or larval stage on it.

Parthenogenesis—asexual reproduction by females without the need of males.

Partial sterilisation—a term used by Williams and Boyko (2012), as 'nutritional castration', where some reproduction still occurs.

Pereon—the thorax. See *body*.

Pereopod (leg, peraepod, pereiopod, thoracopod)—legs of the thorax (cephalothorax, pereon) of crustaceans.

Periodic parasite—acting like a facultative parasite, on a host for short periods of time, but free-living most of the time. Does not obtain most of its nutrition from a host or hosts. Not a serial parasite, temporary parasite, or true parasite.

Permanent parasite—is an obligate parasite, which spends more than one generation without leaving a host. See *temporary parasite*.

Planktotrophic larva—feeds on plankton. See *lecithotropic larvae*.

Pleon—the abdomen. See *body*.

Pleopods (paddle gills)—appendages underneath (ventral) the abdomen (pleon) of crustaceans.

Positive precursor—when the presence of one parasite facilitates infection by another. The interspecific form is fairly common; however, intraspecific forms are rare. This is when one species of a parasite or commensal infects a host first and causes a second species of parasite to be more successful in infecting the same host. See *negative precursor*.

Post-larva (plural: post-larvae) (immature, juvenile, pre-adult)—resembles the adult and characterised by the use of abdominal appendages (pleopods) for propulsion.

Praniza (formerly pranzia)—see *zuphea*.

Pre-adult—a stage after larvae and before adult.

Predisposition—(a) some hosts of crustacean parasites appear to be predisposed to the presence of parasites (Williams et al. 1982); (b) also may refer to a pre-existing condition or behaviour, which makes some process possible (e.g. speciation, life cycle change).

Preferred host—see *secondary host* and *definitive host*.

Pre-larvae (pre-zoae)—the first stage after an egg hatches. Usually held in a marsupium in isopods.

Pre-manca—the isopod brood-pouch stage after eyed embryo before manca and is less developed and has less setae.

Prevalence collection effect—when infected hosts are impaired by their parasites and are more readily to be collected (e.g. dip net, seine, trawl), or less likely to be collected (e.g. hook and line, baited traps), than uninfected ones.

Prey-predator transfer—Fish isopods (cymothoids) from prey fishes can transfer to the predators that eat them. See *prey-predator life cycle* and *transfer host*.

Prey-predator transfer host (prey host)—a resting host for some juvenile fish isopods (cymothoids) on which moults from the six-legged manca juvenile to a post-juvenile stages can occur.

Primary host—see *definitive host*.

Proportional stunting—parasites slowing the growth of their host in a way that cannot be discerned in length-weight condition factors.

Protelean organisms—have larvae that are parasites, usually endoparasites, and free-living adults.

Protopleon larva—the second larval series of jelly parasitoids (hyperiids) with a segmented metasome and imperfect pleopods. It metamorphosed from a pantochelis larva and gives rise to a juvenile.

Pseudoparasite—our term for something that almost everyone accepts as, and calls, a parasite, but is not (e.g. most leeches).

Pullus II (plural pulli)—see *manca larva*.

Pupa—the unique, cigar-shaped, endoparasitic nauplii of larval parasitic copepods (monstrilloids).

Reproductive stage—see *vegetative stage*.

Recently encysted (copepodids 2–3)—pandarid copepodid stage (Lewis 1964). See *late encysted*.

Resting host—a host on which infective larvae or juveniles rest and feed. Larvae do not go through a metamorphosis on this host. See *intermediate host*, *micro-male host*, and *transfer hosts*.

Sea lice—caligoid copepods that infect marine aquaculture fishes, especially salmon. Many recent authors have called them fish lice, which is incorrect. See *lice*.

Secondary host—a host less often infected than the preferred host or definitive host but on which the parasite may complete its life cycle.

Semelparous—females that have only one brood.

Serial parasitoid—similar to a parasitoid in brooding its young in a host, but may use and kill more than one host as a nursery, and also may feed on, and kill, multiple hosts, as an adult.

Serial parasite—an obligate parasite that largely depends on host, or hosts, for nutrition. It is not simply a minipredator, because it associates with a host longer than to feed and leave and has one or more life cycle stages that exist multiple times potentially on and off the same or different hosts. See *temporary parasite*.

Simple life cycle—see *direct life cycle*.

Simple rebrooding—new marsupial reproduction after a single moult. The internal organs are only flattened by a brood pouch with a moderate number of off spring. The female can feed as soon as she moults. See *complex rebrooding*.

Site specific—when a parasite almost always attaches in the same position on or in a host. See *accidental attachment*.

Smaller predator—not a great deal smaller than its prey, attaches to, feeds on, and kills the host. It is an, hitherto, unrecognised life cycle phase (minipredator phase) in parasitic crustacean life. See *micropredator*, *minipredator*, and Table 5.1.

Spillover—a term for the parasites, principally salmon sea lice, produced in fish farms, infecting native fishes. 'Spillover' suggests the pen is so full of free-swimming, infective parasites (copepodids) that a few are forced out. See *filtering*.

Sterilisation—the act of making an animal unable to reproduce. See *partial sterilisation*, *hormonal sterilisation*, and *nutritional sterilisation*.

Strict parasite—see *true parasite*.

Superinfection—a mass infection with about as many parasites that can fit on or in a host. This usually results in the death of the host and the parasites.

Supra-females (post-adult stages, supra-adult)—stages after the first adult female stage with size and/or morphological differences with the first adult and each other. These can be growth stages or instars and often occur in crustaceans.

Supra-males—see *supra-females*.

Tantulus larva—the only larval stage of minute crustacean parasites (tantulocarids) with a dorsal head shield, six-segmented thorax, and biramous urosome.

Temporary parasite—(a) a facultative parasite; (b) a parasite that survives for a time after ingestion by a host species other than its customary host; (c) a minipredator, associated with a prey item just long enough for it to be called a host but largely free-living and rarely found associate with a host; or (d) a parasite with any free-living stage.

Thoracopod—see *pereopod*.

Transfer host (prey host)—a resting host for some juvenile fish isopods (cymothoids) on which moults from the 6-leg manca juvenile to a post-juvenile stages can occur. This is not an intermediate host because no larval stages are involved. See *paratenic host*, *micro-male host*, and *prey-predator life cycle*.

Transitional parasite—a crustacean or roundworm (Nematoda) in the clade Ecdysozoa. They are relatively new parasites with many free-living relatives and little evolved towards a climax parasite state. See *climax parasite*.

Transport host—see *paratenic host*.

Trichogon—injected into a female by a male crypis, of parasitic barnacles (rhizocephalans), and becomes a dwarf male.

Trophic transmission—see *parasite-induced trophic transmission*.

True parasite (good parasite, strict parasite)—a small organism, which feeds from and harms a larger organism. True parasites have a definitive host, which they never leave.

True predator (carnivore)—an organism that hunts, kills and eats other organisms (prey). See *ambushing*, *opossum attack*, and Table 5.1.

Underdispersed (uniform, regular)—see *overdispersed*.

Upward incorporation—adding a new host after the original host with the former definitive host becoming the intermediate host. Begins with parasites surviving in a predator of the original host. Moving higher on the food chain. See *downward incorporation* and *parallel incorporation*.

Urosome—abdomen of arthropods.

Vector mutualists—when a disease or parasite transmitted to a host also benefits the vector. When crustacean parasites are vectors, the infective stage of the crustacean benefits by the invasive transferred organism confusing the immune system of the host and increasing infective crustacean survival. See *viral crustacean mutalists*.

Vegetative stage—is a term we borrowed from botany to describe a feeding and nonreproductive female stage of fish isopods (cymothoids) between stages with a marsupium. See *complex rebrooding*.

Vermigon—a migratory internal stage injected by the kentrogon stage of a parasitic barnacle (rhizocephalans).

Viral crustacean mutualists—a virus benefiting its crustacean host and doing little or no harm to the host.

Virgin female—a term used in the literature for an adult female lacking a marsupium. A vegetative stage is a better term since these stages can occur both before and after stages with a marsupium.

Whale lice—see *lice*.

Y-cypris (plural: y-cyprii)—see *y-nauplius*.

Y-nauplius (plural: y-nauplii)—the first larval stage of y-parasites (facetotectans) and y-cypris the second.

Ypsigon—a slug-like, unsegmented, and limbless form, which may be the infective stage for y-parasites (facetotectans).

Zoea stage (plural: zoeas or zoeae)—the first larval stage of a decapod characterised by the use of the thoracic appendages for swimming and a large dorsal spine.

Zuphea—the first juvenile of fish gnats (gnathiids) with obvious segmentation, which leaves the female, finds a host, feeds, and becomes the second stage, a *praniza* (P1).

5.17 Common Names

Common names are listed alphabetically in bold with and family names in square brackets:

American Alligator, *Alligator mississippiensis* (Daudin, 1802) [Alligatoridae]; **Anchor Worm**, *Lernaea cyprinacea* Linnaeus, 1758 [Lernaeidae] also used as a group name for the genus and/or family; **Antarctic Eelpout**, *Lycodichthys dearborni* (DeWitt, 1962) [Zoarcidae]; **Atlantic Salmon**, *Salmo salar* (Linnaeus, 1758) [Salmonidae]; **Ballyhoo**, *Hemiramphus brasiliensis* (Linnaeus, 1758) [Hemiramphidae); **Barramundi**, *Lates calcarifer* (Bloch, 1790) [Latidae]; **Barrier Reef Chromis**, *Chromis nitida* (Whitley, 1928) [Pomacentridae]; **Beaked Pacu**, *Ossubtus xinguense* Jégu, 1992 [Serrasalmidae]; **Bicolor Damselfish**, *Stegastes partitus* (Poey, 1868) [Pomacentridae]; **Blacktip Grouper**, *Epinephelus fasciatus* (Forsskal, 1775) [Serranidae]; **Blue Crab**, *Callinectes sapidus* Rathbun, 1896 [Portunidae]; **Blue Runner**, *Caranx crysos* (Mitchell, 1815) [Carangidae]; **Bluespotted Ribbontail Ray**, *Taeniura lymma* (Forsskål, 1775) [Dasyatidae]; **Broad Angel Wing**, *Barnea dilatata* (Soulelet, 1843) [Pholidae (angel wings)]; **Brown Chromis**, *Chromis multilineata* (Guichenot, 1853) [Pomacentridae];

Brown Mussel, *Perna perna* (Linnaeus, 1758) [Mytilidae]; **Brownspotted Grouper**, *Epinephelus chlorostigma* (Valenciennes, 1828) [Serranidae]; **Burrowing Crab**, *Raninoides lamarcki* Milne-Edwards & Bouvier, 1923 [Raninidae]; **Button-Crab Parasite**, *Loxothylacus texanus* Boschma, 1933 [Sacculinidae]; **California Bay Pea Crab**, *Parapinnixa affinis* Holmes, 1900 [Pinnotheridae]; **Caribbean Fire Sponges**, *Tedania* spp. [Tedaniidae]; **Caribbean Manatee**, *Trichechus manatus manatus* Linnaeus, 1758 [Trichechidae]; **Cero**, *Scomberomorus regalis* (Bloch, 1793) [Scombridae]; **Common Fish Louse**, *Argulus foliaceus* (Linnaeus, 1758) [Argulidae]; **Coney**, *Epinephelus fulvus* (Linnaeus, 1758) [Serranidae]; **Cressey's Sea Louse**, *Caligus rogercresseyi* (Boxshall & Bravo, 2000) [Caligidae]; **Crevalle Jack**, *Caranx hippos* (Linnaeus, 1766) [Carangidae]; **Doctorfish**, *Acanthurus chirurgus* (Bloch, 1787) [Acanthuridae]; **Dolphinfish**, *Coryphaena hippurus* (Linnaeus, 1758) [Coryphaenidae]; **Epaulette Shark**, *Hemiscyllium ocellatum* (Bonnaterre, 1788) [Hemiscyliidae]; **False King Crab**, *Paralomis granulosa* (Hombron & Jacquinot, 1846) [Lithodidae]; **Foureye Butterflyfish**, *Chaetodon capistratus* Linnaeus, 1758 [Chaetodontidae]; **French Grunt**, *Haemulon flavolineatum* (Desmarest, 1823) [Haemulonidae]; **Glasseye**, *Heteropriacanthus cruentatus* (Lacepede, 1801) [Priacanthidae]; **Goldfish**, *Carassius auratus* (Linnaeus, 1758) [Cyprinidae]; **Graceful Rock Crab**, *Metacarcinus gracilis* (Dana, 1852) (*Cancer* sometimes still used) [Cancridae]; **Harlequin Bass**, *Serranus tigrinus* (Bloch, 1790) [Serranidae]; **Japanese Louse** (also Goldfish Louse), *Argulus japonicus* Thiele, 1900 [Argulidae]; **Jelly Isopod**, *Anuropus* spp. [Anuropidae]; **Jellyfish Barnacle**, *Alepas pacifica* (Pilsbry, 1907) [Heteralepadidae]; **Gray Angelfish**, *Pomacanthus arcuatus* (Linnaeus, 1758) [Pomacanthidae]; **Gray Snapper**, *Lutjanus griseus* (Linaeus, 1758) [Lutjanidae]; **Gray Whale**, *Eschrichtius robustus* (Lilljeborg, 1861) [Eschrichtidae]; **Green Crab**, *Carcinus maenas* (Linnaeus, 1758) [Portunidae]; **King Mackerel**, *Scomberomorus cavalla* (Cuvier, 1829) [Scombridae]; **Largemouth Bass**, *Micropterus salmoides* (Lecepede, 1802) [Centrarchidae]; **Longsnout Bullhead Sculpin**, *Ereunias grallator* Jordan & Snyder, 1901 [Ereuniidae]; **Marine Anchor Worm**, *Pennella* spp. [Pennellidae]; **Non-swimming Fish Lice**, *Chonopeltis* spp. [Argulidae]; **Ochre Copepod**, *Balaenophilus manatorum* (Ortíz, Lalana, & Torrez, 1992) [Balaenophilidae]; **Oyster Pea Crab**, *Zaops ostreus* (Say, 1817) [Pinnotheridae]; **Patagonian Squid**, *Loligo gahi* (Orbigny, 1835) [Loliginidae]; **Peacock Bass**, *Cichla ocellaris* (Bloch & Schneider, 1801) [Cichlidae]; **Pink Salmon**, *Salmo gorbuscha* (Walbaum, 1792) [Salmonidae]; **Polychaete Barnacles**, *Rhizolepas annelidicola*, Day, 1939, and *R. gurjanovae* Zevina, 1968 [Rhizolepadidae]; **Red Bug**, *Tegastes acroporanus* Humes, 1981 [Tegastidae]; **Red Hind**, *Epinephelus guttatus* (Linnaeus, 1758) [Serranidae]; **Red Lionfish**, *Pterois volitans* (Linnaeus, 1758) [Scorpaenidae]; **Rock Beauty**, *Holacanthus tricolor* (Bloch, 1795) [Pomacanthidae]; **Rock Hind**, *Epinephelus adscensionis* (Osbeck, 1765) [Serranidae]; **Salmon Sea Louse**, incorrectly called 'Salmon Louse', *Lepeophtheirus salmonis* (Krøyer, 1838) [Caligidae]; **Scud** [amphipods]; **Sea Firefly**, *Cypridina hilgendorfii* (Müller, 1890) [Cypridinidae]; **Sea Lice**, *Caligus* and *Lepeophtheirus* [Caligidae]; **Sea Turtle Barnacle**, *Chelonibia testudinaria* (Leach, 1817) [Chelonibiidae]; **Shark Barnacle**, *Anelasma squalicola* (Lovén, 1844) [Anelasmatidae]; **Shortfin Smooth Lanternshark**, *Etmopterus joungi* (Knuckey et al. 2011) [Etmopteridae]; **Smooth Hammerhead**, *Sphyrna zygaena* (Linnaeus, 1758) [Sphyrnidae]; **Speckled Crab**, *Arenaeus cribrarius* (Lamarck, 1818) [Portunidae]; **Sperm Whale**, *Physeter macrocephalus* Linnaeus, 1758 [Physeteridae]; **Sponge Shrimp**, various species [Palaemonidae, Alpheidae, etc.]; **Striped Triggerfish**, *Xanthichthys lineopunctatus* (Hollard, 1854) [Balistidae]; **Tongue-replacing Isopod**, *Cymothoa exigua* (Schioedte & Meinert, 1884) [Cymothoidae]; **Toxic Gobies**, *Gobiodon* spp. [Gobiidae], **trunkfishes** [Ostraciidae]; **Yellow Angelfish**, *Centropyge heraldi* Woods & Schultz, 1953 [Pomacanthidae].

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Chapter 6
Effects of Parasitic Crustacea on Hosts

Stewart C. Johnson, Zbigniew Kabata, and Barbara F. Nowak

Abstract This chapter summarises our understanding of the direct effects that parasitic crustaceans have on their invertebrate and vertebrate hosts. At the individual host level, the effects of infection with parasitic Crustacea with respect to host pathological changes and the development of disease states are reasonably well understood. However, we have a much poorer understanding of how infection affects the physiological, immunological and reproductive status of hosts, with much of what is known arising from studies of sea lice (caligid copepods) infections of salmonids. Quantifying sublethal impacts of parasitic Crustacea infection on the biology and ecology of hosts is especially challenging even under controlled laboratory conditions. This is due to the complex and poorly understood interactions between parasite, host and environmental determinants, which ultimately influence the outcome and magnitude of the effect. There is very limited information on the effects that parasitic Crustacea have on their hosts at a population level, as well as on the indirect effects that they may have on species that interact with their hosts (community level effects). Our relatively good understanding of effects of sea lice on salmonids has been brought about due to the large economic impact that these parasites have on farmed salmonids and the necessity to develop new methods for their control. Unfortunately, the progress for other parasites and hosts is much slower which is in part due to the lack of experimental systems, research tools and funding.

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6.1 Introduction

The host-parasite relationship has been defined as the balance between limiting the parasite by host defences and the ability of the parasite to modulate, evade or restrict the host's response (for review, see Wikel et al. 1994). This relationship is based on a series of highly complex interactions between the parasite, its host and the environment in which these interactions take place. Most research on host-parasite interactions for crustacean parasites has focused on caligid copepods, of the genera *Caligus* Müller, 1785, and *Lepeophtheirus* von Nordmann, 1832, and a few salmonid hosts. Data for other species and host groups are mostly limited to field observations or description of the interaction from limited number of individuals only under particular conditions or at a particular point of infection.

It is very difficult to generalise about the nature of the interactions between parasitic Crustacea and their hosts. This is due partly to the fact that the nature of the relationship is influenced by many factors that can be very different for different species of Crustacea. For example, the number of parasites present, the invasiveness of their attachment and their mode and intensity of feeding will affect the host-parasite relationship. For any particular species, these factors can change dramatically over time due to processes such as recruitment of additional parasites, changes in the distribution on the host and changes in their method of attachment and/or feeding. With respect to the host, factors such as genetic background, maturation stage, health status, nutritional condition and the environmental conditions under which they are living will affect these interactions.

The impact of infections with parasitic crustaceans is poorly understood at both the individual and population levels. Kabata (1984) described the difficulties that are commonly associated with determining the effects of infection on the host. These include (1) experimental systems causing laboratory artefacts; (2) uncertainty with respect to the most appropriate host parameters for measurement; (3) establishing a "normal" condition of the host; (4) determining which part of the measurable effect is directly attributable to the presence of the parasite; (5) determining the effect parasite age structure has on the level of host infection; and (6) determining the effect of environmental change on the impact on the host for a particular level of infection and/or parasite population structure. These challenges are discussed in more detail below.

To understand the effects of parasitic Crustacea on their hosts better, controlled laboratory and/or field-based experiments are necessary. With respect to laboratory studies, the development of reliable systems for infecting hosts that enable repeatable and accurate infections to be established is critical. Attaining this goal has been difficult even for parasitic crustaceans that have direct life cycles and hosts that adapt well to laboratory conditions.

By far, the largest number of laboratory infection trials has been conducted with *Lepeophtheirus salmonis* (Krøyer, 1837). This species has a direct life cycle, and its salmonid hosts are easy to maintain in optimal physiological condition in the laboratory. Although a number of different methods for infecting fish with this species have been developed, none are 100% reliable, and the resulting infections often differ from natural infections (Treasurer and Wadsworth 2004; Jones et al. 2006a). As an example, laboratory infections often produce increased numbers of copepods on the gills, when compared to infection of farm-reared or wild salmonids (Treasurer and Wadsworth 2004). In such cases, laboratory-infected fish may differ in their physiological condition when compared to fish infected with an equal number of copepods on body surfaces other than the gills. Another area where laboratory infections differ from natural infections is the rate at which the parasites are acquired. To date, most laboratory studies have infected fish with a single (pulse) exposure of a large number of parasites. This results in relatively high numbers of only a few developmental stages being present at any given time. In comparison, fish infected in the field usually acquire their infections over a much longer period, as shown by a variety of different developmental stages being present. It is reasonable to expect that pulse vs. continuous infections could have different physiological and immunological effects on the host. In the case of other arthropod-host interactions, it has been shown that successive infections result in much different host responses, when compared to single or primary infections, even in situations where resistance to infections does not develop (Schoeler et al. 1999; Szabo and Bechara 1999).

In the case of *L. salmonis*, as with other species of parasitic copepods, it is very difficult to compare between laboratory-based studies. This is in part due to differences between studies in levels of infection, species of hosts, size of the hosts and sampling times. Several methods have been used to enable comparisons within and between studies that have used different sizes of hosts. Most authors standardise the number of copepods to a standard body length or weight. A less commonly used method is to calculate host body surface area and report copepod numbers per unit of area as “lice infection density” (Heuch et al. 2003). Standardisation of copepod numbers improves the ability to compare within and between studies. However, it is still necessary to report the developmental stages that are present and their distribution on the body, as these factors can greatly affect the magnitude of effects on the host.

In studies of host-parasite interactions in infections with Crustacea, relatively few host parameters have been commonly measured. Whether these are the most appropriate parameters for study is often a subject of debate. Part of the reason for this has been a lack of techniques and tools for the study of physiological and immune processes of invertebrates and fish. Historically, most studies have used measures of the physical condition of hosts, gross pathology and/or histology to determine effects of infection. More recently, researchers adopted the use of common indicators of physiological condition and stress, including such parameters as plasma cortisol, plasma glucose, concentration of plasma ions, plasma protein levels and gill Na+/K+-ATPase activity (Fast et al. 2006a). These indicators have often been used in conjunction with some other forms of analysis of immune function. Assays that have been applied to measure immune function include cellular immune function as determined by macrophage respiratory burst activity (Mustafa et al. 2000; Fast et al. 2002) and quantitative studies of immune-related gene expression (Fast 2005, 2014; Fast et al. 2006b, c, 2007; Jones et al. 2007).

The effects of copepods on host’s physical performance have been examined in swim tunnels, as in the case of *L. salmonis* and its salmonid hosts (Wagner et al.

2003, 2004; Wagner and McKinley 2004). Studies of this type have been limited by the availability of specialised equipment and the expertise that is necessary for conducting such research. The identification and selection of additional host parameters for study may be aided by careful review of literature for other parasite-host systems. The development of improved genomic resources and tools for hosts, the application of technologies such as proteomics and metabolomics and continued developments in the field of behavioural ecology will help us to achieve this goal.

It is critical that the "normal" condition of the host is known prior to investigating the effects of parasitic copepods on the host (Kabata 1984). Detailed information on how host parameters vary in the absence of copepods needs to be understood to assign biological significance to results. Such studies need to be conducted for hosts of different age, maturity, etc. over the normal range of environmental conditions to which they are exposed. Without this information, it is impossible to assign biological significance to values of host parameters measured during infections. In the laboratory, this can be achieved by having the appropriate control groups.

A lack of experimental systems that are easy to control and to manipulate accurately, as well as the availability of only limited physiological and immunological tools, makes it difficult to compare effects on hosts between studies even for single parasite species. These difficulties arise in part from the presence of different age distribution of copepods at the time of sampling. As mentioned previously, many copepods change their distribution on the host and the nature of their attachment throughout development. Such changes could have significant effects on the host parameters being measured. As an example, it has been shown for Atlantic salmon heavily infected with *L. salmonis* that the moult to the preadult stage is often associated with host mortality in the absence of lesions (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997; Ross et al. 2000). In this case, it has been hypothesised that the secretion of PGE_2 or other sea louse-derived compounds by preadult and adult stages may reach levels that are toxic to the salmon (Fast et al. 2004; Fast 2005).

In the review by Kabata (1984), the effects of parasitic copepods on host physiology, immune function and performance received little mention due to a scarcity of data. Since its publication, numerous studies covering these areas have been conducted, but most of these studies have been limited to studying the effects of *Lepeophtheirus salmonis* on its salmon hosts (reviewed in Tully and Nolan 2002; Boxaspen 2006; Wagner et al. 2008). Most of this research has been conducted in the laboratory on hosts held under optimal environmental and nutritional conditions, which limits their relevance to understanding natural infections.

6.2 Structural Changes

6.2.1 Invertebrate Hosts

Histological studies of the effects of parasitic crustaceans on their hosts are more common for fish than for other groups of animals. Although many of these studies have limited usefulness for understanding the subtleties of the host-parasite interactions, some do provide us with important clues to processes that may be at work. The effects of crustacean parasites on invertebrate hosts are reviewed in detail below.

6.2.1.1 Respiratory Organs

There are few reports on pathology associated with the attachment and feeding of parasitic copepods on respiratory organs of invertebrate hosts. Lauckner (1983) reviewed the literature on copepods that live in association with bivalves. The information on their pathological effects on the host is limited, both in the number of species and in the level of detail of the observations. Gill lesions have been reported in oysters, *Crassostrea gigas* (Thunberg, 1793) and *Crassostrea angulata* (Lamarck, 1819), infected with the poecilostomatoid *Myicola ostreae* Hoshina and Sugiura, 1953; however, no detailed descriptions of these lesions are available (for review, see Lauckner 1983). The presence of "gall-like structures" on the gills of clams was reported in infections with the poecilostomatoids *Myicola metisiensis* Wright, 1885, and *Lichomolgus leptodermatus* Gooding, 1957. Hypertrophy and an inflammatory response were present at the sites of attachment of an unidentified copepod to the gills of the oyster *Crassostrea virginica* (Gmelin, 1791) (reviewed in Lauckner 1983).

More recently, Cáceres-Martínez and Vásquez-Yeomans (1997) reported on the attachment of the cyclopoid copepod *Pseudomyicola spinosus* (Raffaele and Monticelli, 1885) to gills (without an effect on the host), digestive gland, connective tissue, stomach and intestine of the mussels *Mytilus galloprovincialis* Lamarck, 1819, and *Mytilus californianus* Conrad, 1837. In the catarina scallop *Argopecten ventricosus* (G. B. Sowerby II, 1842), infection of the gills by *P. spinosus* resulted in the rupturing of gill filaments (Cáceres-Martínez et al. 2005). Clarke and Klussmann-Kolb (2003) provided a brief report on the effects of infection by the poecilostomatoid *Epimolgus orientalis* (Heegaard, 1962) (= *Alimeda orientalis*) on the gills of the sea hare *Dolabrifera brazieri* Sowerby, 1870. This copepod attached itself to the base of the gill plicae by means of its second antennae, and its attachment and feeding activities on the epithelium resulted in tearing and maceration of the tissue; however, there was no mention of a host response (Clarke and Klussmann-Kolb 2003).

Information on parasitic crustaceans of cephalopods is very limited despite numerous crustaceans found in association with cephalopods (Hochberg 1990). Castellanos-Martínez and Gestal (2013) reviewed the pathogens and immune response of cephalopods and provided additional information on crustacean parasites. Although numerous species of copepods are reported from cephalopods, there are no reports of gill or other organ damage (Hochberg 1990; Castellanos-Martínez and Gestal 2013). Parasitic isopods and brachyurans are reported occasionally in the mantle cavity of cephalopods; however, these infections are in most cases considered incidental or transitory, and there are no data on host response (Hochberg 1990; Castellanos-Martínez and Gestal 2013).

Fig. 6.1 (**a**) Queensland snapping shrimp, *Alpheus richardsoni* Yaldwyn, 1971, with a bopyrid isopod, *Parabopyrella australiensis* (Bourdon, 1980), inside the gill chamber (arrow), (**b**) removed female bopyrid isopod. Images © Kerry Hadfield and Nico Smit

In regard to the crustacean hosts, there is one report of the siphonostomatoid copepod *Nicothoe astaci* Audouin and Edwards, 1826, causing damage to the gills of the lobster *Homarus gammarus* (Linneus, 1758) (see Mason 1959). This species attaches itself to the gills by means of a suctorial mouth and uses its mandibles to pierce the gill filaments to obtain a blood meal (Mason 1959). The presence of high numbers of this copepod caused the gills to become seriously damaged and misshapen.

Species within the isopod families Bopyridae, Cryptoniscidae, Dajidae and Entoniscidae are recognised as parasites of a number of crustacean genera. Bopyrid isopods inhabiting the branchial cavity of decapod hosts are reported to cause variable levels of host tissue damage (Fig. 6.1). For example, examination of the branchial chamber of the squat lobster *Munida iris* Milne Edwards, 1880, infected with the blood feeder *Munidion irritans* Boone, 1927, identified deformation of the carapace and areas of gills damage that were attributed to the weight of the parasite. Histological examination of the deformed cuticle identified a thickening of and increased blood sinus space within the epidermis and connective tissue layers of the cuticle. Haemocyte density appeared to be higher at sites of mouthpart entry into the blood sinus (Bursey 1978). In areas of damaged gill tissues at and around the periphery of the attachment site, there was an accumulation of haemocytes and necrotic pigment nodules. Deeper gill tissues and underlying muscle tissues were unaffected.

There are a large number of copepod species that live in association with ascidians (reviewed in Monniot 1990). The nature of these associations varies from ones that can be classified as “inquiline” to those that are easily recognised as truly parasitic (also see Chap. 4). Several that are endoparasites of ascidians are found within cysts that are formed of host tissues. In some cases, it is evident that host tissues have been modified for the benefit of the copepod. A well-studied example of such a species is the notodelphyoid copepod, *Scolecodes huntsmani* (Henderson, 1930), which forms cysts within the blood sinus of the branchial basket of several ascidian species (Dudley 1968; Monniot 1990). Adult females are contained within cysts that consist of an elongated sac open to the atrium by means of a ciliated duct or “funnel.” This funnel allows males to access the female as well as provides a route for the release of nauplii. As these cysts do not open into the lumen of the blood vessel, it is thought that *S. huntsmani* obtains its nutrition by feeding on the walls of the cyst or on other host cells within that space (Dudley 1968). Using light and electron microscopy, Dudley (1968) described in detail the structure of cysts associated with the different developmental stages of this copepod within the ascidian *Styela gibbsii* Stimpson, 1864. The walls of cysts that contain adult females are clearly derived from host tissues. The columnar cells that line the ciliated funnel have morphological features similar to host blood vessel endothelial cells. The structure of the sac, which surrounds the copepod, differs from that of the ciliated duct region and the blood vessels of the host. The sac walls are reported to lack a basal lamina, and the cells of the sac wall have irregularly spaced nuclei (Dudley 1968). The earlier developmental stages of this copepod produce cysts that lack ducts and are composed entirely of cuboidal ciliated cells (Dudley 1968). In these cysts, the space between the copepod and the cyst wall contains free-host cells that share morphological features with those making up the cysts of adult females. It appears that the ciliated funnel is formed only after the female reaches the adult stage (Dudley 1968). The manner by which this species stimulates the host to produce this complex cysts structure is unknown. It is possible that *S. huntsmani* produces substances that stimulate and/or alter the development of host cells. If this is the case, this would be a very exciting and important discovery, with implications in developmental biology and many other areas.

6.2.1.2 Other Organs

The cyclopoid copepods *Mytilicola intestinalis* Steuer, 1902, and *Mytilicola orientalis* Mori, 1935, are endoparasites found in the gut of mussels and other bivalves (reviewed in Lauckner 1983). The presence of *M. intestinalis* in the gut of *Mytilus edulis* Linnaeus, 1758, results in dysplasia, resulting in the replacement of the normal ciliated columnar cells by non-ciliated cuboidal cells. In heavily infected individuals, the gut lumen may become occluded and the gut wall distended (see also Moore et al. 1978). Similar observations are reported for *M. orientalis* infecting the gut of the oyster *Crassostrea gigas*. In this instance, heavy infections cause severe erosion of the gut epithelium, with the appendages of the copepods penetrating the underlying connective tissue. Fibrosis of the connective tissues underlying the eroded areas was reported (Lauckner 1983).

Since the review by Lauckner (1983), there has been very limited new data published on the effects of parasitic copepods on molluscs. A number of parasitic copepods that are associated with organs such as the kidneys/pericardia, gonads and digestive glands of opisthobranch molluscs have been reported (Jensen 1987; Schrödl 2002 and references therein). Unfortunately, no histological descriptions of the interactions between these copepods and their host tissues are available. In the case of *Ismaila monstrosa* Bergh, 1867, infecting the sea slug *Ercolania viridis* (Costa, 1867), the anterior portion of the body of the female is positioned beneath the kidney and pericardium of the host, and the abdomen protrudes through the body wall (Jensen 1987). The body of *I. monstrosa*, which eventually occupies most of the body cavity, causes the loss of gonadal tissue and the eventual castration of the host.

Pseudomyicola spinosus has been found embedded in the connective tissue of the digestive gland, as well as within the lumen of the stomach and intestine of the mussels *Mytilus galloprovincialis* and *Mytilus californianus* (see Cáceres-Martínez and Vásquez-Yeomans 1997). It is believed that this species penetrates the wall of the digestive tract, enabling it to gain access to digestive gland connective tissue. In some cases, the copepods' presence within the connective tissue resulted in the formation of granuloma-like structures. Copepods that were encapsulated within these granuloma-like structures were most likely dead. When *P. spinosus* is within the lumen of the stomach (and/or intestine), they are covered by mucus, and there is some evidence of elongation of epithelial cells towards the copepods. Loss of epithelial cells, and in some cases small amounts of haemocyte accumulation and alterations to the basal membrane, was observed at the point of attachment of the copepods' appendages. Attachment of *P. spinosus* to the stomach of the catarina scallop resulted in the detachment and loss of the stomach's epithelium (Cáceres-Martínez et al. 2005).

Numerous species of copepods have been reported from echinoderm hosts, the majority of these being found in the coelomic cavity or digestive tract (for review, see Jangoux 1990). The number of species of parasitic copepods known to be associated with echinoderms has increased significantly since the publication of Jangoux (1990). However, there is little new information with respect to their interactions with their hosts.

The reactions of echinoderms to parasitic copepods range from no host response through to the formation of structurally complex cysts and galls. Depending on the species of copepod and its host species, there are considerable differences in the structure and locations of these cysts and galls. The mechanisms responsible for the formation of these cysts and galls are not understood. In the case of species such as *Scolecodes huntsmani*, which forms cysts that are made up of modified host cells, it should be determined whether these copepods produce substances that are responsible for the modification of the host tissues. If it can be demonstrated that parasitic copepods stimulate and/or alter the development of host cells to produce such structures, this will be a very significant biological finding. There is a large body of research on echinoderm development, as well as rapidly improving genomic resources and tools for this group. These resources are very important as they provide the tools making such investigations possible.

Schuldt and Damborenea (1988) examined the sites of attachment of the cryptoniscus larvae of the bopyrid isopod, *Probopyrus pandalicola* (Packard, 1879) on the shrimp, *Palaemonetes argentinus* Nobili, 1901. Using naturally infected hosts, these authors examined the attachment sites of larvae that attached to areas not within the branchial chamber. These female larvae, which are referred to as "endoparasitic forms" or "tissue cryptonisci", penetrate host tissues for at least a short period. In the case of *P. argentinus*, these larvae were reported to affect connective haemolymphatic tissues with little evidence of a host response. Penetration of areas containing gonadal tissues can result in displacement of ovaries and testis, with little evidence of a host response and no apparent effect on the development of germinal cells. These authors suggested that the lack of a host response was not due to systemic immunological suppression due to the presence of parasites, as there were well-developed inflammatory responses to trematode parasites that were coinfecting the shrimp. The attachment of the adult female *Probopyrus pandalicola* within the branchial chamber of *Palaemonetes argentinus* resulted in thinning of the wall of the branchiostegal and a corresponding reduction in its haemolymph volume in areas undergoing compression by the parasite (Schuldt and Capítulo 1987).

6.2.2 Vertebrate Hosts

6.2.2.1 Respiratory Organs

Earlier literature describing pathological changes associated with parasitic copepod infections of fish was reviewed in detail by Kabata (1970, 1984). With respect to the gills, both damage caused by attachment and feeding activities and damage caused by physical presence of copepods within the gill cavity that are neither attached to nor feeding on the gills were considered. Damage to the gills was classified under the general headings: (1) physical destruction of the filaments by pressure, abrasion and/or feeding; (2) occlusion of brachial circulation leading to the atrophy of gill tissues; and (3) hypertrophy and hyperplasia of the gill tissues (Kabata 1984). For the purpose of this chapter, this system of classification has not been used as pathological changes associated with parasitic copepods on gills can often be classified under more than one of these headings.

Gill responses to parasitic copepods have been described for a variety of elasmobranch species (Benz and Deets 1986; Benz and Adamson 1990; Borucinska and Benz 1999). These studies all report hyperplastic lesions associated with the organs of attachment of adult female copepods. Lesions associated with *Kroyeria caseyi* Benz and Deets, 1986, infection of the night shark, *Carcharhinus signatus* (Poey, 1868), occur at the sites where females attach and embed themselves into the interbrachial septum. No gross pathologies were noted within the deeper tissues of the interbrachial septa; however, a response was reported for soft tissues surrounding the copepod's body (Benz and Deets 1986). Infection of the thresher shark, *Alopias vulpinus* (Bonnaterre, 1788), with the siphonostome copepod, *Nemesis robusta* (Van Beneden, 1851), results in large-scale cellular proliferation and a papillose condition at the site of attachment (Benz and Adamson 1990). In extreme cases, occlusion of interlamellar spaces due to epithelial proliferation was reported. Areas of tissue erosion were reported beneath the cephalothorax. There was no inflammation associated with these lesions. Borucinska and Benz (1999) described the attachment sites of *Phyllothyreus cornutus* (Milne Edwards, 1840) on the interbrachial septa of the blue shark, *Prionace glauca* (Linnaeus, 1758). Grossly visible, soft, papillomatous lesions contained the embedded second antennae of the copepods. In histological sections, lesions were characterised by epithelial hyperplasia and disorganisation of the underlying dermis. These changes overlaid a layer of granulation tissue or fibrosis with lymphoid nodules replacing the lamina propria (Borucinska and Benz 1999). In contrast, lesions associated with the smaller, more mobile male of this species were characterised by regions of epithelial ulceration that were surrounded by a mild hyperplasic response, loss or necrosis of some of the underlying dermis and the presence of subacute inflammatory reactions.

Of all the copepod groups found on gills of teleosts, members of the family Ergasilidae are the most widely studied with respect to their pathological effects. Roubal (1989a) described the effects of *Ergasilus lizae* Krøyer, 1863, and *Dermoergasilus acanthopagri* Byrnes, 1986, on the gills of the yellowfin bream *Acanthopagrus australis* (Günther, 1859). To attach to its host, *E. lizae* uses its second antennae to penetrate the epithelial and subepithelial regions of the basal portions of the gill filaments. Localised host responses to the presence of the antennae include hyperplasia and inflammation. Both reactions occur in gill filaments that are beneath the copepods, and in some instances, these reactions lead to the fusion of adjacent gill filaments. The inflammatory infiltrate contained lymphocytes, eosinophilic cells, macrophages and neutrophils. *Dermoergasilus acanthopagri* attaches itself near the tips of the gill filaments and maintains its position by encircling the filament with its second antennae (Roubal 1989a). This mode of attachment results in occlusion of the blood vessels and tissue compression that ultimately leads to the development of a hyperplastic response in the epithelium and inflammation in the subepithelial tissue. An inflammatory response similar to that seen with *E. lizae* was reported for *D. acanthopagri* (see Roubal 1989a).

Dezfuli et al. (2003) examined the pathology of *Ergasilus sieboldi* Nordmann, 1832, infection on the gills of the bream *Abramis brama* (Linnaeus, 1758). On this host, adult female *E. sieboldi* attached near the base of the primary lamellae by means of their second antennae. This attachment and subsequent feeding activities resulted in the erosion of the primary lamellae, hyperplasia of the intralamellar epithelium, resulting in lamellar fusion, mucous cell proliferation, and enhanced mucus production, congestion and haemorrhaging. Ultrastructural observations revealed the presence of high numbers of eosinophilic granular cells (fish equivalent of mast cells) and rodlet cells, especially in the secondary lamellae at the site of attachment (Dezfuli et al. 2003). Attachment of *Dermoergasilus intermedius* (Kabata, 1992) to gills of tropical fresh water catfish *Arius leptaspis* Bleeker, 1862, resulted in compression of the gill filament where it was encircled by second antennae and necrosis, inflammation and hyperplasia of epithelium (Fig. 6.2; Nowak unpublished).

Heavy infections of the gills of silver carp, *Hypophthalmichthys molitrix* (Valenciennes, 1844), and bighead, *Hypophthalmichthys nobilis* (Richardson, 1845), by the ergasilid copepod, *Sinergasilus polycolpus* (Markevich, 1940), resulted in the clubbing and fusion of gill filaments, as well as some loss of filament tissues (Molnár and Székely 2004). Epithelial proliferation with some infiltration of eosinophilic granular cells and proliferation and degeneration of the connective tissue were reported. Neither granulocytes nor lymphocytes were observed at these sites. The cellular responses reported by Roubal (1989a), Dezfuli

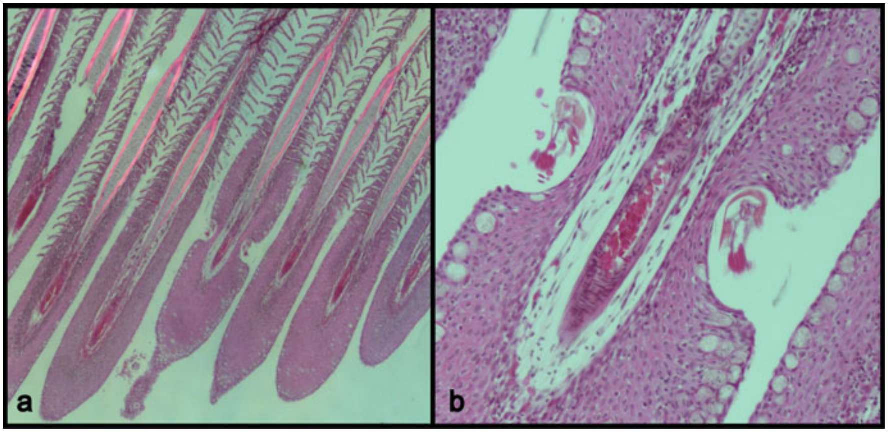

Fig. 6.2 *Dermoergasilus intermedius* (Kabata, 1992) attached to a gill filament of salmon catfish *Arius leptaspis* Bleeker 1862. (**a**) Note compression of the filaments, (**b**) note hyperplasia and inflammation of the epithelium

et al. (2003) and Molnár and Székely (2004) are similar to those reported for *Ergasilus sieboldi* on gills of the tench, *Tinca tinca* (Linnaeus, 1758) and *Ergasilus labracis* on the gills of the striped bass, *Morone saxatilis* (Walbaum, 1792), as reviewed in Kabata (1970, 1984).

Lernanthropid copepods of the genus *Lernanthropus* de Blainville, 1822, are very commonly found on the gills of marine teleosts, especially those of warm waters. Since the publication of Kabata (1984), pathological studies have been completed for four additional species, *Lernanthropus atrox* Heller, 1865; *Lernanthropinus temminckii* (von Nordmann, 1864); *Lernanthropus koenigii* Steenstrup and Lütken, 1861; and *Lernanthropus kroyeri* Van Beneden, 1851, on a number of host species. All of these species attach themselves to the primary lamellae of the host by means of their second antennae, which can penetrate the gill tissues down to the cartilage. Additional attachment support is provided by the maxillipeds and the third leg (Roubal 1989a; Manera and Dezfuli 2003). The large size and blood-feeding habit of *L. atrox* result in massive tissue disruption of the gill lamellae (Roubal 1989a). Epithelial tissues are compressed and deformed, hyperplasia, oedema, cellular infiltration and haemorrhaging being present. In the subepithelial region, there is evidence of haemorrhaging, oedema and leukocyte infiltration (Roubal 1989a). Infection of the sea bass *Dicentrarchus labrax* (Linnaeus, 1758) with *L. kroyeri* is reported to produce similar effects (Manera and Dezfuli 2003). At the gross level, hyperplasia of the interlamellar epithelium and partial fusion of the lamellae were observed. Histological examination of the site of attachment showed that tissues in the immediate vicinity of the copepods were eroded and necrotic with both the filament cartilage and blood vessels frequently exposed. Hyperplasia and proliferation of mucous cells were present in the distal parts of infected primary lamellae. Constriction of the brachial afferent artery and damage to the hemibranch adductor muscle were associated with compression of the tissues by the second antenna

(Manera and Dezfuli 2003). Similar gill responses have been reported for both *Lernanthropinus gibbosus* on greater lizardfish *Saurida tumbil* (Bloch, 1795) and *Lernanthropus koenigii* on black pomfret, *Parastromateus niger* (Bloch, 1795) (see Radhakrishnan and Balakrishnan Nair 1981).

Naobranchia variabilis Brian, 1924, is a common parasitic copepod found on the gills of a wide range of marine fish species in the Atlantic and Indian Oceans. Roubal (1999) described the pathology associated with the attachment of juvenile, subadult and adult *N. variabilis* to the gills of toadfish, *Tetractenos hamiltoni* (Richardson, 1846). This species becomes initially attached to the gills as early juveniles by means of a thin filament that arises from the tips of the second maxillae. As this copepod develops, attachment is afforded by the second maxillae that become permanently fused to form a flat-walled ring encircling the primary lamellae (Kabata 1984; Roubal 1999). Little host tissue proliferation is associated with attachment of the early juvenile stage by its filament or second maxillae; however, the amount of proliferation increases as the copepods mature. Constriction of the gill filament by the second maxillae results in a reduction in the thickness of the lamellar epithelium beneath it and restriction of the afferent and efferent blood vessels. Proliferating tissues adjacent to the second maxillae consisted of hyperplastic epithelial Malpighian cells and some proliferation of the connective tissue within the dermis. There was little evidence of infiltrating cells in these regions. Gill filaments in the vicinity of the mouthparts of juvenile copepods were eroded, and epithelial proliferation was present (Roubal 1999).

Sutherland and Wittrock (1985) reported on the pathology associated with the attachment of *Salmincola californiensis* (Dana, 1852) to the gills of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792). Attachment of the frontal filament to the dermis resulted in little damage and in most cases only a minor host response. As the copepods developed, mucous cell number was reduced, and epithelial hyperplasia was present, in some cases resulting in the fusion of adjacent secondary lamellae. At the gross level, attachment by the adult female caused pale-coloured gills, crypting of the filament and clubbing of their distal ends. At the histological level, well-developed epithelial hyperplasia and hypertrophy were reported in association with the bulla. In this species, the host response is thought to improve the security of attachment to the host. Massive infiltration of eosinophilic granular cells into the epidermis and dermis was noted, as well as the lack of mucous cells within the hyperplastic regions that were within the grazing range of the copepod. Adult females were reported to feed upon the surface of these hyperplastic tissues.

The extent of the pathology associated with the attachment of the lernaeopodid copepod, *Alella pagelli* (Krøyer, 1863), to the gills of the yellowfin bream, *Acanthopagrus australis*, was related to the stage of the copepod development (Roubal 1989b). Grossly, gill filaments to which copepods were attached were frequently reduced in length. Swelling and fusion of the primary lamellae of adjacent filaments were evident, especially when larger immature and adult stages were present. The initial host response to the presence of both the frontal filament and bulla was acute-phase inflammation with large numbers of infiltrating cells in the immediate vicinity of the attachment organ. The magnitude of the granular chronic inflammatory response to the bulla diminished with parasite age and in mature adults. The number of gill surface secretory cells was reduced in the vicinity of the copepod.

Dissonus manteri Kabata, 1966, is a siphonostome copepod that develops through to the adult stages on the gills of its host. The pathology associated with the copepodid, chalimus, preadult and adult stages of this species has been studied for the coral trout, *Plectropomus leopardus* (Lacepède, 1802) by Bennett and Bennett (1994, 2001). In this species, the copepodid stage becomes attached to the gills using its second antennae and maxillipeds and causes lesions that vary in severity depending on the duration of attachment. At the cellular level, a characteristic feature of copepodid attachment was a compressed and hyperplastic epithelium along the anterior margin of the cephalothorax and varying degrees of hyperplasia in tissues posterior to the copepodid. Some minor hyperplasia was associated with the region beneath the thoracic legs. Infiltrating cells were seen in the connective tissue beneath the second antennae and mouthparts of the copepodid. With the moult to the attached chalimus stages, the severity of the associated lesions increased. Chalimus attachment was characterised by localised thickening of host tissues owing to the proliferation of fibroblasts and fibre production around the core of the lamellae. As seen for the copepodid stage, well-developed epithelial hyperplasia occurred immediately adjacent to the anterior margin of the cephalothorax, as well as in the vicinity of the posterior body regions. Some infiltrating cells were observed within the fibrosis and in the vicinity of the basal plate of the frontal filament (Bennett and Bennett 1994). The preadult and adult stages of *D. manteri* were attached to the base of the gill filaments, to the pseudobranchs and occasionally to the surfaces of the buccal cavity (Bennett and Bennett 2001). No pathology was associated with those within the buccal cavity; however, those that were attached to the gills caused significant pathological changes. Attachment to the gills was maintained by use of the maxillipeds, which penetrated the lamellar epithelium and its underlying connective tissues. This resulted in a range of cellular responses from a thickening of the lamellae through to the development of large hyperplastic nodules. Feeding activities initially caused erosion of the epithelium that was then followed by the gradual development of tissue nodules. These nodules, on which the copepods fed, were formed by a hyperplastic response of the epithelial tissues and fibrosis of the underlying connective tissue. Some infiltration of cells occurred in the vicinity of the maxillipeds, as well as in the fibrous connective tissue of the nodules (Bennett and Bennett 2001).

Caligus nanhaiensis Wu and Pan, 1997, is a caligid copepod that has been responsible for disease outbreaks in cultured banded grouper, *Epinephelus awoara* (Temminck and Schlegel, 1842) (cf. Wu et al. 1997). This species feeds on the gills of its host and is reported to cause severe damage of the gill filaments, with little evidence of any host response.

It has been demonstrated that the magnitude of the host responses of naïve chinook, *Oncorhynchus tshawytscha* (Walbaum, 1792); coho, *Oncorhynchus kisutch* (Walbaum, 1792); and Atlantic salmon, *Salmo salar* Linnaeus, 1758, to infection with the salmon louse, *Lepeophtheirus salmonis*, is important with respect to its establishment and maintenance on the host (Johnson and Albright 1992a, b). At 1, 3 and 5 days postinfection (DPI), gills of the resistant species, coho salmon, showed erosion of the epithelium, haemorrhaging, well-developed hyperplasia and acute inflammation. All copepods were lost from the gills by 10 DPI (Johnson and Albright 1992a). In this case, the inflammatory infiltrate consisted primarily of neutrophils and some lymphocytes. In comparison, the gill responses of the more susceptible species, chinook and Atlantic salmon, were minor, with little evidence of hyperplasia or inflammation, especially in Atlantic salmon. In these species, copepods were retained on the gills throughout their chalimus stages (Johnson and Albright 1992a). We know of only one other instance, where the magnitude of the gill response to a particular copepod species is reported to vary between closely related species of fish. Kabata (1984) reported a difference in the magnitude of the response to *Clavella adunca* (Strøm, 1762) between Atlantic cod, *Gadus morhua* Linnaeus, 1758, and haddock, *Melanogrammus aeglefinus* (Linnaeus, 1758). The bulla of this species caused only a minor hyperplastic tissue response in Atlantic cod when compared with a much stronger hyperplastic response seen in haddock.

Infections of striped trumpeter *Latris lineata* (Forster, 1801) with the chondracanthid copepod *Chondracanthus goldsmidi* Tang, Andrews and Cobcroft, 2007, resulted in gross swelling at the attachment site seen histologically as extensive epithelial hyperplasia and necrosis (Fig. 6.3; Andrews et al. 2010). Papilloma-like growth (Fig. 6.3) with numerous eosinophilic granular cells positive for the antimicrobial peptide piscidin surrounded the parasite (Andrews et al. 2010). Upregulation of inflammatory cytokines TNF-alpha, IL-1beta and IL-8 was observed in the gills of striped trumpeter affected by this parasite (Covello et al. 2009). In addition to the gills, *Chondracanthus goldsmidi* can attach to inner opercula and nasal cavities of their hosts, which include a number of marine fish species (Andrews et al. 2010).

There are five descriptions of the histopathological changes associated with attachment and feeding activities of gnathiid isopods (Honma and Chiba 1991; Honma et al. 1991; Heupel and Bennett 1999; Hayes et al. 2007, 2011). Hayes et al. (2007) provide a detailed description of the histopathology associated with gnathiids, identified as *Gnathia pantherina* Smit and Basson, 2002, feeding on the elasmobranch host the puffadder shyshark *Haploblepharus edwardsii* (Schinz, 1822). Attachment and feeding on the gill resulted in loss of epidermal tissues, displacement of cartilage and compression of the dermis and haemorrhaging within the tissues in the vicinity of the mouthparts (Fig. 6.4). Hyperplasia of epidermal tissue was found near the parasite and the infiltration of inflammatory cells to the site of feeding provided evidence of a host response. Similar host responses have been reported for gnathiid isopods infecting gills of stingrays, *Dasyatis* spp. (see Honma and Chiba 1991; Honma et al. 1991) and the epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre, 1788) (Heupel and Bennett 1999). However, sites of larval attachment in the buccal cavity of the epaulette shark were characterised by varying levels of tissue disruption with no evidence of proliferation or other host responses. With respect to teleosts, Hayes et al. (2011) described the host response of single captive blackeye thicklip, *Hemigymnus melapterus* (Bloch, 1791), which died rapidly following a laboratory infection with very large numbers of the gnathiid, *Gnathia aureamaculosa* Ferreira and Smit, 2009, in Ferreira et al. (2009). The presence of the larvae resulted in physical destruction of the gill and production of large amounts of mucus. No inflammation was observed which might be due to the rapid death of the host that occurred 30 minutes following exposure.

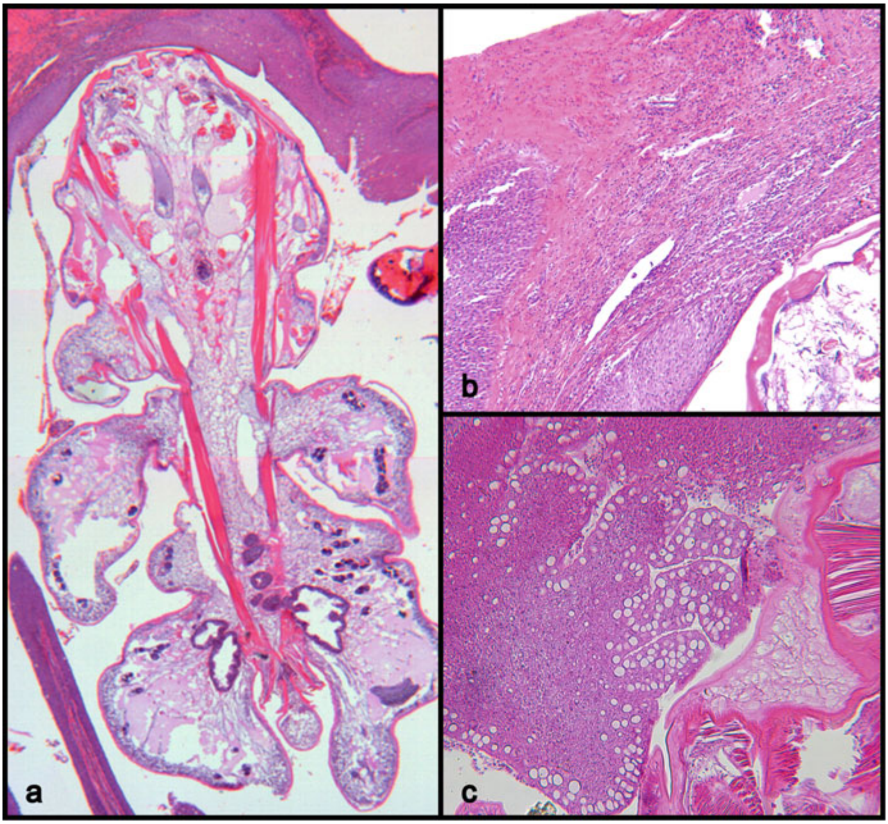

Fig. 6.3 (**a**) Pressure atrophy, (**b**) necrosis and (**c**) papilloma-like growth caused by *Chondracanthus goldsmidi* Tang, Andrews and Cobcroft, 2007, at the attachment site. Note an increase in the numbers of mucous cells. Images © Dr Melanie Andrews

It is possible that some of the gill changes may be due to stress associated with infection. For example, stress-related changes in gill morphology have been reported for infections of *Lepeophtheirus salmonis* on salmonids (Nolan et al. 1999, 2000b). Nolan et al. (1999) infected post-smolt Atlantic salmon with either three, six or ten preadult *L. salmonis* and examined changes in the epithelial structure using scanning and transmission electron microscopy. Although *L. salmonis* was not found on the gills, lifting of the epithelium, intracellular swelling, infiltration by leukocytes and increased chloride cell turnover were observed in the gills of infected fish. The magnitude of these effects was positively correlated with the number of copepods present and their time on the host. These changes were thought to occur in response to the stress of infection. Similar changes were evident in infected rainbow trout only after the application of a confinement stress (Nolan et al. 2000b). Changes that were reported for infected fish included epithelial cell and lamellar swelling, thickening of the lamellar bases at the junction with the filament, detachment of the epithelium, apoptosis of chloride cells and increased mucus production.

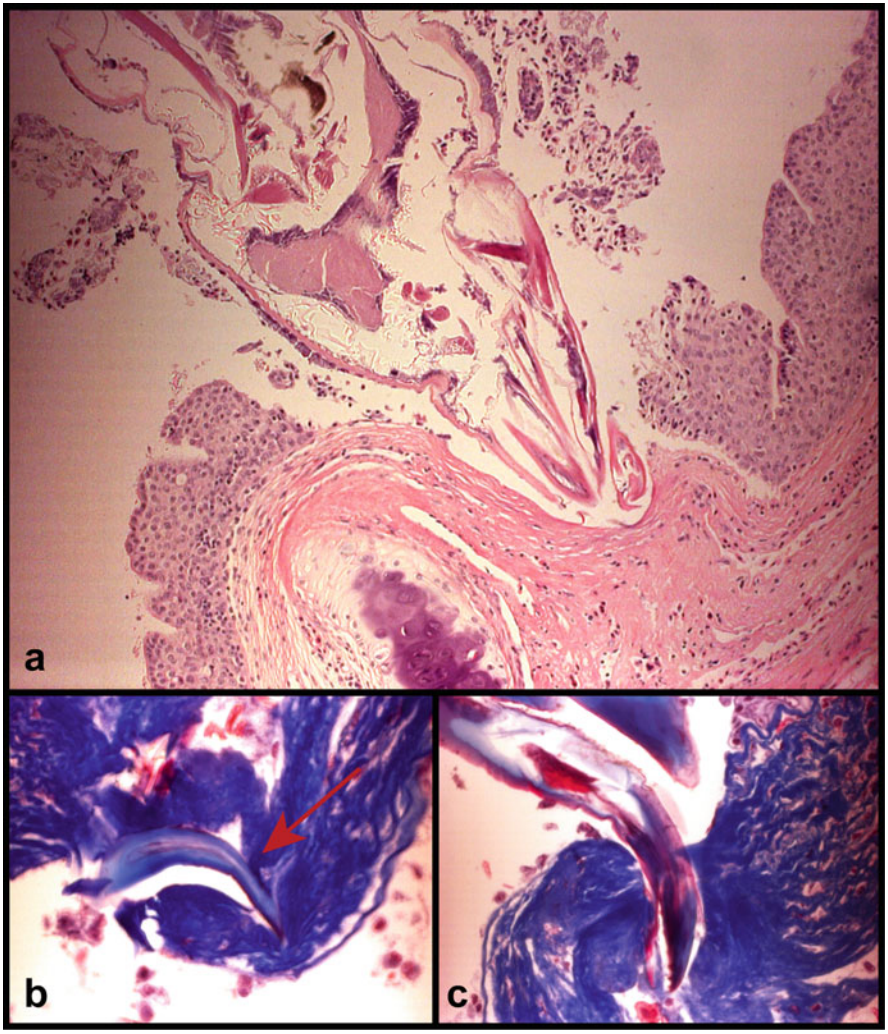

Fig. 6.4 (**a**) Displacement of cartilage, loss of epidermis and compression of the dermis where the gnathiid mouthparts attach, (**b**) hooked dactylus of gnathopod (arrow) penetrating dermis, (**c**) gnathiid mandible penetrating and lifting the dermis. Images © Nico Smit and Polly Hayes

6.2.2.2 Other Organs

Kabata (1984) provided a detailed review of the effects of parasitic copepods on the integument, musculature, sense organs and internal organs of fish. The severity of damage attributed to a single copepod species often varies widely. Since the publication of Kabata (1984), there have been numerous studies on pathology associated with copepod infection of non-respiratory organs of fish. Unfortunately,

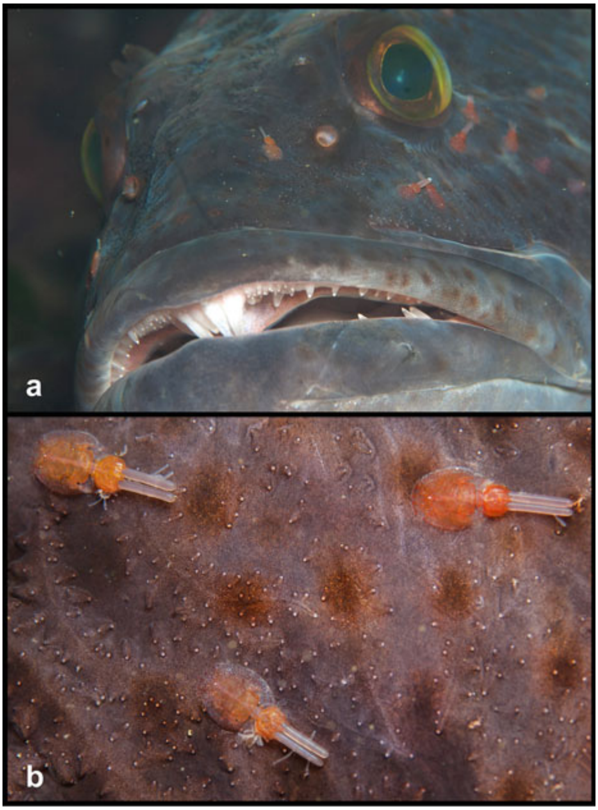

Fig. 6.5 *Caligus* sp. on the skin of lingcod *Ophiodon elongatus* Girard, 1854. (**a**) Note the position on the head of the lingcod, (**b**) close-up of three female parasites attached to the skin. Images © Jon Bryan

the majority of these have been limited to species within the family Caligidae, due in part to the economic importance of this family as parasites of both cultured and wild fish.

With regard to gross pathology caused by caligid copepods, it is often reported that there is little evidence of damage caused by the early developmental stages (copepodid and chalimus) of caligid copepods. The later developmental stages (preadults and adults) are generally reported to cause only minor damage to their hosts (Fig. 6.5; Ogawa 1992; Roubal 1994; Johnson et al. 1996). However, when these copepods are abundant, significant pathology may occur. For example, extensive areas of skin erosion and haemorrhaging on the head and back and a distinct area of erosion and subepidermal haemorrhage in the perianal region have been reported for both wild and farmed salmonids heavily infected with *Lepeophtheirus salmonis* (see Johnson et al. 1996; Pike and Wadsworth 1999). Similar types of lesions have also been reported for Atlantic halibut, *Hippoglossus hippoglossus* (Linnaeus, 1758), infected with large numbers of *Caligus elongatus* von Nordmann, 1832, and the rabbit fish, *Siganus fuscescens* (Houttuyn, 1782), infected with large numbers of *Caligus oviceps* Shiino, 1952, and *Lepeophtheirus atypicus* Lin, Ho and Chen, 1996 (cf. Lin et al. 1996; Bergh et al. 2001). Infection of sea bass, *Dicentrarchus labrax*, with large numbers of

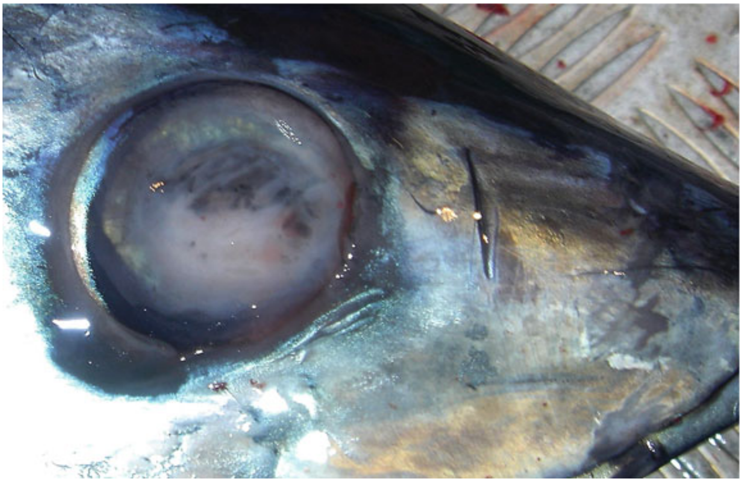

Fig. 6.6 A damaged perforated eye leading to blindness. A positive relationship has been reported between the presence of copepod *Caligus chiastos* Lin and Ho, 2003, and eye damage in farmed tuna. Image © Dr. Craig Hayward

Caligus species [*C. minimus* Otto, 1821; *C. pageti* Russell, 1925; *C. mugilis* Brian, 1935; and *C. apodus* (Brian, 1924)] resulted in the development of lesions on the head and in and around the buccal cavity that ranged in severity from pinpoint lesions through to dispersive ulcerative lesions (Ragias et al. 2004). Gross eye damage has been reported in southern bluefin tuna, *Thunnus maccoyii* (Castelnau, 1872), infected with *Caligus chiastos* Lin and Ho, 2003 (see Fig. 6.6; Hayward et al. 2008). This association was present at most sampling occasions for both ranched and experimental tuna (Hayward et al. 2008, 2009). The damage has been either due to direct effect of sea lice attachment and feeding or due to the infected fish rubbing against net and other objects to get rid of the parasites (Hayward et al. 2008).

The histopathology associated with the copepodid and early chalimus stages of *Lepeophtherius salmonis* has been described for laboratory and naturally infected Atlantic salmon (Jones et al. 1990; Johnson and Albright 1992a). Under both situations, there is minor, if any, host response to the second antennae, maxillipeds or feeding activities of the copepodid stage. With respect to the chalimus stages, there was little to no cellular response and only mild hyperplasia associated with the frontal filament. Epidermal hyperplasia, with abundant areas of focal necrosis, was reported along the margins of the lesions with increased levels of melanisation of the stratum granulosum evident beneath the hyperplasia (Jones et al. 1990). In contrast, infection of naïve coho salmon with *L. salmonis* resulted in a marked hyperplasic and inflammatory responses of fin tissues that resulted in the loss of copepods from the body (Johnson and Albright 1992a, b). The fin responses of chinook salmon were intermediate in intensity between those of Atlantic and coho salmon (Johnson and Albright 1992a). Administration of hydrocortisol to naïve coho salmon resulted in the suppression of these responses and increased the survival rate of *L. salmonis* to a level similar to that seen on Atlantic salmon (Johnson and Albright 1992b). Examination of the attachment and feeding sites of chalimus larvae of *L. salmonis* on the fins of heavily infected sockeye salmon, *Oncorhynchus nerka* (Walbaum, 1792), revealed mild epithelial hyperplasia associated with the frontal filaments, epidermal erosion at the sites of feeding and a small amount of inflammatory infiltrate (Johnson et al. 1996).

Using histology, MacKinnon (1993) examined the attachment and feeding sites of *Caligus elongatus* on naturally infected Atlantic salmon. Lesions associated with the chalimus stages extended through the epithelium to the basement membrane. In some instances, epithelial cells at the periphery of the lesions became detached from the basement membrane. There was no evidence of inflammatory responses to these stages. A small proportion of lesions associated with older chalimus larvae (chalimus IV) showed evidence of epithelial hyperplasia in the surrounding tissues. At feeding and attachment sites of both the copepodid and chalimus stages of *Caligus epidemicus* Hewitt, 1971, on yellowfin bream, *Acanthopagrus australis* (Owen, 1853), there was also little evidence of an inflammatory response, although some cellular infiltration was occasionally present (Roubal 1994).

Jónsdóttir et al. (1992) studied the histopathology associated with the preadult and adult stages of *Lepeophtheirus salmonis* on the skin of naturally infected Atlantic salmon. In their study, the severity of lesions was seen to vary widely, and this was attributed to the ability of these stages to move around on their hosts. Tissues were generally more heavily damaged beneath the cephalothorax than under other regions of the parasite's body, with the cells showing a loss of surface structure as determined by scanning electron microscopy (SEM). In addition, the thickness of the epidermis varied relative to the thickness of the underlying layers, and there was evidence of swelling and splitting of the epidermal layer. Basal cells became hypertrophic and developed large granular nuclei. In some cases, the basement membrane and pigment layer increased in thickness, whereas in other cases, it was ill-defined or broken (Jónsdóttir et al. 1992). An inflammatory response to the copepod was reported in the tissues surrounding the periphery of the lesions. Open lesions on seriously diseased sockeye salmon increased in depth towards the centre, where the entire epidermis and dermis were removed exposing underlying muscle (Johnson et al. 1996). There was congestion in the blood vessels of the exposed muscle, but little evidence of inflammation. In some lesions, secondary bacterial infections were noted. Using scanning and transmission electron microscopy, Nolan et al. (1999) reported marked epithelial changes in the skin of Atlantic salmon infected with preadult *L. salmonis* at sites that were distant from their point of attachment and feeding. Changes included necrosis of the pavement cells, increased apoptosis of cells within the epidermis and widening of intracellular spaces. These changes were interpreted as an indirect effect of the infection, as they were similar to changes described for other species of fish upon exposure to a wide variety of stressors.

Ragias et al. (2004) reported on the histopathology associated with mixed infection of *Caligus* spp. on sea bass. In their study, pathology was attributed primarily to older (preadult and adult) stages of *Caligus minimus*, and to a lesser extent *Caligus mugilis*. The sites of copepod attachment showed ulceration of the epidermis with a marked inflammatory response within the dermis. Epithelial hyperplasia was evident at the point of attachment of the second antennae, as well as around the periphery of the lesions. Cells that were immediately adjacent to the lesions showed signs of necrosis, and there was also degeneration of basal cells and the development of diffuse areas of spongiosis. In many cases, fibroplasia and spongiosis were evident within the dermal collagenous connective tissue (Ragias et al. 2004).

Shariff and Roberts (1989) provided a detailed account of the histopathology of *Lernaea polymorpha* Yü, 1938, infection in bighead carp, *Aristichthys nobilis* (Richardson, 1845). With respect to the naïve host, there was evidence of severe tissue damage and haemorrhage immediately following host penetration. Over time, an acute inflammatory response developed, with large numbers of mononuclear leucocytes and neutrophils present within the exudate. A predominant feature was the development of massive vascularisation within the periphery of the lesion at 64 h postinfection (HPI). There was also evidence of the formation of a thin-walled capsule around the cephalic region of the copepod at that time. The extent of tissue vascularisation and capsule development increased with time. At 128 HPI, there was further degeneration and myophagia of the muscle tissues in the vicinity of the copepods. In addition, large numbers of the inflammatory cells were undergoing degenerative changes. Mononuclear cells became abundant in the periphery of the lesion. At 256 HPI, the epidermal cell layer around the lesion thickened, and additional fibrous tissue had formed around the copepod and beneath the lesion. Mononuclear cells were very abundant. At the end of the study (512 HPI), mononuclear cells were still abundant, and eosinophilic granular cells and cells resembling lymphocytes were first reported. Lesions in fish that were assumed to be immune differed from those of naïve fish. The epidermis around the lesion was thickened and spongiotic with large and distinct areas of infiltration of eosinophilic granular cells and lymphocytes. In addition, the underlying dermis was oedematous with extensive areas of haemorrhage and eosinophilic granular cells and lymphocytes present around a distended vasculature. Mononuclear infiltrates were present within scale pockets containing *Lernaea cruciata* (Lesueur, 1824) in naturally infected largemouth bass, *Micropterus salmoides* (Lacepède, 1802) (see Noga 1986). Eosinophilic granular cells were often seen in close association with the copepod. Secondary bacterial infections were common especially in older lesions (Noga 1986).

Gross morphological and histological descriptions of sites of attachment of *Dichelesthium oblongum* (Abildgaard, 1794) on wild Atlantic sturgeon, *Acipenser oxyrinchus* Mitchill, 1815, have been made (Fast et al. 2009). Lesions associated with juvenile *D. oblongum* were quite large (7–12 mm), often located on the operculum or at the base of fins. These lesions consisted of focal areas of ulceration surrounded by a raised border. Histologically, there was necrosis or complete loss of the epidermis and dermis, haemorrhage and focal necrosis of the underlying musculature. Foci of epidermal spongiosis were observed in the vicinity of lesions where the epidermis was still intact. There was no evidence of secondary bacterial infections.

Adult females pennelid copepods from the genus *Lernaeocera* Blainville, 1822, and *Haemobaphes* Steenstrup and Lütken, 1861, parasitise the heart of the final host,

Fig. 6.7 *Haemobaphes* sp. Note only the genital segment is exposed (arrows) in the buccal cavity of silver dory *Zenopsis nebulosa* (Temminck and Schlegel, 1845). Image © Mark Boulter

with the parasite head in the vicinity of the bulbous arteriosus and only the genital segment exposed to the environment (Fig. 6.7; Baily et al. 2011 and the references therein). Chronic infection resulted in swelling of the ventral aorta and nodular thickening in the wall of the bulbous arteriosus and ventricle as well as pigmented nodules in the pericardium (Baily et al. 2011; Behrens et al. 2014). Histologically, formation of granulomas and proliferation of fibrovascular tissue were present (Baily et al. 2011; Behrens et al. 2014). The parasites were often degenerated, and it was proposed that they were eliminated from the vascular system when a thrombus formed as a reaction to the endothelial damage (Baily et al. 2011).

Gnathiid isopods are parasitic as juveniles on a variety of elasmobranch and teleost hosts (reviewed by Smit and Davies 2004). After hatching, the unfed juveniles ("zupheas") locate and establish themselves on a host and begin a period of blood feeding (Fig. 6.8). During feeding, relatively large volumes of blood are stored within their bodies, and these juveniles are referred to as "praniza" larvae. After feeding is completed, the first praniza leaves the host, digests the blood meal and moults into the second zuphea stage. The process of reinfection, feeding and

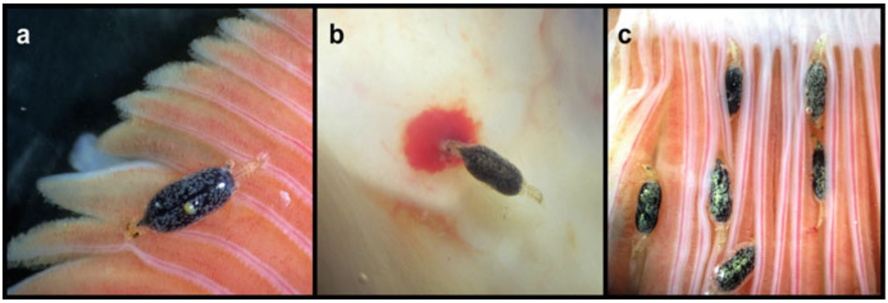

Fig. 6.8 (**a–c**) Gnathiid isopod larvae in the branchial (pharyngeal) cavity of the Giant shovelnose ray *Glaucostegus typus* (Anonymous [Bennett], 1830). Note the damage and bleeding at the site of attachment (**b**). Images © Kerry Hadfield and Nico Smit

moulting is repeated until a third-stage praniza is produced which matures into a nonfeeding adult. The duration of host contact and feeding ranges from hours to weeks. The variation in the reported effects of this group of isopods on their hosts may be due to their highly variable periods of host contact.

A leatherjacket louse *Ourozeuktes bopyroides* (Lesueur, 1814) infects a range of leatherjacket species including *Meuschenia freycineti* (Quoy and Gaimard, 1824) (see Friese 1978). Juvenile stages of this isopod attach to the host and burrow through the body wall using their anterior, dactyli-equipped pereopods. Host response results in encapsulation of the parasite by a thin epithelial membrane (pouch) isolating the parasite from the host's internal organs. The posterior part of the parasite stays outside the host through a narrow aperture which remains open (Fig. 6.9a) to allow respiration (Friese 1978). The parasite is very large relative to the host size (Fig. 6.9b) and causes a significant displacement of the host's internal organs (Friese 1978) and pressure atrophy (Nowak unpublished data).

Some parasitic isopods cause degeneration of the tongue of their host and then replace the tongue with their own body (Fig. 6.10). For example, *Cymothoa exigua* Schioedte and Meinert, 1884, replaces the tongue of snapper *Lutjanus guttatus* (Steindachner, 1869) without apparent adverse effects on the host other than the lack of normal tongue (Brusca and Gilligan 1983).

Crustaceans may stimulate a host response, or the host to produce specialised tissues or structures to improve their attachment, and possibly limit their exposure to the host's immune system. Examples of this may be found in the families such as the Pennellidae and Lernaeopodidae, where fibrosis of the host's tissues around the embedded regions of the copepods body may improve their attachment and limit exposure to the immune response. Indirect effects related to the host's integrated stress response have been demonstrated to occur in areas distant from the site of attachment and feeding (see Nolan et al. 1999). In general, the magnitude of these changes is very small, and therefore they are likely to be unrecognised unless scanning or transmission electron microscopy is used.

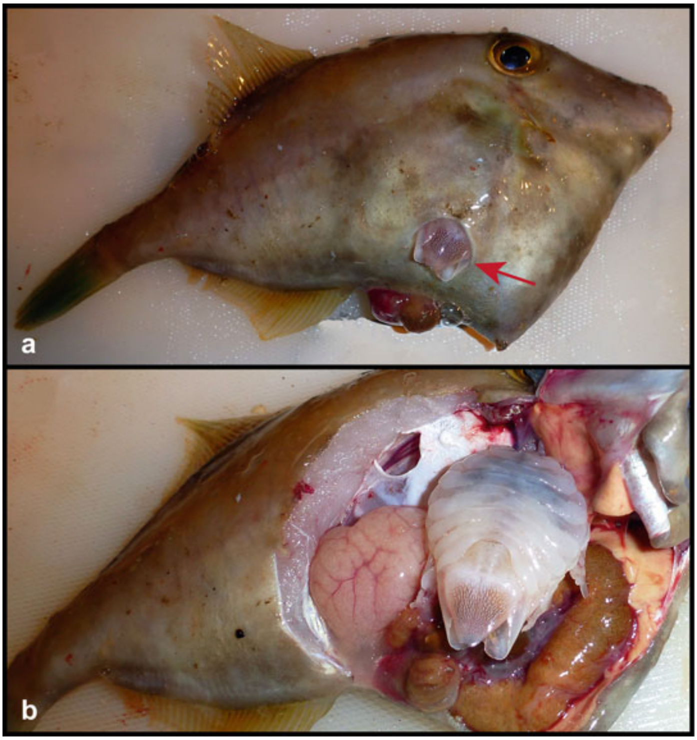

Fig. 6.9 Leatherjacket, *Meuschenia freycineti* (Quoy and Gaimard, 1824) with the leatherjacket louse, *Ourozeuktes bopyroides* (Lesueur, 1814). (**a**) The narrow aperture seen on the side of the host (arrow) remains open allowing contact of the posterior part of the parasite with the external environment, (**b**) note the size of the parasite relatively to the host. Images © Dr Mark Powell

6.2.3 Higher Vertebrate Hosts

There are few reports of pathology associated with parasitic crustacean infection of higher vertebrates. Badillo et al. (2007) reported that the feeding activities of the harpacticoid copepods, *Balaenophilus* spp., on loggerhead sea turtles, *Caretta caretta*, (Linnaeus, 1758) could have resulted in the development of lesions. Unfortunately, no description of the lesions is available. Kupferberg et al. (2009) described outbreaks of *Lernaea cyprinacea* Linnaeus, 1758, in Foothill yellow-legged frogs, *Rana boylii* Baird, 1854. Although the authors did not provide a description of the lesions, they did report an increase in the prevalence of morphological abnormalities, especially in the hind limbs, of infected frogs in 1 out of the 2 years studied. They suggested that the development of morphological abnormalities was related to the developmental stage of the frog when it was infected. Frogs infected earlier in their development have a greater chance of developing morphological abnormalities.

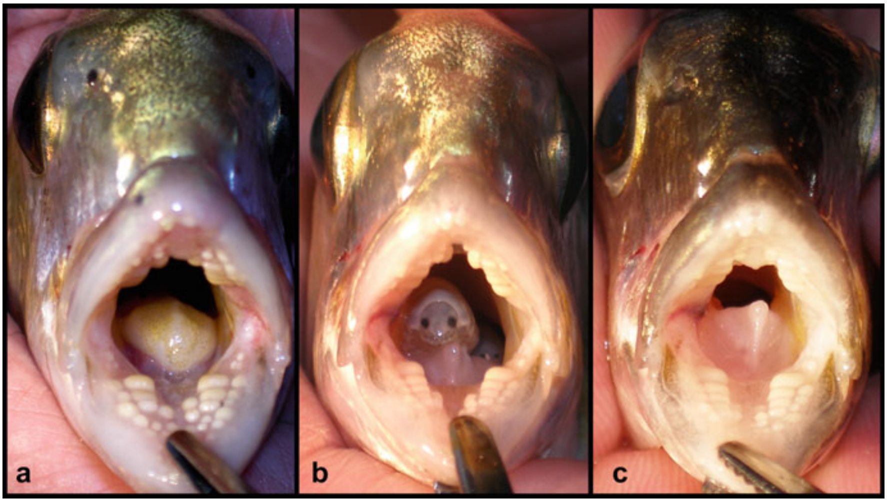

Fig. 6.10 (**a**) Uninfested tongue of *Sparodon durbanensis* (Castelnau, 1861), (**b**) *Sparodon durbanensis* infested with "tongue-biter" cymothoid *Ceratothoa famosa* Hadfield, Bruce and Smit, 2014, (**c**) the damaged and stunted tongue of *S. durbanensis* caused by *C. famosa*. Images © Nico Smit

Dailey (1985) reviewed the diseases of Cetacea and made only a brief mention of infection of the baleen whale, *Balaenoptera acutorostrata* (Lacepède, 1804), by *Pennella* sp. More recently, histological examination of a striped dolphin, *Stenella coeruleoalba* (Meyen, 1833), and a Russo's dolphin, *Grampus griseus* (G. Cuvier, 1812), infected with *Pennella* sp. revealed the presence of inflammatory reactions (infiltration of lymphocytes and eosinophils) and microhaemorrhages in the vicinity of the holdfasts (Cornaglia et al. 2000). Infection of a northern elephant seal, *Mirounga angustirostris* (Gill, 1866), with *Pennella balaenoptera* Koren and Danielssen, 1877, was reported by Dailey et al. (2002). Associated with this infection were large, raised, ovoid subdermal masses in which parts of dead copepods were visible. These masses were filled with mucopurulent discharge and tissue debris and were secondarily infected by a number of bacterial species. After initial treatment of the animal, these lesions had failed to resolve, and samples of the lesions containing copepod structures were submitted for histological analysis. These masses consisted of dense dermal infiltrates of degenerate and viable neutrophils, macrophages, scattered lymphocytes and plasma cells (Dailey et al. 2002). The magnitude of the host response to the copepod body parts was more severe than that reported for cetaceans, leading the authors to postulate that in this case, the copepods may have infected already formed lesions.

Amphipods of the family Cyamidae (whale lice) complete all stages of their life cycle on the cetacean hosts. Little is known about the nature of their associations with their hosts. Four species of whale lice were recovered from humpback, *Megaptera novaeangliae* (Borowski, 1781), and right, *Eubalaena glacialis* (Müller, 1776), whales (Rowntree 1996). These species feed on the outer-pigmented skin off their host, relying on other organisms on the surface of the skin for additional nutrition (Rowntree 1996; Osmond and Kaufman 1998). While structural changes have not been reported for those parasites, increased numbers have been observed on weak individuals (Osmond and Kaufman 1998) and have been used to determine poor condition of humpback and right whales (Knowlton and Kraus 2001).

It is possible to identify both direct and indirect (stress-related) effects on host tissues caused by parasitic copepods using histological techniques. With respect to direct effects, the changes reported are primarily the result of physical and possibly enzymatic disruption of host tissues. The observed histopathological effects may be in part due to the presence of secondary agents such as bacteria and fungi.

As discussed below, it is likely that many species of parasitic copepods will be found to produce immunomodulatory substances that modify the host response thereby reducing immunological responses such as hyperplasia and inflammation. Only a few histological studies provided evidence for the presence of such substances. The lack of histological evidence may be in part due to failure to examine tissues adjacent to the feeding sites where immunomodulatory effects on host tissue responses may not be present.

6.2.4 Modulation of Structural Responses by Crustacean Parasites

The ability of parasitic Crustacea to modify their environment through the modulation of host responses would confer many advantages to them. Depending on the species, these could include (1) protection and improved security of attachment (e.g. formation of galls or cysts, development of fibrous host tissues around attachment organs); (2) improved food resources (e.g. stimulation of host tissues to proliferate at the feeding site); and (3) avoidance of host innate and adaptive immune responses.

As discussed previously, there are numerous examples, especially for invertebrates, where parasitic copepods are associated with specialised structures such as cysts or galls, both derived from host tissues. The mechanisms responsible for the formation of these structures remain unknown. The physical presence of the copepod alone may be sometimes sufficient to result in a host response that eventually leads to the encapsulation of the copepod and the formation of morphologically simple cysts or galls. However, for species such as *Scolecodes huntsmani* that occupy complex structures derived from host tissues, it is difficult to imagine how the physical presence of the parasite alone could stimulate host cells to differentiate and produce such structures. It is unknown whether some species of parasitic copepods produce substances that stimulate host tissues and/or modify the host immune response to produce such structures. Research in this area would improve our understanding of parasitic copepod-host interactions, as well as possibly provide insights into basic cell biology process such as cell regulation and differentiation.

With respect to provision and security of the food supply, some copepod species are reported to stimulate the host to produce specific types of host tissues, on which they feed. In the case of *Dissonus manteri*, proliferation of gill epithelial and fibrous tissue has been suggested to benefit the copepod by serving as a food resource (Bennett and Bennett 2001). Adult females *S. huntsmani* are reported to feed on host tissues that make up the walls of the cysts in which they are found or on other host-derived cells present within the cyst (Dudley 1968). Infection of leatherjackets with the isopod *Ourozeuktes bopyroides* results in formation of a “pouch” which is an epithelial membrane rich in mucous cells that have been suggested to provide the parasite with nutrients (Friese 1978). In such instances, stimulation of host tissues provides a renewable food resource and, in the case where these tissues are poorly vascularised, possibly some protection from host immune responses.

In regard to protection from host immune responses, arthropod parasites are known to release numerous substances within their saliva that serve to enable establishment and maintenance on their hosts. These substances include immunomodulators such as proteases, phosphatases and prostaglandins, which generally make up the major salivary constituents (reviewed in Wikel 1996). In addition to these, a large number of other substances such as macrophage migration inhibitory factors, apyrases, peroxidases and many others as yet unidentified products are also present in salivary secretions (Wikel 1996; Jaworski et al. 2001; Bowen et al. 2010).

There are several observations providing reasonable indirect evidence for substances being produced by parasitic crustaceans that may aid in their establishment and maintenance on their hosts. For example, ergasilid copepods release enzymes onto the surface of the host resulting in the process of “extra-buccal digestion” (Kabata 1984). Observation of red blood cell degeneration shortly after host penetration by *Lernaea polymorpha* suggests the production of enzymes or other substances that are involved with penetration of the host tissues (Shariff and Roberts 1989). Preadult and adult stages of caligid copepods are reported to produce imprints of their cephalothorax on the surface of their hosts, with inflammation in the host tissues limited to the periphery of these imprints (Jónsdóttir et al. 1992; Roubal 1994). The secretion and retention of copepod-derived substances such as enzymes or other salivary components beneath the carapace, as well as the actions of the mouthparts and thoracic legs, may contribute to the formation of these imprints and possibly limit the inflammatory response to the periphery (Johnson and Fast 2004). As previously mentioned, there is often little to no host tissue response associated with frontal filaments of live caligid copepods (Sutherland and Wittrock 1985; Jones et al. 1990; Johnson and Albright 1992a, b; Bennett and Bennett 1994; Johnson et al. 1996). However, frontal filaments of *Caligus epidemicus* and *Lepeophtheirus salmonis* abandoned by copepods provoke strong tissue responses that include epithelial hyperplasia, and infiltration of neutrophil-like cells, macrophages and lympocytes (Jones et al. 1990; Roubal 1994).

Bell et al. (2000) reported the presence of glands associated with the mouthparts of *L. salmonis* and *Caligus elongatus* that stained positively for the presence of peroxidase activity. They suggested that the production of peroxidases might confer protection against host-derived reactive oxygen species and/or be involved in the production of prostaglandins.

6.3 Effects on the Individual

6.3.1 Effects on Stress Physiology and Immune Response

Through their attachment and feeding, parasitic Crustacea affect the physiological status and immune function of their hosts both directly and indirectly, as the result of the stress response. The magnitude of such effects will depend on (1) the parasite species, (2) their abundance, (3) the developmental stages present, (4) their distribution on the host, (5) the species of host and (6) the environmental conditions under which the host is held.

6.3.1.1 Caligid Copepod Parasites

With respect to *Lepeophtheirus salmonis*, the majority of laboratory studies have standardised copepod number per unit of fish wet weight and have used infection levels that range from 0.1 to 3.0 copepods g^{-1} of fish (Johnson and Fast 2004). Studies on susceptible hosts, such as Atlantic salmon, that have used high levels of infection ($>$0.6 copepods g^{-1} of fish) have generally reported osmoregulatory problems, high levels of plasma cortisol, the development of gross lesions and morbidity. For example, Grimnes and Jakobsen (1996) examined the physiological responses of Atlantic salmon (average weight 40 g) infected with an average of 1.0 *L. salmonis* g^{-1} fish. They reported no significant effect on serum protein, serum albumin, plasma chloride and haematocrit, while the copepods were present as chalimus larvae. However, with development to the preadult and adult stages, significant differences in plasma chloride, serum protein, serum albumin and haematocrit became evident, when compared to controls. Host morbidity started after the moult to the preadult stage without any evidence of the development of gross lesions. In another study, Atlantic salmon infected with an average of 0.6 *L. salmonis* g^{-1} fish showed elevated levels of cortisol, when compared to controls, at 7 days postinfection (DPI) (Finstad et al. 2000). Fish became moribund, and mortalities occurred at the moult to the preadult stage without the development of gross lesions (Finstad et al. 2000). At higher levels of infection, Atlantic salmon infected with an average of 3.0 *L. salmonis* g^{-1} fish were reported to have elevated levels of plasma cortisol that average between 100 and 170 $nmol^{-1}$ as early as 3 DPI (Ross et al. 2000). One hundred percent morbidity occurred within a 24-h period of the moult to the first preadult stage without the development of gross lesions. These authors also reported increased protease and alkaline phosphatase activity in mucus collected from the infected fish. This protease activity was later determined to be the result of *L. salmonis* secretory activities (Firth et al. 2000). Studies on sea trout, *Salmo trutta*, heavily infected with *L. salmonis* have reported similar results for laboratory studies and from field-collected individuals (Bjørn and Finstad 1997; Bjørn et al. 2001).

Only a few studies have investigated the effects of lower levels of infection by *Lepeophtheirus salmonis* on host physiology. Nolan et al. (1999) infected Atlantic salmon with low numbers of copepods and reported physiological changes similar to those reported in response to general stress. These effects included disruption of the skin and gill epithelia over large areas of the body, increased turnover rates of chloride cells on the gills and some small-scale effects on osmoregulation. Ross et al. (2000) examined the effects of lower levels of *L. salmonis* infection (0.4 *L. salmonis* g^{-1} fish) on Atlantic salmon. At this level of infection, there was no significant increase in cortisol in the infected fish and no mortality.

The role that parasitic Crustacea play in the ability of their hosts to respond to other stressors and disease-causing agents is an important area of research that has received little attention. Ruane et al. (2000) investigated whether infection of rainbow trout with *Lepeophtheirus salmonis*, in the absence of cortisol or other physiological responses, would affect their ability to deal with additional stressors. The infected fish did not show elevated plasma cortisol or glucose levels, when compared to uninfected controls. However, infected fish exposed to an additional stressor had a significantly greater stress response (higher levels of plasma cortisol and glucose) when compared to uninfected fish.

A few laboratory infection studies involving *Lepeophtheirus salmonis* have included both measurements of physiological and immune-related parameters. Effects on the immune system have been examined using functional assays and immune-related gene expression. Bowers et al. (2000) infected Atlantic salmon with approximately 0.3 *L. salmonis* g^{-1} fish and monitored plasma cortisol, glucose, electrolytes, thyroid hormones (T3 and T4) and haematocrit over a 29-day period. They reported significantly elevated levels of plasma cortisol at 3, 7, 21 and 29 DPI, and glucose at 3, 7, 14, 21 and 29 DPI, when compared to controls. Levels of plasma cortisol and glucose increased abruptly when preadult copepods were present. However, there was no significant relationship between the cortisol or glucose levels and the copepod numbers (Bowers et al. 2000). This is in contrast to the work of Bjørn et al. (2001) who found a significant positive relationship between the levels of plasma cortisol and copepod numbers. With the exception of 29 DPI mean haematocrit values were significantly higher in infected fish when compared to controls. Increased haematocrit values are another indicator of stress in salmonids (Mazur and Iwama 1993). There was also evidence of osmoregulatory failure, as evidenced by elevated plasma sodium and potassium levels, in infected fish from 7 DPI onwards. There was no clear relationship between the levels of plasma proteins, plasma potassium, thyroid hormones and infection with *L. salmonis*. In a companion paper, Mustafa et al. (2000) reported a significant reduction in respiratory burst and phagocytic activity in head kidney macrophages that were isolated from infected fish at 21 DPI, when the average cortisol level was 178.9 nmol l^{-1}. In a second experiment, Atlantic salmon infected with an average of 0.5 *L. salmonis* g^{-1} fish had significantly higher levels of cortisol and glucose at 7, 14 and 21 and 14 and 21 DPI, respectively. At 21 DPI when average cortisol levels of the infected fish exceeded 60 nmol l^{-1}, both the respiratory burst and phagocytic activities of isolated head kidney macrophages were significantly reduced (Mustafa et al. 2000). It was suggested that the decrease in macrophage function was due to the prolonged elevated levels of cortisol experienced by the infected fish.

Atlantic salmon, coho salmon and rainbow trout infected with a relatively low number of *Lepeophtheirus salmonis* (0.16 *L. salmonis* g^{-1} fish) generally showed no evidence of elevated plasma cortisol levels nor osmoregulatory problems, when compared to uninfected fish over a 21-day study period (Fast et al. 2002). However, with respect to immune function, a significant reduction in macrophage respiratory burst and phagocytic activity was observed for rainbow trout at 21 DPI and Atlantic salmon at 14 and 21 DPI. The lack of an effect on coho salmon immune function was thought to be due to the rapid loss of *L. salmonis* from this species.

It is reasonable to expect that the presence of parasitic crustaceans will affect the ability of their hosts to deal with stressful changes in their environment. However, few experimental data demonstrate this. Nolan et al. (2000a) examined the effects of subsequent exposure to a stressor in rainbow trout that were previously exposed to *Lepeophtheirus salmonis*. The application of a continuous net confinement stress resulted in a decrease in skin mucous cell number and increased gill Na+/K+ ATPase activity in fish that had been infected, when compared to uninfected controls. These changes were thought to represent an increased energetic cost due to stress in the previously infected fish.

More recent studies on the effects *Lepeophtheirus salmonis* have on their hosts used quantitative reverse transcription polymerase chain reaction (QPCR) to quantify both constitutive and inducible immune-related gene expression (Fast et al. 2006b, c; Jones et al. 2007; Fast 2014). QPCR has also been used to identify immunomodulatory activities within the secretions of *L. salmonis* (Fast et al. 2007; Fast 2014). To date, the number of immune-related genes that have been included in these studies is limited. This is in part due to a lack of sequence information for immune-related genes in the different host species. Genes involved in inflammation and the acute-phase response that have been studied include interleukin-1 (*IL-1ß*), interleukin-8 (*IL-8*) and tumour necrosis factor alpha (*TNFα*). Of these, IL-1ß and TNFα are also very important with respect to their interactions with the neuroendocrine system. Other genes that have been studied include major histocompatibility class I and II (*MHI*, *MHII*), transforming growth factor-β (*TGFβ*)-like cytokine and cyclooxygenase-2 (*Cox2*). These genes are involved in antigen processing and presentation, cell differentiation and proliferation and the production of prostaglandins, respectively.

Fast et al. (2006c) were the first to report on host immune-related gene expression during a parasitic copepod infection, studying the effects of a low-level *Lepeophtheirus salmonis* infection (ca. 8–11 lice/fish) on the expression of *Cox2*, *MHI*, *MHII*, *IL-1β* and *TNFα* at 12 and 21 DPI. In the absence of a cortisol stress response, there was no effect on expression of *Cox2* and *TNFα* in head kidney at either time point. Significant differences included (1) a two- to tenfold decrease in expression of *MHI* at 21 DPI; (2) a significant increase (>tenfold) in expression of *MHII* at 12 and 21 DPI; and (3) a threefold increase in expression of *IL-1β* at 21 DPI. Leukocytes isolated from the kidney of the infected fish did not have the ability to increase expression of *Cox2* and *MHI* after stimulation with LPS at 12 and 21 DPI, respectively. No other significant effects were noted, which was due in part to high levels of variability in gene expression between leukocyte samples.

In another study, Fast et al. (2006b) examined the effects of successive infections of *Lepeophtheirus salmonis* on the immune status of Atlantic salmon. This study used an initial low level of infection that was followed at 14 days by a second infection with higher numbers of copepods. Copepod numbers declined following both the initial and second infection with an average of 50 *L. salmonis* per fish present at 40 days post-initial infection (DPII). Infected fish showed significantly higher plasma cortisol levels at 26, 33, 40 DPII and had higher PGE2 levels at 9, 33 and 40 DPII, when compared to controls. Infection also resulted in significantly higher expression of *COX2*, *IL-1β*, *TNFα* and *TGFβ* in infected fish at 9 DPII. Interestingly, stimulation of the immune system by the first infection had little effect on the ability of *L. salmonis* to reinfect these hosts. Following the second infection, *MH1* and *TNFα* expressions were higher in infected fish at 26 and 33 DPII. At the later time points, *MHII* and *TGFβ* expressions were significantly higher at 33 DPII and *IL-1β* and *TNFα* significantly higher at 40 DPII when compared to uninfected fish. At 40 DPII, *MHI* expression was significantly depressed in infected fish.

Jones et al. (2007) investigated the consequences of high- (735 copepodids fish^{-1}) and low-level (243 copepodids fish^{-1}) exposures of *Lepeophtheirus salmonis* on juvenile pink and chum salmon. Copepod loss on both species was rapid, with relatively few copepods present at the end of the experiment. With the exception of a transient cortisol response that was observed in chum salmon at 21 DPI in the low-level exposure, there were no significant trends in plasma cortisol. However, consistently lower numbers of *L. salmonis* on pink salmon were reported when compared to chum. This was associated with an earlier and significantly higher expression of the pro-inflammatory genes *IL-8*, *TNFα-1* and *IL-1β* in fin and head kidney of pink salmon when compared to chum salmon. This, and the earlier work by Fast et al. (2006b, c), suggests a role of pro-inflammatory cytokine genes such as *IL-8*, *IL-1β-1* and *TNFα-1* in controlling the abundance of *L. salmonis* on salmonids. The inflammatory lesions that were reported for gill and fin of both pink and chum salmon support the view that epidermal inflammation and hyperplasia are important in the response of *Oncorhynchus* spp. to *L. salmonis* infection (Johnson and Albright 1992a, b). In a more recent study, Skugor et al. (2008) examined gene expression in Atlantic salmon at various stages following a single pulse infection with *L. salmonis*. Using cDNA microarrays and real-time qPCR, a large number of genes in the skin, head kidney, liver and spleen were differentially expressed in response to the infection. The initial response (3 DPI) of the skin involved the induction of a mixed inflammatory response. This response was followed by a diminished degree of responsiveness characterised by restricted inflammation, and delayed healing of wounds may account for the limited ability of Atlantic salmon to reject *L. salmonis*. These results supported the earlier histological observations of *L. salmonis* attachment and feeding sites on Atlantic salmon.

Host-specific pathways contributing to species resistance to parasitic caligids were proposed on the basis of histochemistry and transcriptomics (Braden et al. 2015a). The resistant species tested, coho salmon, showed early pro-inflammatory

Th1-type pathway followed by regulatory Th2-type processes in the skin following infection with *L. salmonis*. In contrast, IL4 was suppressed or not detectable in Atlantic salmon and sockeye salmon during the first 72 h postinfection (Braden et al. 2015a). The ability to regulate inflammation, limit pathology and have an adaptive tolerant response was suggested as characteristics of a resistant species. Downregulation of MHCII, CRP, *IL-1β*, *IL-8* and *COX-2* genes was characteristic for mature pink salmon *Oncorhynchus gorbuscha* (Walbaum, 1792) but not the juveniles after infection with *L. salmonis* (see Braden et al. 2015b). Juveniles of this species are more resistant to sea lice infection than mature individuals and have higher numbers of $IL\text{-}1\beta^+$ and $MHII\beta^+$ cells as well as mucous cells in their skin during infection (Braden et al. 2015b).

These studies provide good evidence that infection with *Lepeophtheirus salmonis* can have both physiological and immunological costs that change throughout the infection. With respect to the immune system, these effects can be seen at the site of attachment as well as in other organs. As some of these effects are reported in the absence of a cortisol stress response, the role of stress in modulating these responses remains unclear. The interpretation of the role of the stress response is further complicated by studies of higher vertebrates which document that endogenous glucocorticoids at physiological doses are not universally immunosuppressive and in some cases can enhance immune function (reviewed in Engelsma et al. 2002). In addition, there is bidirectional communication between the neuroendocrine and immune system that allows animals to respond appropriately to physiological and psychological disturbances and pathogen challenge (Engelsma et al. 2002).

Unfortunately, little is known about the relationship between neuroendocrine and immune system of fish. This lack of knowledge along with some differences in the immune responses of fish when compared to higher vertebrates makes it difficult to interpret the immunological results obtained from experimental challenges. Future studies on the interactions between parasitic copepods and salmonid hosts will benefit from the ever-increasing amounts of genomic information for salmonids, as well as ongoing developments in methods to study and analyse transcriptional responses (e.g. RNA-seq).

6.3.1.2 Other Parasitic Copepods

As mentioned previously, outside of the Caligidae studies on effects of parasitic copepods on host physiology and immune response are almost non-existent. Two Russian studies reported severe anaemia in the sturgeons *Acipenser stellatus* Pallas, 1771, and *Acipenser gueldenstaedtii* Brandt and Ratzeburg, 1833, when infected by large numbers of *Pseudotracheliastes stellatus* (Mayor, 1824) (reviewed in Bauer et al. 2002). More recently, Fast et al. (2009) examined the serum chemistry of wild Atlantic sturgeon, *Acipenser oxyrinchus*, infected with *Dichelesthium oblongum*. This suggested that infestation with *D. oblongum* had an effect on serum chemistry and overall physiological robustness. However, serum chemistry was affected also by site of sampling, indicating that the fish may have been exposed to varying levels or different stressors at the different sampling sites, which were also affecting their physiological equilibrium.

Suppression subtractive hybridisation (SSH) was used to characterise genes in the grass carp *Ctenopharyngodon idella* (Valenciennes, 1844) that were upregulated in response to a natural infection with the gill-dwelling copepod, *Sinergasilus major* (Markevich, 1940) (see Chang et al. 2005). In this study, a SSH cDNA library was produced from pools of gill and liver tissue, and a total of 122 clones were selected for sequencing. Of these, 23 clones contained inserts for immune-related genes and 16 for genes related to tissue repair. The majority of the immune-related genes were involved in innate immunity. Although this is a modest project with respect to the numbers of sequences obtained, it is a good example of how molecular biological techniques can be applied in the study of copepod-host interactions.

Data for other copepod species is limited to laboratory trials that have involved reinfecting previously infected fish with the goal of studying acquired immunity. Shields and Goode (1978) reported variable reinfection of goldfish *Carassius auratus* (Linnaeus, 1758) with *Lernaea cyprinacea* suggesting the possibility that acquired immunity had developed. Shariff (1981) studied the distribution and abundance of adult female *Lernaea piscinae* Harding, 1950, growing on big head carp, *Aristichthys nobilis*. In this study, copepods were retained for a longer period of time in the eyes when compared to other body regions. This led him to suggest that, as the eyes are an immunologically privileged site, there is good evidence of the importance of the immune response in this interaction. Woo and Shariff (1990) reported for *L. cyprinacea* growing on kissing gourami, *Helostoma temminckii* Cuvier, 1829, that (1) upon reinfection previously infected fish lost copepods faster than naïve hosts; (2) a higher portion of egg sacs were lost from copepods growing on previously infected fish than naïve fish; and (3) eggs from copepods growing on previously infected hosts either failed to develop or produced copepodids that had a lower infectivity when compared to copepodids hatched from eggs of copepods growing on naïve hosts. It was proposed that changes in the structure of the lesions or the production of antibodies that interfered with feeding or digestion may be responsible for these observations. Kularatne et al. (1994) reported that acquired immunity was not important in the interactions between *Lernaea minuta* (Scott, 1900) and the Javanese carp *Puntius gonionotus* (Bleeker, 1850). This conclusion was based on an infection trial in which no significant difference in *L. minuta* intensities was observed between fish that (1) were naïve, (2) had recovered from infection, (3) had been injected with plasma from recovered fish and (4) had been injected with plasma from naïve fish. Interestingly, previously infected fish were reported to start losing their parasites a few days before the naïve group. Furthermore, the failure of plasma from recovered fish to immobilise the first naupliar stage of *L. minuta* in vitro was also considered as evidence for the lack of an acquired immune response. Thoney and Burreson (1988) reported that there was no evidence of antibody production by the spot croaker, *Leiostomus xanthurus* Lacepède, 1802, against the tissue dwelling copepod, *Lernaeenicus radiatus* Le Sueur, 1824. They attributed the lack of an antibody response to the presence of a thick capsule of host tissue that surrounds the head and the neck of this copepod that they felt would limit antigenic stimulation of the host. The susceptibility to reinfection with *Lernaeocera branchialis* (Linnaeus, 1767) was investigated in the Atlantic cod under laboratory conditions (Khan 1988). In this study there was no evidence of adaptive immunity as previous infection conferred no protection agains reinfection.

6.3.1.3 Parasitic Isopods

Grutter and Pankhurst (2000) examined the stress response of the blackeye thicklip *Hemigymnus melapterus* (Bloch, 1791) that were naturally infected with a maximum of 27 gnathiid isopods (*Gnathia* sp.) per fish. In this study, there was no significant relationship between plasma cortisol or glucose levels and isopod abundance, even when host size was taken into consideration, suggesting that gnathiid isopods at this natural level of infection did not act as a stressor in *H. melapterus*.

6.3.2 Avoidance of Host Immune Response

To date, the production of substances with possible immunomodulatory activities has been confirmed only for the parasitic copepod *Lepeophtheirus salmonis*; two cymothoid isopods, *Ceratothoa oestroides* (Risso, 1826) and *Anilocra physodes* (Linnaeus, 1758); and the gnathiid isopod, *Paragnathia formica* (Hesse, 1864) (see Romestand and Trilles 1976a, b; Manship et al. 2012; Fast 2014). *Lepeophtheirus salmonis* is known to secrete compounds such as proteases that may aid in feeding and/or avoidance of host immune responses (Firth et al. 2000; Ross et al. 2000; Fast et al. 2002, 2003). Trypsin is a major component of these secretions, and the site of its production has been localised in gut tissues (Firth et al. 2000; Johnson et al. 2002). Trypsin and trypsin-like enzymes are important in maintaining other arthropod host-parasite relationships (reviewed in Johnson and Fast 2004; Wagner et al. 2008). Additionally, the presence of prostaglandin E_2 (PGE_2) has also been identified in these secretions (Fast et al. 2004). This substance is a potent immunomodulator, known in other parasites to play a variety of roles in feeding and avoidance of host immune responses such as inflammation. In addition to trypsin and PGE_2, there also appears to be other immunomodulatory agents present in the secretions of *L. salmonis*. Using a combination of biochemical, proteomic and molecular techniques, substances other than PGE_2 were identified and partially purified from these secretions (Fast 2005; Fast et al. 2007). Mass spectrometric analysis of size-fractionated secretions revealed the presence of trypsin, as well as other peptides that showed identity with genes of *L. salmonis*. Expression studies of three of the non-trypsin genes revealed that two were significantly upregulated upon copepodid attachment and initiation of feeding (Fast 2005). In addition, it was demonstrated that aside from PGE_2 and trypsin, other components of the secretions of *L. salmonis* inhibited the expression of Atlantic salmon immune-related genes in vitro (Fast 2005; Fast et al. 2007). In a more recent study, Lewis et al. (2014) *used* in vitro assays to examine differences in the response of SHK-1 cells and head kidney macrophages from different salmon species following exposure to *Aeromonas salmonicida* in the presence or absence of *L. salmonis* secretory products. These secretory products modified the cellular immune response as determined by phagocytic rates and respiratory burst activity. These modifications were not consistent across species and may be related to the difference seen between these species with respect to their susceptibility to infection with *L. salmonis*.

Using the presence of trypsin activity as an indicator of secretory activity, *Lepeophtheirus salmonis* was shown not to produce secretions in the presence of mucus of coho salmon and winter flounder, *Pleuronectes americanus* (Walbaum, 1792), any more frequently than they did in the presence of seawater alone (Fast et al. 2003). As mentioned previously, coho salmon is resistant to infection, and the winter flounder is not a host species. It is possible that the strong tissue response to *L. salmonis* seen in coho salmon occurs due to reduced copepod secretory activities. Alternatively, the immune system of coho salmon may respond differently to the presence of immunomodulatory substances, compared with the response of species more susceptible to infection, such as Atlantic salmon. This latter viewpoint is supported by the work of Lewis et al. (2014).

Antithrombin activity against fish blood was biochemically identified to be present in the salivary glands of adult cymothoid isopods *Ceratothoa oestroides* and *Anilocra physodes* (see Romestand and Trilles 1976a, b). A variety of enzymes, enzyme inhibitors and anticoagulants have been identified in the gnathiid isopod, *Paragnathia formica*, using biochemical techniques (Manship et al. 2008, 2012). Manship et al. (2008) identified cathepsin-like cysteine proteinases in the digestive system of unfed (zuphea) and fed (praniza) third-stage juveniles with highest levels of activities in the digestive glands of the praniza. These authors assumed that these proteases were primarily involved in digestive functions. However, as noted earlier, cathepsin L activity has been observed in the secretions of *L. salmonis* and other parasites, observations that suggest the role for this enzyme in the establishment and maintenance of parasites on hosts (McCarthy et al. 2012). Whether this is the case for *P. formica* remains to be determined. In a follow-up study, these authors examined first-stage zuphea for bioactive compounds with a focus of identifying those that could be involved in evasion of host responses (Manship et al. 2012). Based on their analysis of crude and partially purified zuphea extracts, these authors identified three trypsin inhibitors that ranged from 18 to 22 kDa in size, as well as fractions containing antithrombin activity against human plasma. Due to the small size of the stage 1 larvae, whole-body homogenates were used in their study; therefore, tissues involved in the production of these proteins were not identified.

6.3.3 Cardiac Function and Swimming Performance

There is little new information on the physiological consequences of infection with parasitic crustaceans outside of what was reviewed in Kabata (1984). The effects of *L. salmonis* infection on Atlantic salmon's cardiac output and swimming performance were investigated in a series of studies (Wagner et al. 2003, 2004; Wagner and McKinley 2004). At an infection level of 0.02 adult *L. salmonis* g^{-1} fish, there was no change in blood chloride levels during exercise or swimming performance when compared to uninfected fish (Wagner et al. 2003). However, at higher levels of infection (0.1 adult *L. salmonis* g^{-1} fish), there was a significant increase in plasma chloride levels during exercise and a significant decrease in swimming performance, when compared to the fish with lower numbers of *L. salmonis* and the uninfected controls. Several studies have reported that salmonids heavily infected with *L. salmonis* will prematurely return to fresh water in an effort to restore the osmotic and ionic balance and to remove the parasite (Bjørn et al. 2001 and references therein). To further investigate this, Wagner et al. (2004) studied the effect of the short-term transfer from seawater to fresh water on blood chemistry and physiological performance (critical swimming speed and cardiovascular performance) of Atlantic salmon infected with *L. salmonis*, as measured by critical swimming speed and cardiovascular performance. Fish infected with 0.08 *L. salmonis* preadults and/or adults g^{-1} fish had reduced swimming performance when compared to uninfected controls only in seawater. In contrast to the previous studies, there was no evidence of increased plasma chloride levels during exercise in seawater. These authors suggested that reduced energy expenditure by infected fish to maintain osmotic and ionic balance in fresh water might be responsible for their improved swimming performance. Their results supported the existence of a link between the physiological effects of *L. salmonis* and premature return of salmonids to fresh water, as suggested by Bjørn et al. (2001) and references therein.

Nendick et al. (2011) examined the effects of *L. salmonis* infection on juvenile pink salmon, *Oncorhynchus gorbuscha* (Walbaum, 1792), swimming performance and ionic homeostasis. This is a very interesting study as pink salmon enter seawater soon after emergence from gravel and as such are exposed to *L. salmonis* infections at a very small size. Their small size at seawater entry was thought to put them at great risk from *L. salmonis* (see Morton et al. 2004; Krkosek et al. 2006). It was reported that for the smallest pink salmon (average weight 0.34 g), infection with a single *L. salmonis* (chalimus II through preadult) had large and significant negative impacts on swimming performance and postswim whole-body ions. However, tripling the number of *L. salmonis* present did not affect the fish any further. Larger pink salmon (average weight 1.1 g) showed no sublethal impacts at these levels of infection. These authors suggested that the disruption of swimming ability is due to ionoregulatory imbalance rather than to increased surface drag caused by the presence of *L. salmonis*. Only low rates of mortality were seen during their experiments. This is in contrast to predictions of much higher levels of mortalities at these levels of infection (Krkosek et al. 2006).

The parasitic copepod *Lernaeocera branchialis* had a negative effect on cardiorespiratory function of its final host Atlantic cod, *Gadus morhua* Linnaeus, 1758 (see Behrens et al. 2014). Specifically, cardiac output and specific dynamic action were reduced in all naturally infected cod. Cardiac rhythm was irregular and amplitude reduced in cod with macroscopically visible parasites.

6.3.4 Anaemia

Infection with *Lepeophtheirus salmonis* reduced haematocrit in several host species that may be caused by stress and/or feeding activities (Grimnes and Jakobsen 1996; Bowers et al. 2000; Jones et al. 2007). The effects of repeated blood loss on swimming performance of rainbow trout has been studied and related to blood feeding by *L. salmonis* (Wagner and McKinley 2004). These authors used a *L. salmonis* blood-feeding model to predict the point at which blood feeding can cause anaemia. They estimated that blood makes up 15–25% of the host tissues that are ingested by *L. salmonis*. Based on these values, they suggested that at higher levels of infection ($\geq$ 0.5 lice g^{-1} fish), feeding activities would likely cause anaemia. Anaemia in combination with osmotic and ionic imbalances induced by *L. salmonis* could have contributed to the observed decrease in swimming performance and host morbidity in infected fish (Wagner and McKinley 2004). Accidental infection of farmed Atlantic salmon with pennelid copepod, *Haemobaphes disphaerocephalus* Grabda, 1976, resulted in anaemia (Kent et al. 1997). The closely related genus *Lernaeocera* has also been reported to cause anaemia in its hosts (Khan et al. 1990).

As mentioned previously, blood feeding can have direct as well as indirect effects on haematological parameters. Direct effects are due to blood loss due to feeding, whereas indirect effects include those resulting from stress associated with parasite attachment and osmotic imbalances caused by wounding.

The effects of blood feeding by parasitic isopods on host haematological parameters have in most cases been assessed by comparing naturally infected and noninfected fish sampled from fish farms or wild populations. With respect to cymothoids and aegiids, literature published prior to 2003 has been reviewed by Horton and Okamura (2003). Infection of fish with cymothoid isopods generally resulted in anaemic conditions as characterised by significant decreases in erythrocyte counts, with corresponding decreases in haematocrits and haemoglobin levels. The effect on leucocyte populations is less clear with some authors reporting increases in leucocyte numbers and others declines in infected fish. In a later study, blackeye thicklip, *H. melapterus*, infected with large numbers of juvenile gnathiid isopods (*Gnathia* sp.) under laboratory conditions had a reduced haematocrit (Jones and Grutter 2005). In that study, infection levels ranged from 278 to 1251 isopods per fish, which are orders of magnitude higher than reported for this host species in the field (Grutter and Pankhurst 2000). There was no significant relationship between isopod numbers and haematocrit levels, which was attributed to the transitory nature of their attachment and feeding activities. What was not determined in any of these studies was whether observed changes in haematology were of sufficient magnitude to compromise the host.

6.3.5 *Effects on Growth*

Crustacean parasites may reduce the amount of energy that is available for host growth and reproduction, as well as affecting their survival. Depending on the magnitude of the energy reduction, infected hosts may either show the same energy allocation pattern as uninfected hosts or respond to infection by adjusting the proportion of energy allocated to each of these functions. The effects that crustacean parasites have on host growth, reproduction and survival are related to relative size of parasite in comparison to the host, the number of parasites present on the host, the duration of feeding on the host, the invasiveness of their feeding activities and the availability of host food resources. With respect to parasitic copepods, Kabata (1984) noted the lack of quantitative data on their effects on host growth and reproduction. A similar situation exists with respect to other groups of parasitic crustaceans. Unfortunately, the situation for parasitic copepods has improved little since the publication of Kabata (1984) and laboratory-based studies on these topics remain almost non-existent. Condition factor (K) and other indices such as hepatic somatic index (HIS) and gonadic somatic index (GSI) have been used to determine the effect of parasitic crustaceans on host growth and reproductive potential. These indices are most often calculated for naturally infected hosts collected in the field.

6.3.5.1 Condition Factor

The condition factor (index), which is a relationship between body weight and length, is considered to be more reliable in long-term studies, and changes may indicate alterations in nutritional states. Interpretation of field-collected data on the effects of copepods on host condition factor is difficult. For example, it is impossible to determine whether a low condition factor is the result of infection, or an indication that the host was already in poor condition at the time of infection. Furthermore, it is difficult to compare condition factors of hosts collected at different times or from different regions due to the potential for differences in the availability of food resources, the stage of their reproductive cycle and other factors.

With respect to invertebrates, there was a negative relationship between the numbers of the gill-dwelling copepod, *Pectenophilus ornatus* Nagasawa, Bresciani and Lutzen, 1988, and the dry weight condition index of the Japanese scallop, *Mizuhopecten yessoensis* (Jay, 1857) from July to September (Nagasawa and Nagata 1992). The reduction seen at higher levels of infection was suggested to be due to the blood-feeding habit of the copepod, as well as to gill damage that limits host respiratory capacity (Nagasawa and Nagata 1992). Significant negative correlations between the presence of *Pseudomyicola spinosus* and the condition index of *Mytilus galloprovincialis* and *Mytilus californianus* and the catarina scallop, *Argopecten ventricosus*, have been reported at some sites in Baja, Mexico (Cáceres-Martínez et al. 1996, 2005). However, it is unclear whether this was a consequence of infection by the copepod or the result of some other factors such as host spawning.

In the northern Atlantic, infection of Pacific oysters, *Crassostrea gigas*, by *Mytilicola orientalis* had no effect on oyster condition or chemical composition, when mean abundance ranged from 0.6 to 1.48 copepods oyster^{-1} (De Grave et al. 1995; Steele and Mulcahy 2001). In Pacific oysters infected with much higher levels of *M. orientalis*, reduced host condition was noted when compared to uninfected hosts (Katkansky et al. 1967; Deslous-Paoli 1981).

At the individual level, infection of the gills and mantle cavity of short-finned squids, *Illex coindetii* (Vérany, 1839) and *Todaropsis eblanae* (Ball, 1841) by the copepod, *Pennella* sp. had a negative effect on the condition of both host species. The condition factor (Fulton Index) at the individual level showed a strong negative correlation with copepod abundance (Pascual et al. 1997). However, this effect was not observed at the population level as there were no significant differences in population growth based on a comparison of length-weight regression between copepod infested and uninfested squid groups. These authors proposed that this observation was due to the highly skewed distribution of copepods within infected populations. Pascual et al. (2005) examined the relationship between infection with *Pennella* sp. and size at age in *I. coindetii* and showed that the infestation contributed to variability in squid growth, as well as to the strength of age-length relationships in this host species.

Based on field-collected samples, a negative relationship between the abundance of parasitic copepods and the condition factor of their fish hosts has been reported. Arctic cod, *Boreogadus saida*, infected with *Haemobaphes cyclopterina* (Müller, 1776) and the tidepool sculpin, *Oligocottus maculosus* Girard, 1856, infected with *Haemobaphes intermedius* Kabata, 1967, had lower condition factors than uninfected individuals (Khan et al. 1997). Nagasawa et al. (1998) reported that the condition factor of brook trout, *Salvelinus fontinalis* (Mitchill, 1814), was related to the intensity of infection with *Salmincola carpionis* (Krøyer, 1837). They reported that fish infected with >50 copepods had condition factors that were lower than fish that were lightly infected (1 to 18 copepods). Farmed sea bass infected with *Lernanthropus kroyeri* at intensities of 1 to 24 parasites per host had significantly lower condition factors when compared to uninfected hosts (Manera and Dezfuli 2003). Katakura et al. (2004) studied the effects of infection with *Haemobaphes diceraus* Wilson, 1917, and *Clavella perfida* Wilson, 1915, on the growth and sexual maturity of the walleye pollock, *Theragra chalcogramma* (Pallas, 1814), and reported decreases in the host's condition factor and hepatic somatic index with increasing numbers of *H. diceraus*, but not *C. perfida*. The infection of lanternfishes, *Diaphus theta* Eigenmann and Eigenmann, 1890, and *Tarletonbeania crenularis* (Jordan and Gilbert, 1880), by the pennelid copepod *Cardiodectes medusaeus* (Wilson, 1908) was studied at two sites off central California (Sakuma et al. 1999). At both sites, the occurrence of *C. medusaeus* was significantly greater on *D. theta* when compared to *T. crenularis*. There was a significantly higher rate of parasitism reported for *D. theta* from one site, when compared to the other. However, there was no difference between the sites in the level of parasitism seen on *T. crenularis*. At the site where copepods were most abundant, significantly lower host dry weights were observed for infected *D. theta* and *T. crenularis*, when compared to uninfected co-specifics. In the Pacific cod, *Gadus macrocephalus* Tilesius, 1810, infection of young-of-the-year individuals with *Haemobaphes diceraus* resulted in lower body mass and larger liver mass when compared to uninfected fish (Poltev 2010). In contrast to these studies, Moser and Taylor (1978) reported that lanternfish, *Stenobrachius leucopsarus* (Eigenmann and Eigenmann, 1890), parasitised by *Cardiodectes medusaeus*, were actually larger when compared to non-parasitised specimens of the same age. This was hypothesised to be due to suppression of reproduction in infected fish that increased the available energy for somatic growth. For southern bluefin tuna, *Thunnus maccoyii*, a negative correlation was observed between the number of *Caligus chiastos* and condition factor during early stages of infection (Hayward et al. 2008). However, infections of farmed fish with species of *Caligus* were reported to have an inconsistent effect on host condition factors within and between years (Hayward et al. 2009). This inconsistency may have been due to the relatively small number of hosts examined and/or their reporting and analysing together three species of *Caligus*, which may differ in pathogenicity.

Gomiero et al. (2012) examined the effects of infection with the cymothoid *Paracymothoa astyanaxi* Lemos de Castro, 1955, on the length-weight relationship and the condition factor of the fresh water fish *Astyanax intermedius* Eigenmann, 1908. These authors reported that unlike the condition factor of noninfected hosts that differed between seasons and sexes, infected hosts showed no seasonal or sex-specific differences having a lower condition factor than comparable infected hosts. Infection with isopod, *Ourozeuktes bopyroides* affected condition factor only in juvenile (below 50 mm length) variable leatherjacket, *Meuschenia freycineti*, while there was no significant effect on larger hosts (Friese 1978).

6.3.5.2 Growth

Hyperiid amphipods are found within the pelagic zone and are mostly commensals and parasitoids of gelatinous zooplankton such as cnidarians, ctenophores or salps. Depending on the species, their association with gelatinous zooplankton can be for only part of their life cycle. Hyperiids feed on host tissues, as well as, in some cases, on food items that were captured by their host (reviewed in Laval 1980). Depending on the species, as well as its relative size to its host, feeding can result in the destruction of host tissues which if not regenerated may ultimately cause the death of the host. Laval (1972) cited in Laval (1980) reported an infestation of *Lestrigonus schizogeneios* (Stebbing, 1888) on the medusa *Phialidium* sp. resulting in decreased growth of the medusa that was caused by feeding on host tissues and/or diversion of host food resources.

Heagney et al. (2013) identified differences in otolith microchemistry between yellowtail scad, *Trachurus novaezelandiae* (Jordan and Gilbert, 1880), infected with a cymothoid, *Ceratothoa* sp. and those that were not. Otoliths of parasitised individuals were characterised by significantly lower lithium, calcium, magnesium and higher strontium and barium levels when compared to those of unparasitised individuals from the same subpopulation. These differences in otolith microchemistry indicated that this isopod affected its host, but it remains unclear as to whether these differences arose due to differences in physical, metabolic, chemical and behavioural processes, or combinations thereof, between infected and noninfected individuals. This is an important observation in that otolith microchemistry is used to delineate stocks, to study fish movements and to determine natal origin.

There are only a couple of laboratory studies that have reported on the effects of copepod infection on host growth. The effects of infection with *Lernaeocera branchialis* on Atlantic cod, *Gadus morhua*, have been investigated (Khan 1988, Khan and Lee 1989). Khan (1988) reported that Atlantic cod, which survived infection with *L. branchialis*, showed reduced growth and a lower condition factor that was related to reduced food intake and a lower conversion factor, when compared to uninfected controls. The magnitudes of these effects were dependent on the number of copepods present. In a subsequent study, the relationship between Atlantic cod growth and infection with *L. branchialis* was studied in more detail (Khan and Lee 1989). In this study, adult Atlantic cod were infected in the laboratory and their growth and food consumption monitored every 2 months for a period of 16 months. From 4 to 10 months postinfection, infected cod generally showed a significant reduction in weight and condition factor, when compared to controls. This difference was more apparent in fish infected with more than one *L. branchialis*. At 13 and 16 months after the copepods had reproduced, there were marked improvements in weight and condition factors of infected fish. To examine this change in more detail, food consumption, food conversion efficiency and condition factor of adult cod that were uninfected, recently reinfected and infected with postmature copepods (more than 1 year old) were examined in a series of 2-month-long trials. Over the first month, food consumption and percentage weight gain in both groups of infected fish were higher than that of uninfected fish. Atlantic cod with postmature copepods gained more weight than controls or the reinfected hosts over the second month. Reinfected hosts had a significant decrease in weight gain when compared to uninfected fish at 2 months. At both 1 and 2 months, food conversion rates in the infected groups were significantly lower than that of the uninfected fish. Interestingly, immature Atlantic cod differed in their response to infection with recently infected fish having lower food consumption and therefore lower weight gain, food conversion and condition factors when compared to uninfected fish.

Duston and Cusack (2002) conducted laboratory trials to determine the efficacy of emamectin benzoate against the gill copepod *Salmincola edwardsii* (Olsson, 1869) on brook trout. They reported a significant increase in condition factor and mean specific growth rate in treated fish, when compared to untreated hosts as copepod numbers were reduced from an average of 118 copepods fish^{-1} to 49 copepods fish^{-1}. However, in a second trial, where initial and final average numbers of copepods on the treated fish were 56 and 35 copepods fish^{-1}, respectively, there were no significant differences in condition factor and mean specific growth rate between groups. Appetite suppression was noted in the more heavily infected fish in the first trial, and improved appetite following the removal of the copepods was thought to be responsible for the increased condition factor and higher growth rates of treated fish.

In a field study, which used a mark recapture technique, the effects of natural infection with *Pharodes tortugensis* Wilson, 1935, on the bridled goby, *Coryphopterus glaucofraenum* Gill, 1863, growth, reproduction and survival were assessed (Finley and Forrester 2003). With respect to growth, there was a negative correlation between parasitism and growth, with significant reductions in growth in parasitised fish. Higher respiration rates and lower feeding rates were correlated with the presence of the copepod.

Studies of caligid copepods infecting a variety of host species have generally found no relationship between copepod numbers and host condition factor or feeding rate. The exceptions are studies that have reported extremely high levels of infection under laboratory conditions. For example, there was no correlation between the intensity of infection and condition factor in sea trout, *Salmo trutta* Linnaeus, 1758, that were naturally infected with preadult and adult *Lepeophtheirus salmonis* and *Caligus elongatus* (see Mo and Heuch 1998; Schram et al. 1998). Atlantic salmon, *Salmo salar*, smolts infected in the laboratory with high numbers of *L. salmonis* copepodids were examined at 12, 21 and 30 DPI using X-rays and radio-opaque markers in the feed to determine individual dry weights, condition factor, specific growth rates and mean food consumption rates (Dawson et al. 1999). At 21 DPI, when the majority of the copepods were preadults (average of 51.5 copepods fish^{-1}), a decrease in mean food consumption occurred in the infected group due to a reduction in the number of fish that were actively feeding. However, by 30 DPI, when the copepods had reached the adult stage and healing of the lesions caused by the earlier developmental stages had started, mean food consumption returned to the same level as the uninfected fish. With respect to dry weight, specific growth rate and condition factor, there were no significant differences between infected and uninfected fish over the study (Dawson et al. 1999). Jones et al. (2006b) examined 1309 three-spine sticklebacks, *Gasterosteus aculeatus* Linnaeus, 1758, and reported co-infection of these hosts with copepodid and chalimus stages of *L. salmonis* and *Caligus clemensi* Parker and Margolis, 1964. The intensity of these infections was 18.3 and 4.2, respectively. There was no correlation between copepod abundance and host condition factor. However, at highest levels of infection, *L. salmonis* may have caused a reduction in host weight. As mentioned previously, Jones et al. (2007) reported that the abundance of *L. salmonis* was consistently higher on chum salmon, when compared to pink salmon following a laboratory infection. At the highest level of challenge (735 copepodids fish^{-1}), a significant reduction in the weight of chum salmon was reported as early as 14 DPI, when compared to uninfected fish. More recently, Mańin et al. (2009) experimentally infected the common jollytail, *Galaxias maculatus* (Jenyns, 1842), with *Caligus rogercresseyi* Boxshall and Bravo, 2000, and monitored their survival and growth. Although *C. rogercresseyi* has not been reported on wild common jollytail, the laboratory infections were successful and demonstrated superficial damage, weight loss and mortality associated with the infection.

Although some authors suggested that isopod-host interactions are relatively benign (e.g. Maxwell 1982; Carrassón and Cribb 2014), the vast majority of studies have identified negative impacts on host growth and condition arising from infections. For example, Lanzing and O'Conner (1975) examined wild-caught luderick, *Girella tricuspidata* (Quoy and Gaimard, 1824), infected with *Ceratothoa banksii* (Leach, 1818), and reported based on analysis of length-weight relationships that infected hosts were in poorer condition than uninfected hosts and that this was especially true when the hosts harboured more than one parasite. Anderson (1977) examined the effect of parasitism by the bopyrid isopod *Probopyrus pandalicola* on growth and metabolisms of the daggerblade grass shrimp *Palaemonetes pugio* Holthuis, 1949, under laboratory conditions. This author reported a variable effect of parasitism on host growth and metabolism throughout the year with growth in some months higher in parasitised hosts. Cymothoid isopod, *Anilocra pomacentri* Bruce, 1987, infection of the coral reef fish, *Chromis nitida* (Whitley, 1928), resulted in significant reductions in growth rate and condition of the host (Adlard and Lester 1994). Five-lined cardinalfish, *Cheilodipterus quinquelineatus* Cuvier, 1828, infected with single female *Anilocra apogonae* Bruce, 1987, showed significantly reduced condition (Fogelman et al. 2009). When corrected for age, infected fish had significantly lower weights, lower hepatosomatic indices and lower growth for both sexes when compared to uninfected individuals. Similarly, in the Kuro shrimp, *Argis lar* (Owen, 1839), infection with the bopyrid isopod *Argeia pugettensis* resulted in lower body masses for a given carapace length in infected hosts (Seo et al. 2014). Examination of wild-caught goldblotch grouper, *Epinephelus costae* (Steindachner, 1878), infected with gnathiids, showed no evidence for a negative effect on growth or general condition of infected fish although high numbers of parasites were present (Ercument et al. 2011). This lack of an effect may be due to the transitory nature of attachment and feeding within this group of isopods.

6.3.6 Reproduction

According to Kabata (1970, 1984), parasites may interfere with reproductive activities of their hosts by (1) physical disruption or destruction of the gonads, (2) the production of toxins or other factors that act selectively on the gonads and (3) causing general debilitation of the host, thus indirectly depressing gonadal development and function. In addition, parasitism may affect reproductive behaviours and the development of secondary sexual characteristics. With respect to parasitic copepods, it is the debility of the host that is probably the most common cause of observed effects on gonads (Kabata 1984). With respect to other groups of parasitic Crustacea, castration of hosts is the most commonly reported effect of infection on reproduction. The mechanisms by which castration and/or modification of sexual features or behaviours occur are not understood. In some cases, it is apparent that isopod parasites can directly utilise and destroy host's gonadal tissues. In other cases, energetic demands of the parasite may simply reduce the energy available for reproduction and/or the parasite may selectively target host reproductive energy by producing substances that directly manipulate host energy allocation away from reproduction.

6.3.6.1 Invertebrate Hosts

Reinhard (1956) reviewed aspects of parasitic castration of crustaceans and suggested that, as a rule, infection with epicarideans leads to suppression or regression of female gonads but to a lesser extent the gonads of the male host. An entoniscid species, *Portunion* sp., occurs in the grapsid crabs *Cyclograpsus lavauxi* Milne Edwards, 1853, *Hemigrapsus crenulatus* (Milne Edwards, 1837) and *Austrohelice crassa* (Dana, 1851) in New Zealand waters (Brockerhoff 2004). Infection by this isopod resulted in the castration of females due to the loss of ovarian tissues. There was no effect on the structure of the testis and associated structure or secondary sexual characteristics (chelae size) of males. Similarly, parasitised male squat lobsters, *Munida gregaria* (Fabricius, 1793), infected with the bopyrid, *Pseudione galacanthae* Hansen, 1897, showed normal gonad development, whereas parasitised females had smaller eggs but similar fecundity to non-parasitised females (Varisco and Vinuesa 2011). Parasitism had no effect on the secondary sex characters in this species.

Portunion conformis Muscatine, 1956, is an entoniscid isopod that infects and castrates the shore crabs *Hemigrapsus oregonensis* (Dana, 1851) and *Hemigrapsus nudus* (Dana, 1851). Interestingly, these hosts are reported to be able to regenerate ovarian tissues upon the death of *P. conformis*. This isopod is an internal parasite, which as it develops in the host becomes surrounded by a host-produced cellular sheath (Kuris et al. 1980). This cellular sheath is thought to be formed of two or three layers of host blood cells which were classified as phagocytic amoebocytes (Kuris et al. 1980). The role of this sheath in the host-parasite relationship is unknown, although it is possible that they form part of the host defence response. Alternatively, they may be created by the isopod to avoid an immune response and/or to protect its developing eggs and provide access for larval escape from the host. In the case of the sheath surrounding the entoniscid isopod, *Priapion fraissei* (Giard and Bonnier, 1886), in the swimming crab, *Liocarcinus holsatus* (Fabricius, 1798), it is believed that it is formed by an invagination of the wall of the branchial chamber (Choy 1986).

Bopyrid isopods (Bopyridae) utilise free-living decapod crustaceans as their definitive hosts, and many of the members of this family are reported to cause parasitic castration of their hosts. Parasitic castration by bopyrid isopods has been reported for *Probopyrus pandalicola* infecting the shrimp, *Palaemonetes pugio* (Anderson 1977). Seo et al. (2014) reported significant reduction in growth and a marked reduction in the gonadosomatic index and breeding rate in Kuro shrimp, *Argis lar*, infected with *Argeia pugettensis* Dana, 1853. In the laboratory, Calado et al. (2008) examined the effects of *Argeiopsis inhacae* Kensley, 1974, infection on female reproduction in the stenopodid shrimp, *Stenopus hispidus* (Olivier, 1811). There was no effect of infection on intermoult duration or mating behaviours (Calado et al. 2008). However, when mated with unparasitised males, parasitised females showed no evidence for the development of vitellogenic oocytes and therefore produced no egg clutches. Infection of the burrowing mud shrimp, *Upogebia pugettensis* (Dana, 1852), with a recently introduced bopyrid, *Orthione griffenis* Markham, 2004, had a negative impact on host reproduction and population size (Griffen 2009). Using field-collected data and simulation modelling, a number of testable hypotheses were proposed that may explain how increased metabolic demands due to infection may affect patterns of interactions between this parasite and its host that were observed in the field (Griffen 2009).

Infection of the shrimp, *Palaemonetes argentinus*, by *Probopyrus oviformis* (syn. of *P. pandalicola*) resulted in an interruption of oocyte maturation with development arrested at the end of primary oogenesis (Schuldt and Capítulo 1985). The reproductive function of males was not affected. Similar observations were made by Petrić et al. (2010) who examined field-collected specimens to determine the effects of infection of the gill chamber by *Pleurocrypta* sp. on growth and reproduction in the shrimp, *Munida rutllanti* Álvarez, 1952. Histological examination of ovaries collected through the year revealed delays in oocyte development and suppression of egg development past the previtellogenic stage. This was proposed to be due to depletion of lipids or energy by the parasite. In the case of infected males, delayed spermatozoa and spermatophore development was reported, as well as some feminisation of secondary sexual characteristics. Feminisation of secondary sexual characteristics in males of the shrimp *Thor floridanus* Kingsley, 1878, infected with *Bopyrinella thorii* (Richardson, 1904) has also been reported (Romero-Rodríguez and Román-Contreras 2011).

The effects of bopyrid isopods on reproductive output of shrimp *Lysmata* spp. have been examined for a number of species. Members of this genus first mature as males but as they age change to become functional simultaneous hermaphrodites, although most reproductive effort in the hermaphroditic stage is devoted to embryo production and incubation (Bauer 2006). Isopods that are parasitic within the abdomen of their hosts such as *Eophrixus lysmatae* (Caroli, 1930) have been reported to cause castration of the female function of their hosts although male function is retained (Calado et al. 2005 and references therein). In the case of infection of the brachial cavity with *Parabopyrella* sp., a significant reduction in embryo production, but not embryo quality, was reported for *Lysmata amboinensis* (de Man, 1888) (Calado et al. 2006).

In the porcellanid crab, *Pachycheles rudis* Stimpson, 1859, infection with the bopyrid isopod, *Aporobopyrus muguensis* (Shiino, 1964), resulted in delayed sexual maturity in female crabs, as well as substantial reductions in their fecundity, which may in part be related to reduced growth rates of infected crabs (Van Wyk 1982). Feminisation of secondary sexual characteristics seen as a reduction in size of the major chela was reported for the fiddler crab, *Uca uruguayensis* Nobili, 1901, infected with *Leidya distorta* (Leidy, 1855) (Roccatagliata and Jordá 2002).

Hirose et al. (2005) determined the state of gonadal maturation, as well as the number of eggs and embryos per zooid in the ascidian, *Diplosoma virens* (Hartmeyer, 1909), from populations that were heavily or occasionally parasitised by parasitic copepods of the family Notodelphyidae. They reported significantly lower numbers of eggs/embryos per zooid in the ascidian population that was heavily infected with copepods. These copepods are known to feed on the host's tunic matrices but not on the host's reproductive products. The energy requirements necessary to repair damage caused by copepod feeding may be responsible for the suppression of host sexual reproduction (Hirose et al. 2005). The presence of endoparasitic copepods within the body segments of polychaetes, *Polydorella* spp., has been reported to interfere with their asexual reproduction (Williams 2004). Interestingly, the presence of copepods was also thought to result in an increase in the number of body segments and body length, when compared to uninfected hosts.

Infection of sea slug *Ercolania viridis* with copepod *Ismaila monstrosa* caused the loss of gonadal tissue and the eventual castration of its host (Jensen 1987). However, infection with *Ismaila belciki* Ho, 1987, did not result in castration, only in significantly lower reproductive output, and reduced the survivial of the nudibranch *Janolus fuscus* O'Donoghue, 1924 (see Wolf and Young 2014).

6.3.6.2 Vertebrate Hosts

Kabata (1984) presented evidence for detrimental effects on host fish reproductive capacity caused by infections with the pennellid copepods, *Lernaeocera branchialis* and *Peroderma cylindricum* Heller, 1865. Since publication of his review, a limited number of additional reports based on field-collected materials and laboratory studies have become available. Infection of lantern fish with *Cardiodectes medusaeus* arrested egg development at the oocyst stage (Moser and Taylor 1978). Infected hosts were larger than uninfected hosts of the same age, and there was no significant difference in caloric content when compared to noninfected hosts. This prompted the authors to suggest that this copepod may control host reproduction through the production of substances such as hormones rather than through limiting energy available for reproduction. Laboratory infection of Atlantic cod with *Lernaeocera branchialis* resulted in a reduction of the proportion of animals that were in spawning condition, when compared to uninfected fish (Khan 1988). At 9 months postinfection, both male and female Atlantic cod with two or more copepods had significantly lower gonadosomatic indices.

Katakura et al. (2004) reported a reduction in the gonadalsomatic index of both male and female walleye pollock, *Theragra chalcogramma*, that was negatively correlated with numbers of *Haemobaphes diceraus*. The lack of atretic oocytes in ovaries from infected hosts during the normal spawning season suggested that infection might result in earlier spawning or possibly the suspension of spawning. Infection of the bridled goby, *Coryphopterus glaucofraenum*, with parasitic copepod *Pharodes tortugensis* was correlated with a reduction in the ovary size, with infected hosts having gonads that were significantly smaller than uninfected hosts of comparable body sizes (Finley and Forrester 2003).

Parasitic isopods can affect reproduction of their fish hosts. The gonadosomatic index of *Chromis nitida* infected with *Anilocra pomacentri* Bruce, 1987, was significantly lower when compared to uninfected individuals (Adlard and Lester 1994). In addition, a reduction of 88% in the fecundity of *C. nitida* was estimated as infection resulted in fewer, yet similar sized eggs being produced. Furthermore, migratory movements of the fish to reef slopes were reduced in parasitised individuals, presumably due to the effect of *A. pomacentri* on the development of the gonads. Infection with a single female isopod *Anilocra apogonae* resulted in significantly lower gonadosomatic index and castration of female five-lined cardinalfish, *Cheilodipterus quinquelineatus*. With respect to male breeding success, infection resulted in a failure to mouthbrood their offspring, and when mouthbrooding occurred lower numbers of eggs were present (Fogelman et al. 2009). The absence of sex-specific proteins in plasma and inhibition of gonadal development in male and female *Cyphocharax gilbert* (Quoy and Gaimard, 1824) were caused by fresh water cymothoid isopod *Riggia paranensis* Szidat, 1948 (see Da Silva et al. 2005). These authors suggest that *R. paranensis* might interfere with the regular hormonal process of vitellogenesis. As mentioned above, isopod infections of decapods have also been reported to affect vitellogenesis.

6.3.7 Survival

As noted previously, the environment plays an important role in modulating the impacts on the host for a particular level of infection and/or parasite. This has been demonstrated for the bopyrid isopod, *Probopyrus pandalicola* infecting the daggerblade grass shrimp, *Palaemonetes pugio* (Sherman and Curran 2013). These authors compared the survival time of *P. pugio* during starvation for groups of parasitised, deparasitised and unparasitised shrimp at 20 and 25 °C. At higher water temperature, infected shrimp carrying this bopyrid isopod and those that had the isopods removed immediately prior to the experiment both had significantly reduced survival times when compared to unparasitised individuals (Sherman and Curran 2013). Reduced survival in deparasitised individuals was due to the compromised nutritional state of the shrimp (Sherman and Curran 2013). At the lower water temperature, there was no significant difference in survival times between these groups.

With the exception of studies on three species of damselfish, *Pomacentrus amboinensis* Bleeker, 1868; *Pomacentrus moluccensis* Bleeker, 1853; and *Dischistodus perspicillatus* (Cuvier, 1830), there are few data on the effects of gnathiid isopods on their host's biology (Grutter et al. 2008, 2010, 2011; Jones and Grutter 2008; Penfold et al. 2008; Ercument et al. 2011). Laboratory challenge trials have been used to examine effects of gnathiid infections on hosts. For example, Jones and Grutter (2008) exposed juvenile *D. perspicillatus* to 0, 1 or 2 *Gnathia falcipenis* Holdich and Harrison, 1980, and held them for 8 days to examine effects on mortality and growth. Fish exposed to two gnathiids had a significantly shorter standard length and weight when compared to unexposed fish. Laboratory exposures of the damselfishes *Acanthochromis polyacanthus* (Bleeker, 1855) and *Neopomacentrus azysron* (Bleeker, 1877) to one or two gnathiid resulted in mortalities in larval and recently settled stages (Grutter et al. 2008). Grutter et al. (2011) determined the impact of infection with a single gnathiid, *Gnathia aureumaculosa*, on survival of juvenile damselfish, *Acanthochromis polyacanthus*. Previously infected and uninfected fish were transferred back to the wild and their survival monitored. In most instances, fish that had been infected in the laboratory disappeared before controls.

6.3.8 Host Behaviour

Kabata (1984) concluded that anecdotal evidence exists for parasitic copepods having an impact on the behaviour of fish hosts. However, he suggested that "systematic well designed studies were needed to provide insight into its impact and mechanism". Since Kabata's review, there have been additional field-based reports of parasitic copepods causing behavioural changes in hosts but few experimental studies.

Numerous authors mentioned changes in fish behaviour that are associated with the development of disease caused by parasitic copepods in the laboratory and aquaculture settings. In general, these changes are similar to those that would be seen to occur in response to a variety of parasitic and other diseases and include changes in swimming behaviour, changes in colouration, loss of equilibrium and hyperinflation of the swim bladder. For example, net-pen-reared Atlantic salmon that are heavily infected with *Lepeophtheirus salmonis* or other caligid copepods can show increased flashing and jumping activity and reduced appetite prior to morbidity. Atlantic cod infected in the laboratory with *Lernaeocera branchialis* were reported to be hyperactive and to swim in an erratic manner (Khan 1988). Others were reported to have overinflated swim bladders and a darkened colouration.

There are a few reports of changes in behaviour of wild fish infected with copepods. The majority of these reports refer to infections of caligid copepod, causing changes in host's swimming behaviour and their residence time in seawater (Tulley et al. 1993a, b; Birkeland 1996; Grimnes and Jakobsen 1996; Birkeland and Jakobsen 1997; Bjørn et al. 2001). In both Ireland and Norway, sea trout were observed to return prematurely to estuaries and rivers, the fish that returned being heavily infected with *Lepeophtheirus salmonis* (Tulley et al. 1993a, b; Birkeland 1996; Bjørn et al. 2001). Birkeland and Jakobsen (1997) experimentally infected sea trout smolts with *L. salmonis* and studied their behaviour and timing of return to fresh water. Fish that were infected with *L. salmonis* prior to their release returned to the estuarine area and migrated into fresh water earlier, when compared to uninfected control fish that were released at the same time. In this study, the control fish acquired a heavy infection with *L. salmonis* following their release that affected their eventual return to fresh water. In both groups, osmoregulatory problems caused by *L. salmonis* and high infection pressure were thought to be responsible for their premature return to estuarine areas and fresh water. Dawson et al. (1999) reported changes in the dominance hierarchy of Atlantic salmon infected with *L. salmonis* in the laboratory. Whether *L. salmonis* can affect social structure of fish populations under more natural conditions remains to be determined.

Kabata in his review reported on the "abnormal" behaviour of several species of non-salmonid fish which included instances of obviously aberrant behaviour which were mainly signs of distress (Sproston and Hartley 1941; Hotta 1962; Rosenthal 1967; Guthrie and Kroger 1974). More recently, Poulin (1999) examined the effects of parasitism on the social behaviour of three-spined, *Gasterosteus aculeatus*, and blackspotted, *Gasterosteus wheatlandi* Putnam, 1867, sticklebacks by quantifying the prevalence and intensity of infection with the copepod *Thersitina gasterostei* (Pagenstecher, 1861) and with another crustacean parasite, *Argulus funduli* Krøyer, 1863. With respect to *T. gasterostei*, a relationship between shoal size and the prevalence and intensity of infection was reported, with fish in larger shoals having more severe infections. Due to the fact that this study was conducted in a predator-free habitat and that infection with *T. gasterostei* can cause death under some environmental conditions, it was concluded that *T. gasterostei* may be responsible for the formation of smaller shoal sizes; however, this remains to be proven.

Laboratory exposures of the damselfishes *Acanthochromis polyacanthus* and *Neopomacentrus azysron* to one or two gnathiids resulted in impaired swimming behaviour in larval and recently settled stages (Grutter et al. 2008). Grutter et al. (2011) determined the impact of infection with a single gnathiid, *Gnathia auresmaculosa*, on swimming performance, oxygen consumption, settlement and survival of juvenile damselfish, *Acanthochromis polyacanthus*. Infection resulted in a reduction in critical swimming speed, and fish that had been previously parasitised had 35% higher oxygen consumption when compared to fish that had never been infected.

With respect to invertebrate hosts, behavioural changes were identified in grass shrimp *Palaemonetes pugio* infected with the bopyrid *Probopyrus pandalicola*. Based on tank observations, there were differences in prey capture rate between parasitised and non-parasitised hosts for *Daphnia* but not *Artemia* which the authors attributed to differences in the level of prey activity (Bass and Weis 1999). With respect to predation, parasitised hosts were preferentially selected by the visual predator, *Fundulus heteroclitus heteroclitus* (Linnaeus, 1766). This was attributed to lower levels of activity in the parasitised grass shrimp.

6.3.9 Factors Increasing the Susceptibility of Hosts to Infections with Crustacea

Situations that result in chronic stress and/or poor health of hosts are considered to play very important roles in determining their susceptibility to infection with parasites. With respect to caligid copepods, it is well recognised that poorly smolted or otherwise unhealthy salmonids are more susceptible to infection with *Lepeophtheirus salmonis* (cf. Grimnes and Jakobsen 1996; Finstad et al. 2000). In pond culture, overcrowding and poor water quality have been attributed to be responsible for the development of disease caused by parasitic copepods (Singhal et al. 1986; Tareen 1986). Exogenous administration of cortisol has been widely used to experimentally mimic stress physiology (Iwama et al. 2005). Using this technique, Johnson and Albright (1992b) were able to increase the survival rate of *L. salmonis* on coho salmon, a species that is resistant to infection, to a level similar to that seen on Atlantic salmon. This increased survival was related to the suppression of the epithelial hyperplasia and inflammatory response of the host due to the elevated cortisol levels. The value of exogenous cortisol administration as a model of stress in fish is questionable, especially in those instances where cortisol administration results in the elevation of levels beyond the normal physiological range. Furthermore, administration of cortisol often results in sustained high levels of cortisol, a condition that is not seen over the long term in chronically stressed fish (Barton et al. 1987; Basu et al. 2001; Hosoya et al. 2007). For these reasons, studies such as that of Johnson and Albright (1992b) can be used as evidence for the importance of innate immune responses in controlling *L. salmonis* infections, but not as evidence for an effect of stress on susceptibility of hosts to infection.

To determine whether a stress event can have long-term effects on susceptibility to parasitism by copepods, Saarinen and Taskinen (2005) subjected a group of fresh water clams, *Anodonta anatina* (Linnaeus, 1758), to a 25-day period of low oxygen. Eleven months after the stress, these clams, along with a non-stressed control group, were exposed to a natural infection of the ergasilid copepod, *Paraergasilus rylovi* Markevich, 1937. The clams within the stress group became more heavily parasitized when compared to the non-stressed clams. However, these clams also had lower growth, lower reproduction and lower survival than the unstressed clams suggesting that their health had been seriously compromised.

Changes in host physiology, immune response and behaviour associated with reproduction have been related to higher prevalence and intensity of parasitism in a number of host-parasite systems. With respect to parasitic copepods, only one study has examined whether such relationships exist. Taskinen and Saarinen (1999) examined the relationship between the reproductive status of the fresh water clam *Anodonta piscinalis* and the abundance of *Paraergasilus rylovi* in three lakes in Finland. They reported that after correction for host size, the abundance of *P. rylovi* was two times higher in female clams that were brooding glochidia larvae, when compared to non-reproducing females. There was no explanation for this difference, although they did propose several mutually non-exclusive hypothesis, including (1) increased feeding rates of brooding clams resulting in an increased exposure to *P. rylovi*, (2) changes in energy allocation during reproduction resulting in a decline in immune defences and (3) the possibility that *P. rylovi* may benefit by the reproductive activities by possibly feeding on glochidia larvae.

The importance of the diet in modulating immune function and the resistance of fish to disease is well established (Waagbø 1994). With respect to parasitic copepods, Jones et al. (2007) examined the effect of reduced feed ration on the susceptibility of very small (1.6 to 8.9 g) pink and chum salmon to infection with *Lepeophtheirus salmonis*. Body weight and condition factor in both species were significantly lower in the reduced ration group. However, there were no significant effects on prevalence or abundance of *L. salmonis* or the rate at which the copepods developed.

6.3.10 Effects on Host Resistance to Other Diseases

There is still relatively little known about how the presence of parasitic crustaceans affects the ability of their hosts to deal with stressful conditions, including exposure to pathogens. Kabata (1984) noted that with respect to disease resistance, results were inconclusive. More recently, it has been demonstrated that Atlantic cod infected with *Lernaeocera branchialis* (Linnaeus, 1767) were less resistant to oil exposure when compared to uninfected fish (Khan 1988). Furthermore, infected cod had a higher rate of mortality following infection with the blood-dwelling protozoa, *Trypanosoma murmanensis* Nikitin, 1927 (cf. Khan 1988). In several instances, a relationship between infectious diseases and the presence and abundance of parasitic copepods have been suggested. For example, Hammell and Dohoo (2005) reported a relationship between outbreaks of infectious salmon anaemia (ISA) in Atlantic salmon and the presence and abundance of *Lepeophtheirus salmonis*. The exact nature of the relationship between *L. salmonis* and infectious salmon anaemia virus (ISAV) remains unclear. It is possible that high numbers of *L. salmonis* may predispose their hosts to outbreaks of ISA. Alternatively, carriers of ISAV may be more susceptible to infection with *L. salmonis*. A third possibility is that *L. salmonis* may serve as a vector for this disease as it does for pancreas disease (PD) (Petterson et al. 2009; see Chap. 7). In the case of pancreas disease, several epidemiological studies have proposed that high numbers of *L. salmonis* are a risk factor for this disease (Rodger and Mitchell 2007 and references therein). However, even as *L. salmonis* burdens have significantly decreased in areas of endemic PD, the disease incidence increased. This has led to the suggestion that *L. salmonis* is not essential as either a stressor for disease development or as a vector for the causative agent of this disease (Petterson et al. 2009 and references therein).

To date, the only direct evidence for parasitic copepods reducing the resistance of their hosts to other diseases is provided by Mustafa et al. (2000). These authors demonstrated under laboratory conditions that infection of rainbow trout with *L. salmonis* resulted in impaired host macrophage activity that predisposed the fish to subsequent infection with the microsporidian parasite, *Loma salmonae*.

6.4 Population-Level Effects

There are very few studies evaluating the effects of crustacean parasites on host fish populations. Field and laboratory studies on the parasitic isopod *Anilocra pomacentri* (Cymothoidae) on the population dynamics of the reef fish *Chromis nitida* (Pomacentridae) at Heron Island, Great Barrier Reef, Australia, showed that parasites significantly depressed growth, reproduction and survivorship (Adlard and Lester 1994). The mortality of infected juvenile *C. nitida* (LCF 15–30 mm) in the field was at least 88% in contrast to the mortality of uninfected fish, which was 66% in the first 70 days after recruitment of the fish (Adlard and Lester 1994). The effect of the infection on survivorship was further confirmed by laboratory experiments, where the mortality of the infected juveniles ranged from 78% for small fish (mean LCF 15.0 mm) to 28% for larger fish (mean LCF 24.9 mm) within 4 days of experimental infection (Adlard and Lester 1994).

The parasitic copepod *Pharodes tortugensis* had a significant effect on mortality and reproduction of its host bridled goby *Coryphopterus glaucofraenum*, and as a result, it was suggested that this parasite has an effect on the population dynamics of the host (Finley and Forrester 2003).

Field and laboratory observations suggested that isopod *Ourozeuktes bopyroides* had no significant effect on variable leatherjacket *Meuschenia freycineti* under normal conditions with up to 40% of the host being infected (Friese 1978). When the fish were deprived of food for 5 weeks, the mortality of infected individuals was significantly greater (30.5% infected and 10.6% control); however, most of the surviving fish (23 out of 25) rejected the parasites (Friese 1978).

6.5 Concluding Remarks

In summary, the nature of the interactions between parasitic Crustacea and their hosts, and how these interactions affect hosts at the individual and population levels, remain poorly understood. To date, the majority of studies have examined the infection of salmonids, primarily Atlantic salmon with *Lepeophtheirus salmonis*. These studies have (1) improved our understanding of the types of interactions that occur, (2) identified difficulties in conducting such studies and (3) demonstrated how difficult it is to compare between studies, as well as to extrapolate results from lab studies to the field. The effects of parasitic Crustacea on their hosts depend on a large number of factors. With respect to the copepods, these include (1) numbers of the different development stages present, (2) their level of invasiveness, (3) their distribution on the host and (4) how long they have been on the host. Host factors include (1) the species of host, (2) the age/size of the host and (3) the hosts' physiological, immune and nutritional status at the time of infection. The physical, chemical and biological characteristics of the environment also play a role in determining whether a given level of infection will have a measurable effect on the host. All of these factors need to be considered in the design and interpretation of studies of copepod host-parasite relationships.

Histopathological studies have shown that there are both direct and indirect effects on host caused by parasitic Crustacea. Direct effects include changes resulting from the physical and possibly enzymatic disruption of host tissues due to the parasites attachment and feeding activity. In some cases, the pathology may be in part due to the presence of secondary pathogens, such as bacteria and fungi. Indirect effects are related to the host's integrated stress response, and they may occur at sites distant from the site of attachment and feeding.

It is likely that most species of parasitic Crustacea will be found to produce immunomodulatory substances that modify host immunological responses such as hyperplasia and inflammation. Recently, a number of immunomodulatory substances have been isolated and characterised from the salmon louse, *Lepeophtheirus salmonis*. Similar types of studies need to be conducted for other species of parasitic Crustacea to see how widespread the uses of such substances are. Some species of parasitic Crustacea stimulate their hosts to produce specialised tissues and/or structures to improve the security of their attachment and possibly limit their exposure to the host's immune system. One of the most interesting examples is *Scolecodes huntsmani* that forms cysts with a distinct structure that is made up of modified host cells. The mechanism by which these cysts are formed is unknown, although it is hard to imagine that they are simply the result of the physical presence of the parasite. It is possible that in such cases, the parasites produce substances that stimulate and possibly modify host cellular development. If present, the characterisation and study of such substances could provide new insights into cell development and regulation processes.

In most studies of host-parasite interactions for crustacean parasites, there is little biological data provided that can be used to put the magnitude of the reported effects into context. For example, information on the intensity of the infection, stages of developmental stages present, presence of other diseases, physiological condition of the host and environmental conditions at the site of collection are often not provided. All of these factors will have an impact on the magnitude and type of host response reported.

A large number of publications report on aspects of the susceptibility of species (or strains within species) to infection with copepods. Many of these studies use the number of copepods present on the host at a particular time (or time points) as an indicator of susceptibility. The question arises as to whether this is the best variable for measurement, especially in studies examining differences between closely related species (or strains) of hosts. In such cases, other parameters, such as copepod development rates and/or survival to particular developmental stages, should be considered.

It is well recognised that high numbers of parasitic copepods can cause morbidity and death of hosts due to loss of physiological homeostasis and in some cases development of a secondary infection. However, there is a great deal of disagreement on to how low levels of infection affect hosts and host populations. To develop a better understanding of these effects requires the use of controlled infection studies. In addition, research is needed to identify the most appropriate host parameters for measurement as well as to assign biological significance to the measured values.

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Chapter 7
Parasitic Crustacea as Vectors

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Abstract In assessing the role of parasitic crustaceans as vectors, it is interesting to note that the relevant literature appears to be limited to a handful of species. Isopods of the genus *Gnathia* (family Gnathiidae) likely act as definitive hosts and vectors of fish blood parasites of the genus *Haemogregarina*. They may also transmit fish viruses (such as VEN) and may be intermediate hosts for nematode larvae. Furthermore, cymothoid isopods (family Cymothoidae) may transmit lymphocystis virus to fishes. Recent studies show barnacles (subclass Thecostraca) on the carapace and gill filaments of crabs could be potential reservoir hosts for shrimp viruses. Copepods of the genus *Caligus* and *Lepeophtheirus* (family Caligidae) are noted as potentially important mechanical vectors or alternative hosts of a number of viral diseases between fishes, and *Lepeophtheirus* can transfer pathogenic bacteria between fishes. Ergasilids (family Ergasilidae) parasitic on the gill filaments of fishes can support the replication of shrimp viruses and likely act as viral vectors and transmit lymphocystis. Branchiurans, specifically from the genus *Argulus*, are thought to serve as mechanical vectors of several viruses to fishes, especially carp, as well as acting as intermediate hosts for dracunculoid and skrjabillanid nematodes of fishes. All of these vector examples are further discussed within the chapter, and areas of possible future research are identified.

7.1 Introduction

Several groups of crustaceans are reported to be parasitic on a number of different hosts including fish, invertebrates and even other crustaceans. However, these parasitic crustaceans can also act as definitive and intermediate hosts as well as hypersymbionts (see Chap. 8). If the crustacean can carry and transmit an infectious pathogen into its host, it is called a vector. A vector can be biological or mechanical.

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A biological vector transports the pathogen, and the pathogen is able to develop and replicate inside the vector (becoming infective) before reaching a new host. A mechanical vector merely transports the vector without biological development or replication (sometimes just through physical contact) to a susceptible host.

Cusack and Cone (1986) briefly revised some of the fish parasites which act as vectors of bacteria and viruses. They found that most of the known vectors at that time were tissue feeders that were able to breach the host epidermis (through feeding or attachment) and were able to transfer from one host to another (thus transferring the pathogen too). Some of these vectors can cause severe impacts on fish in aquaculture, resulting in monetary losses (Overstreet et al. 2009). Although vectors are noted to spread disease (and often with great efficiency), pathogens are not dependant on vectors for disease transfer. Many pathogens can be transmitted in several other ways including passive transmission directly through the water or directly from host to host and through organic material (blood, faeces, urine, mucus, etc.).

Most research on arthropod vector associations has been focused on terrestrial organisms, with only a few reported from the aquatic environment. Needless to say, there are even less recorded incidences of parasitic crustaceans acting as vectors, but some of these will be discussed below.

7.2 Isopoda

There are a number of isopod families that are parasitic on fish or crustaceans. Within the suborder Cymothoida, there are three families with possible vector associations. The family Cymothoidae are permanent obligate ectoparasites of marine and freshwater fishes; the Entoniscidae are endoparasites of crustaceans (usually crabs), while the family Gnathiidae are temporary ectoparasites, with only the larval stages being parasitic on marine fish.

7.2.1 Cymothoidae

The first report of an isopod being associated with lymphocystis is that of *Livoneca redmanii* Leach, 1818 (as *Livoneca ovalis* (Say, 1818)). Lymphocystis is a communicable disease occurring in freshwater and marine fishes caused by the iridovirus known as lymphocystivirus or lymphocystis disease virus (LCDV). Infected fish have small, wart-like nodules generally found on the fins, skin or gills. Lawler et al. (1974) noticed that 95% of the silver perch, *Bairdiella chrysoura* (Lacepède, 1802), with gill lesions caused by the lymphocystis had one or more *L. redmanii* associated with the lesion (Fig. 7.1). The isopod potentially irritates the gills and allows the virus to enter, or it is possible that the isopod transmits the virus. Of the 20 fish with isopod gill infections, 14 had internal infections suggesting that the virus is transferred to the internal tissues via the gills (Lawler et al. 1974).

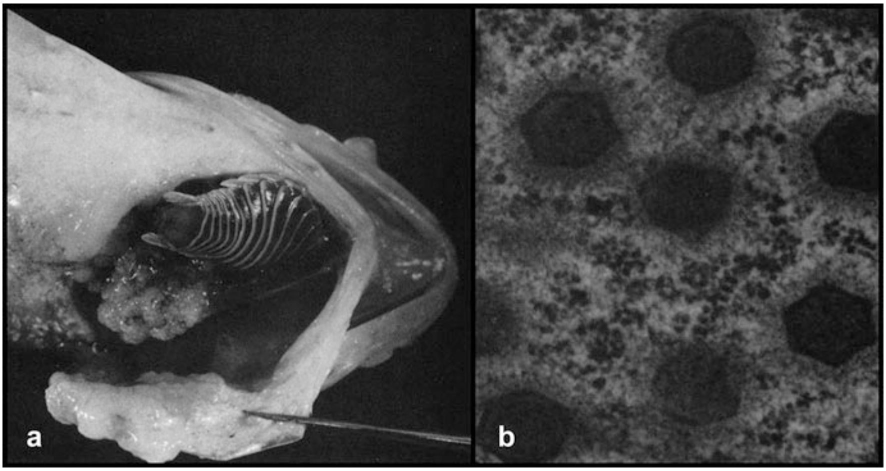

Fig. 7.1 (**a**) *Livoneca redmanii* Leach, 1818 (as *Livoneca ovalis* (Say, 1818)) in the gills of the silver perch, *Bairdiella chrysoura* (Lacepède, 1802) showing gill hypertrophy and lymphocystis cells on the skin, gills and operculum, (**b**) electron micrograph displaying virus particles in the lymphocystis cell cytoplasm from the gill operculum. Images from Lawler et al. (1974)

The presence of cymothoid isopods can also lead to secondary infections at the site of attachment. Rameshkumar et al. (2013) noted that bacterial and fungal pathogens associated with carangid fishes infested with three *Nerocila* Leach, 1818 species could be infectious and negatively affect fish populations.

7.2.2 Entoniscidae

The entoniscid isopod *Portunion conformis* Muscatine, 1956 infects common shore crabs, such as *Hemigrapsus oregonensis* (Dana, 1851), and castrates its host. In 1979, Kuris et al. discovered two viruses within the parasitic isopod. One was a relatively large, unidentified virus (58 nm), and the other was a smaller, more abundant RNA picorna-like virus (25 nm). Although a high prevalence of viral infection was seen to kill the isopod in some cases, thus benefitting the crab host, there are still uncertainties regarding the presence of viral particles in both the host and parasite. Kuris et al. (1979) hypothesised that the isopod could transmit the virus to its progeny that would go on to infect other crabs. The different isopod stages and the effect of infective isopods on uninfected crabs (virus free) would need to be studied.

7.2.3 Gnathiidae

The possibility of a gnathiid isopod being a vector of fish haemogregarines was first suggested by Davies and Johnston (1976). Up to this point, only leeches were

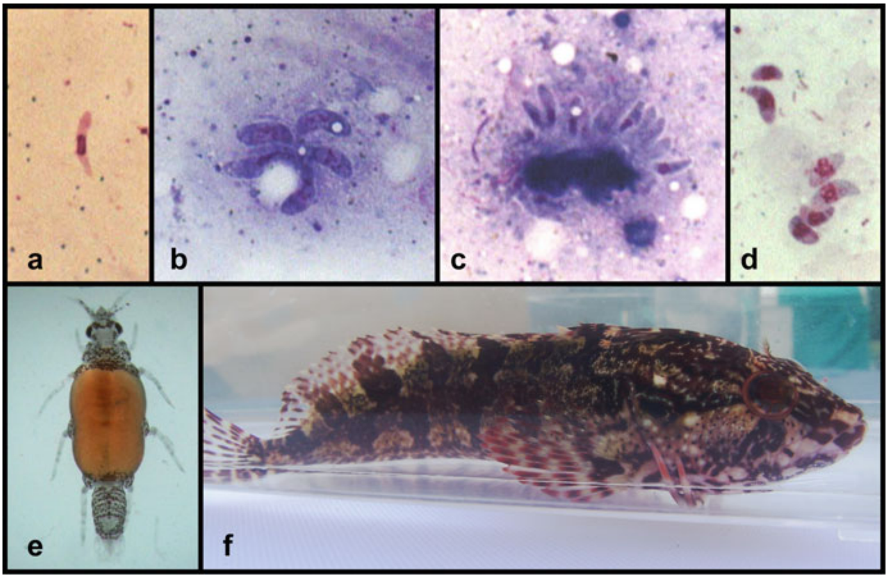

Fig. 7.2 Life cycle stages of *Haemogregarina bigemina* (Laveran & Mesnil, 1901) in the gnathiid isopod, *Gnathia africana* (Barnard, 1914) and the South African fish host, *Clinus superciliosus* (Linnaeus, 1758). (**a**) Free gamont of *H. bigemina*; (**b**) formation of five sporozoites (sporogony); (**c**) slender, immature merozoites produced from second-generation meront; (**d**) third-generation merozoites; (**e**) praniza larva of *G. africana*; (**f**) the fish host, *C. superciliosus*. Images (**a**)–(**d**) from Davies and Smit (2001); image (**e**) © Nico Smit; image (**f**) © Maryke Ferreira

recognised as transmitting blood parasites. Several papers thereafter reported gnathiids on infected host fish and showed evidence of the haemogregarines in certain gnathiid larvae; however, it was only in 2001 that Davies and Smit were able to show the full development of the blood parasite in both the fish host and the gnathiid isopod. The life cycle of *Haemogregarina bigemina* (Laveran & Mesnil, 1901) in the South African fish host, *Clinus superciliosus* (Linnaeus, 1758), and the gnathiid isopod, *Gnathia africana* (Barnard, 1914), included the transmission of the blood parasite from the host to the gnathiid as well as its developmental stages in the gnathiid (Fig. 7.2, Davies and Smit 2001). The authors believed the haemogregarines were most likely transmitted when infected gnathiids were ingested by fishes rather than infecting fishes during another blood meal (as they have three infective juvenile stages). More recently, Curtis et al. (2013) provided evidence that gnathiids most likely act as vectors of haemogregarines from tropical coral reefs. They found that squashes of *Gnathia aureamaculosa* (Ferreira & Smit, 2009) in Ferreira et al. (2009) that had fed on triggerfish, *Rhinecanthus aculeatus* (Linnaeus, 1758), infected with *Haemogregarina balistapi* (Smit, Grutter, Adlard & Davies, 2006) contained not only gamont stages but also all the different haemogregarine developmental stages similar to those found by Davies and Smit (2001). This study on the Great Barrier Reef, Australia, thus provided strong evidence that *G. aureamaculosa* is the definitive host of *H. balistapi* and further supports for the inclusion of gnathiids on the list of vectors of fish haemogregarines.

Gnathiids were also suspected to be vectors of viral erythrocytic necrosis (VEN), which affects the red blood cells of marine and anadromous fish. In a study by Davies et al. (2009), VEN-like bodies were seen in both the erythrocytes of the host fish, *Rhinecanthus aculeatus*, and within the juvenile gnathiid isopods feeding on it. The presence of the VEN-like bodies within the digesting blood meal of the gnathiids indicated that these parasites may act as vectors for this virus. Other associations with parasitic gnathiids, such as protozoan and fungal-like structures as well as foraminifers, are less clear and involve symbiotic organisms that could be hyperparasites or commensals (Smit and Davies 2004). Monod (1926) reported on the rare occurrence of nematode larvae encysted in the ovary of *Paragnathia formica* (Hesse, 1864) as well as a nematode in a praniza pleon. Smit and Davies (2004) also noted a nematode in the anterior hindgut of juvenile *Gnathia pantherina* (Smit & Basson, 2002) as well as flagellates and fungal-like structures in the body and anterior hindgut of *Gnathia maxillaris* (Montagu, 1804), respectively. The lack of further reports on theses associations could be that no one is looking for these organisms within these tiny crustacean parasites. Whether these parasites are intermediate hosts, vectors or accidental infections remains to be seen and requires further research.

7.3 Cirripedia

Many thoracican barnacles are considered to be commensals on numerous aquatic organisms (including corals, sponges, molluscs, whales, turtles and other crustaceans); however, there are several species which are true parasites inflicting harm on their respective hosts. Most natural barnacle diseases were overlooked due to the difficulty in observing the specific symptoms of disease on an organism covered in calcareous plates. Thus, the first recorded viral disease of a barnacle was made by Leibovitz and Koulish as recently as 1989. The ivory barnacle, *Amphibalanus eburneus* (Gould, 1841) (previously *Balanus eburneus*), was infected with a large (222 nm × 175 nm), mature enveloped icosahedral DNA iridovirid-like virus (Leibovitz and Koulish 1989).

In 2009, Overstreet and colleagues exposed two barnacles on the gills of *Callinectes sapidus* Rathbun, 1896 (blue crab) to three different viruses (as well as an ergasilid, see Sect. 7.4.2). Both barnacles, the potentially parasitic acorn barnacle *Chelonibia testudinaria* (Linnaeus, 1758) (as *Chelonibia patula* (Ranzani, 1818)) on the carapace and the gooseneck barnacle *Octolasmis lowei* (Darwin, 1852) (as *Octolasmis muelleri* (Coker, 1902)), were shown to be potential reservoir hosts for Taura syndrome virus (TSV). Taura syndrome is one of the more harmful diseases affecting shrimp populations worldwide. The second virus, another highly infectious and harmful virus called white spot syndrome virus (WSSV), did not replicate in either barnacle. However, these barnacle parasites could potentially also be vectors of the third virus, yellowhead virus (YHV), for a short time period if continuously exposed. Yellowhead disease is highly contagious and lethal and turns the cephalothorax of infected shrimp and prawns yellow. The study, however, showed decreased virus levels over the 2-week study, and thus they are not considered to be reservoirs for this particular virus (Overstreet et al. 2009).

The question of whether or not the barnacle could transfer a virus and infect shrimp (or any other host) remains unanswered. Theoretically, there is the opportunity for shrimp to feed on infected barnacle fragments and thus transmit the virus; however, no publications have yet substantiated this theory.

7.4 Copepoda

Parasitic copepods can be located on external surfaces as well as within the body cavities of their aquatic hosts. In most cases, the co-infection of a fish host with both a parasite and a pathogen increases the risk of the disease as well as the transmission of the pathogen to other hosts. Some copepods are prospective vectors of biotoxins, viruses and bacteria via trophic transfer (infected copepods are eaten by the host). However, only two families are currently known to contain species which act as parasitic vectors, namely, Caligidae (sea lice) and Ergasilidae. A third family, Lernaeidae has the potential for vector associations and is thus discussed here too.

7.4.1 Caligidae

Lepeophtheirus salmonis (Krøyer, 1837), also referred to as salmon lice, are known to feed on mucus, epithelial cells and blood of the salmon hosts. They can cause large wounds at the site of attachment and leave the salmon susceptible for secondary infections by pathogenic bacteria and viruses. One such virus is the infectious salmon anaemia virus (ISAV). This virus is characterised by severe anaemia, haemorrhages, organ enlargement and necrosis, and can cause high mortalities over time to farmed Atlantic salmon. Nylund et al. (1993) identified ISAV in the copepod gut and stated it could be a vector for the virus, although they were unsure how long the virus could reside in the lice. A year later, Nylund et al. (1994) reported on the transmission of ISAV from infected sea lice to noninfected Atlantic salmon. These lice were noted as potentially important vectors in both epidemic and endemic phases. Although not the exclusive mode of transmission, the copepods appear to be the most effective transfer of the virus, and future studies should concentrate on the survival times of the virus in the copepod and the fish, as well as the spread of the virus to other geographical regions.

Infectious haematopoietic necrosis virus (IHNV) is a rhabdovirus which causes infectious haematopoietic necrosis (IHN). This infectious disease occurs in both marine and freshwater fish and can cause mass mortalities in aquaculture. Using IHNV, Jakob et al. (2011) established an in vivo virus-parasite challenge to determine if *L. salmonis* has the capacity to transfer a virus to another host. Under laboratory conditions, the salmon louse was able to become infected with the virus, from a water bath exposure as well as from feeding on infected salmon, and transmit it to naïve Atlantic salmon through parasitism. The transient association of the virus and the louse indicates that *L. salmonis* acts as a mechanical vector (rather than a biological vector or reservoir).

Lepeophtheirus salmonis can also function as a vector and reservoir for secondary invader pathogenic bacteria, such as *Aeromonas salmonicida* (Lehmann & Neumann 1896) Griffin et al. 1953. Nylund et al. (1993) attempted to study this interaction and were able to locate the virus in the gut of the copepod but were unable to prove that the salmon lice could transfer furunculosis. Similarly, another three bacteria species, *Tenacibaculum maritimum* (Wakabayashi, Hikida & Masurmura, 1986) Suzuki et al. 2001, *Pseudomonas fluorescens* (Flügge 1886) Migula, 1895, and *Vibrio* Pacini 1854 spp., were isolated (internally and externally) from *L. salmonis* but still required further studies to determine its role as a biological vector (Barker et al. 2009). Recently, Novak et al. (2016) investigated this interaction between the copepod and bacteria in a manner similar to Jakob et al. (2011) above. Novak et al. (2016) were able to acquire bacteria both internally and externally from a water bath exposure (higher prevalence seen with higher concentration and exposure) as well as from parasitising infected fish. However, only those bacteria which were acquired internally through feeding on an infected host fish were able to transfer the pathogen to smaller, naïve fish hosts via parasitism (Novak et al. 2016). Future work should include identifying whether the male or female copepod is a better vector (as they have different feeding habits), whether *L. salmonis* acts as a biological or mechanical vector (does the bacteria replicate inside the parasite) and what the transmission of the pathogen would be in nature (as compared to the laboratory conditions used previously).

Salmon alphavirus (SAV) or salmon pancreas disease virus (SPDV) is responsible for pancreas disease and sleeping disease in Atlantic salmon, *Salmo salar* (Linnaeus, 1758), and rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792), respectively. Although the virus has been positively identified from the salmon lice (Petterson et al. 2009), no evidence was present regarding the replication of the virus within the copepod or if it is able to transmit the pathogen to other fish. Thus, it remains as a possible vector for this virus.

Neoparamoeba perurans Young, Crosbie, Adams, Nowak & Morrison, 2007 is the aetiological agent of amoebic gill disease (AGD), which is a potentially fatal disease to marine fish. This disease is characterised by build-up of mucus on the gills of infected fish, which causes white mucoid spots and plaques, and epithelial hyperplasia and lamellar fusion (Adams et al. 2004). Recently, *Lepeophtheirus salmonis* has been identified as a potential vector for this marine amoeba (Nowak et al. 2010).

Another caligid louse has also been suspected of pathogenic transfer. *Caligus rogercresseyi* Boxshall & Bravo, 2000 was identified as a mechanical vector for infectious salmon anaemia virus (ISAV). Oelckers et al. (2014) noted that the copepod was able to transmit ISAV to a naïve fish up to 48 hours after being removed from an infected host. The prevalence and amount of the virus decreased the longer it was away from the infected host indicating that the virus was not replicating within the lice. The ISA virus was also found to not be vertically transmitted from adult to nauplii larvae.

Elgendy et al. (2015) identified *Caligus elongatus* von Nordmann, 1832 as a potential vector for *Photobacterium damsela* subsp. *piscicida*. This bacterium causes a disease called photobacteriosis, which is an acute bacterial septicaemia and leads to extensive mortalities in sea bass as well as other marine fishes.

7.4.2 Ergasilidae

Ergasilids are, in their own right, species of economical and commercial importance, specifically regarding the pathology these parasites can cause when attached to the gills of their fish host (Fig. 7.3). These parasites are also implicated as a possible disease vector. In his study on lymphocystis, a common and non-lethal chronic viral disease of marine and freshwater fish, Nigrelli (1950) noted a correlation between the number of parasites on a fish and the degree of the disease, strongly suggesting the copepod is involved with the transfer of the virus. Lymphocystis disfigures the fish to the point where the growths inhibit the fish's ability to swim and eat or breathe, and this (along with secondary infections) can lead to the death of the host. Jones and Hine (1983) noticed a similar pattern with *Ergasilus rotundicorpus* Jones & Hine, 1983 on *Siganus guttatus* (Bloch, 1787) fingerlings.

In order to determine the role of ergasilid parasites in association with a pathogenic virus, Overstreet et al. (2009) exposed three viruses to *Ergasilus manicatus* Wilson, 1911 (along with two species of barnacles, see Sect. 7.3). The three viruses were

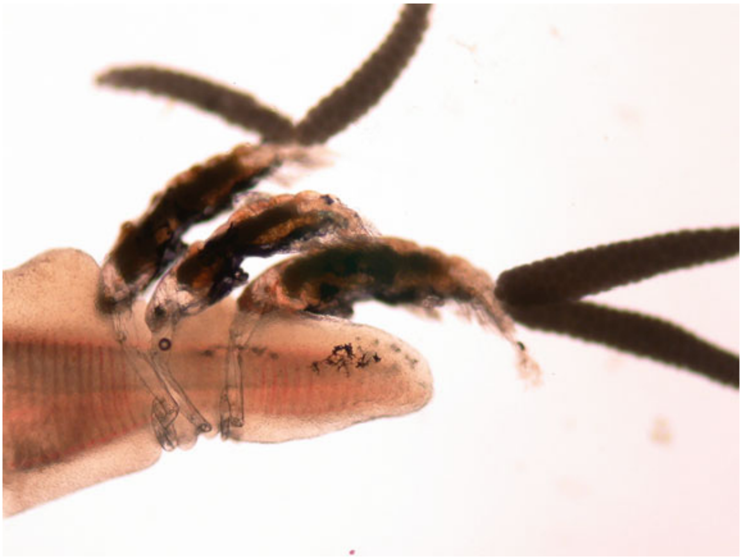

Fig. 7.3 Three female *Ergasilus* von Nordmann, 1832 species attached to the gill filament of the blackspotted squeaker, *Synodontis nigromaculatus* Boulenger, 1905, from the Okavango Delta, Botswana. Image © Liesl van As

Taura syndrome virus (TSV), spot syndrome virus (WSSV) and yellowhead virus (YHV). The first virus, TSV, was able to replicate within the copepod for at least 2 weeks and still be infective. This marks this parasite as a potential reservoir host for the virus. Evidence was also provided to suggest that the second virus, WSSV, replicates within *E. manicatus*. Lastly, YHV (as seen previously with the barnacles) gradually declined over the 2-week period. The copepod could be a vector for YHV if continuously exposed but will not act as a reservoir for the virus. Thus, all three viruses were associated with the copepod. This could mean that the infected parasites could disperse the virus to habitats and hosts not usually exposed to these pathogens. Overstreet et al. (2009) also mentioned how other local ergasilid parasites, which are larger and from more migratory hosts, could potentially be better vectors for these viruses.

7.4.3 Lernaeidae

The epizootic haematopoietic necrosis virus (EHNV) is an Australian iridovirus which causes high mortalities in certain fish species, such as the redfin perch, *Perca fluviatilis* Linnaeus, 1758, and rainbow trout, *Oncorhynchus mykiss*. Langdon (1989) experimented on the transmission and pathogenicity of the virus on 12 different fish species and tried to determine the parasitic vector for the virus. Unfortunately, the virus could not be located in any of the common parasitic crustaceans associated with the host fish; however, the copepod, *Lernaea cyprinacea* (Linnaeus, 1758) (which was not tested in the study), was mentioned as a possible vector as it is often found on the fish later in the summer. To our knowledge, no other studies have recorded *Lernaea* as a vector, and thus studies on this genus could provide more insight into this possible pathogen carrier.

7.5 Branchiura

The genus *Argulus* Müller, 1785 is the largest of the four genera in the family Argulidae and one of the more problematic parasitic crustaceans. It is a common and widespread parasite and can cause disease in various fish hosts, often with severe consequences in aquaculture.

One such disease is spring viraemia of carp (SVC). It is an infectious rhabdovirus disease of carp and other cyprinid fishes, with a high mortality rate and can cause substantial economic losses to the aquaculture industry. Spring viraemia of carp virus (SVCV) was found to be transmitted by *Argulus foliaceus* (Linnaeus, 1758) from infected to healthy carp (Pfeil-Putzien 1978). The parasite functions as a mechanical vector as no multiplication of the virus takes place within the parasite (Ahne 1985).

Argulus has also been found to be associated with carp pox. Carp pox is identified by the white to pink waxy spots covering the scales and fins of infected fish and is caused by

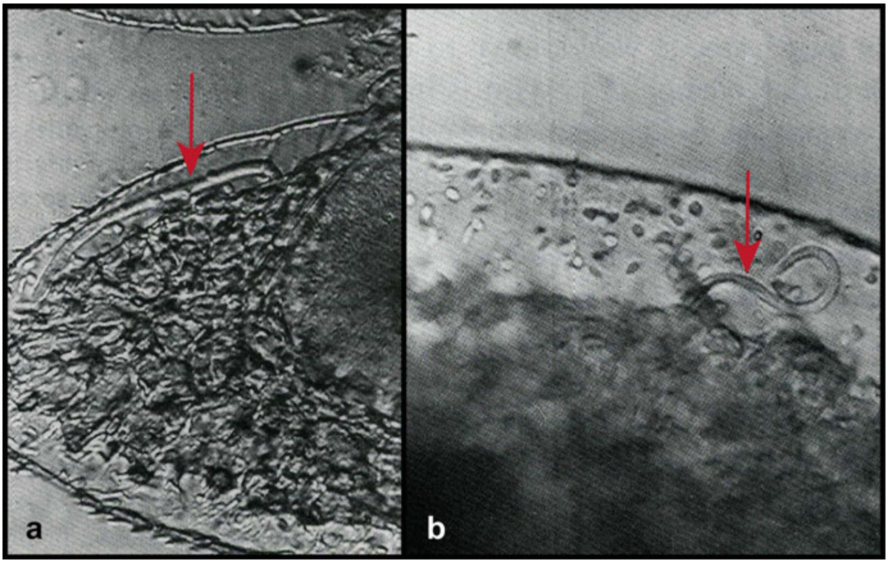

Fig. 7.4 Skrjabillanid nematode larva from the branchiuran *Argulus foliaceus* (Linnaeus, 1758) removed from common carp. (**a**) Skrjabillanid larva observed in the uropod of *A. foliaceus*, (**b**) skrjabillanid larva from the lateral section of the body of *A. foliaceus*. Images from Molnár and Székely (1998)

the cyprinid herpesvirus-1. Timur (1991) noted that the presence of *Argulus* with the infected fish supports the idea that this parasite is a vector for the virus. After removal or decline of the *Argulus* parasite, a noticeable reduction in visible carp pox symptoms has been noted (Landsberg 1989).

In addition to viruses, *Argulus* has also been associated with nematode larvae. Over the years, *Argulus foliaceus* has been identified as an intermediate host for skrjabillanid and daniconematid nematode larvae (Fig. 7.4, Molnár and Székely 1998; Moravec et al. 1999). Larvae of *Skrjabillanus scardinii* (Molnár, 1966) have been shown to develop within the branchiuran thoracopods (where they undergo two moults) and then migrate to the suckers where they will become infective. Once in the suckers, they will be able to enter the skin of a new host when the *Argulus* starts feeding (Tikhomirova 1970; Moravec 1994).

7.6 Concluding Remarks

As stated previously, there are only a few recorded cases of parasitic crustaceans functioning as vectors, with many researchers having overlooked these parasites as disease-carrying agents. It is probable that vectors have not been identified as researchers are not actively looking for them within the parasitic Crustacea. Most known vectors are associated with economically important hosts due to the impact they have on the host fish, but the possibility exists that there are several unknown crustacean parasites functioning as vectors that await discovery. Other aspects on mode of transmission, duration of viability, tolerance of the vector and pathogen, etc. are still very much unknown in many cases, and more research is needed for better understanding of these crustacean vectors. The presence of metazoa, myxozoa, protozoa, bacteria or viruses associated with a fish host and a parasitic crustacean thus warrants further studies and could provide valuable information on this scantly researched topic.

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Chapter 8
Hypersymbionts and Hyperparasites of Parasitic Crustacea

Liesl L. van As

Abstract Microsporidians, peritrich ciliates, udonellids, tantulocarids and parasitic isopods have been found associated with parasitic crustaceans, i.e. Branchiura, parasitic Copepoda and Isopoda, as well as Rhizocephala (parasitic Cirripedia). Information on the Microsporida found in parasitic Copepoda are scarce, whilst infestation in gregarines, myxosporidia, cestodes and trematodes has been reported. Information is provided from known records of hypersymbiont infestations, as well as some unpublished data collected of peritrichs (*Epistylis* and *Vorticella*) found on the fish parasites *Dolops* and *Argulus* (Branchiura), members of *Lernaea* and *Opistolernaea* (Copepoda: Lernaeidae) and *Ergasilus* (Copepoda: Ergasilidae). The genus *Doropygus* (Copepoda), found in the branchial chamber of redbait (Ascidiacea), also harbours peritrichs. These hypersymbionts take the association to the next level, as the ciliates themselves harbour zoochlorellae. Helminths of the family Udonellidae are found associated with caligids and sometimes branchiurans, which occur on the skin of marine fishes. Tantulocaridans (*Hypertantulus siphonicola*) have been reported from siphonostomatoid copepods. Cabiropidae (*Cabirops*) are hyperparasites found in the brood pouch of bopyrid hosts, and *C. orbionei* might be considered as biological control for bopyrids, which are found on penaeid shrimps. Four genera of the family Cryptoniscidae (*Liriopsis*, *Cryptoniscus*, *Hemioniscus* and *Danalia*) and one genus of the family Cabiropidae (*Perezina*) are parasites of rhizocephalans that are parasitic on decapod hosts.

8.1 Introduction

Epibiosis (Greek *epi* "on top"; *bios* "life") is a non-symbiotic facultative, interspecific association of two organisms: the epibiont and the basibiont. Epibiotic associations are rarely species-specific, as numerous sessile organisms live either as basibionts or as epibionts or both simultaneously (Harder 2008). Epibionts include organisms that

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during the sessile phase of their life cycle are attached to the surface of a living substratum, whilst the basibiont lodges and constitutes a support for the epibiont. In general, epibiosis has been viewed as a commensal relationship (Abdallah et al. 2011).

In an epibiotic (or hyperepibiotic) life style, the hypersymbionts would require a stable substratum. Epibiosis is a direct consequence of surface limitation, and the result is a close association between two or more living organisms that can belong to the same or different species (Harder 2008). The majority of colonisers will be non-specific substratum generalists, and the ecological consequence for the overgrown host (the basibiont or secondary parasite in this case) and the coloniser (hypersymbiont or parasite in this case) can be both positive and negative. Bozkurt and Genc (2009) found that although it has been reported that ciliate epibionts have negative effects on free-living zooplankton hosts, they could not find any severe "health" problem in the infested zooplankton. They concluded that under natural conditions the level of infestation that may be tolerated by the hosts depends on the general viability with regard to abiotic environmental parameters. However, the presence of epibionts might have a harmful effect on the hosts, even if there is no direct action, for example, in the case of parasitic protozoans (Bozkurt and Genc 2009). The epibionts hinder the host's movement and compete for food (this might not be the case for the parasitic copepods, but may be to a lesser extent for branchiurans) which might shorten the life span of the host. Animals infested with epibionts are more visible to predators and therefore easier to capture. The question arises, what will the situation be in the case of hypersymbionts and hyperparasites found on parasitic crustaceans?

Epibiosis is a typical aquatic phenomenon, commonly found amongst marine and freshwater Crustacea, with numerous records of this kind of association occurring on the majority of crustacean taxa (Fernandez-Leborans 2009). According to Freeman (2005), the term hyperparasite (hypersymbiont) refers to an organism that parasitises another parasite, i.e. a secondary parasite (secondary parasitism). He uses the term hyperparasite to refer to obligate parasites only and not to organisms displaying facultative epibiosis, for example, the infestation of parasitic crustaceans by stalked ciliates. Freeman (2005) also refers to hyperparasites that are found externally as ectohyperparasites and to those that occur internally (e.g. microsporidians found inside caligids that parasitise fish) as endohyperparasites.

Although many crustaceans have been studied in terms of behaviour, few research studies examined their associates and symbionts, and virtually nothing is known of the interactions between the epibionts and their hosts (basibionts). According to Williams and McDermott (2004), investigations into the physical and biological factors of these communities related to the establishment of symbioses, as well as for hypersymbioses and predator-prey relationships, should prove an important area of research for the future. However, a decade later we are still in the dark. Studies on hypersymbionts found on parasitic crustaceans are not well known, incomplete (Ohtsuka and Boxshall 1998) or scarce (Abdallah et al. 2011). To date, this remains unchanged. Studies of epibiotic ciliates are abundant in literature; however, little is known regarding the ecological aspects of this relationship in ecosystems. The same applies to the variety of hypersymbionts and hyperparasites found associated specifically with parasitic crustaceans.

Each section in this chapter will contain some basic characteristics of the hypersymbiont or hyperparasite (both terms will be used in the chapter, depending on the kind of association with the host) and parasitic crustaceans. This will be followed by information and data on those symbionts found attached to branchiurans, parasitic copepods, tantulocaridans, isopods and parasitic barnacles. Where necessary and applicable, symbiotic or parasitic species are summarised in tables. The chapter also includes a section on the effect these symbionts or parasites might have on parasitic crustaceans. In two of these cases, the hyperparasites may be used as possible biological agents. The last section of this chapter under the heading “Babushkas” refers to multiple associations in single individuals, which will be followed by concluding remarks and references used in this chapter.

8.2 Hypersymbionts and Hyperparasites and Their Different Hosts

8.2.1 Microsporidians in Parasitic Copepoda

8.2.1.1 Microsporidia

Traditionally microsporidian taxonomy has been based on characters associated with structure, patterns of development and interactions with the host visualised by electron microscopy (Jones et al. 2012). Phylogenetic inferences based on molecular data tended not to support this traditional taxonomy fully, and a consensus has not been reached on the extent to which molecular and traditional data may be integrated to form a unified microsporidian taxonomy. The group is sufficiently distinct to be classified as a separate phylum, the Microsporidia (see Smith 2009; Jones et al. 2012), and although previously considered primitive eukaryotes, they have been recognised as highly evolved organisms constituting a phylum of the kingdom Fungi (Freeman et al. 2003; Vossbrinck et al. 2004). Microsporidians are obligate intracellular, spore-forming fungi that infect nearly every major animal group, i.e. insects, fish, mammals and even other parasites. According to Vossbrinck et al. (2004), microsporidians have evolved the most remarkable adaptation to intracellular parasitism, i.e. the polar filament. The spore organelle is wrapped around the periphery of the inside of the spore and extends upon germination, forming a hollow tube through which the microsporidian injects itself into a cell of the host. To date, over 1200 species from 143 genera are known. Reports of microsporidian infections in marine and freshwater Crustacea are numerous and include various genera infecting brine shrimp, cladocerans, ostracods, copepods, shrimps, amphipods, freshwater crayfish, marine lobsters and crabs (Freeman et al. 2003; Freeman and Sommerville 2009).

8.2.1.2 Hyperparasitic Microsporidia

A few species of hyperparasitic microsporidians have been found in endoparasitic myxosporeans, acanthocephalans and gregarines (Freeman et al. 2003), and hyperparasitic microsporidia have been reported in trematodes on numerous occasions

(Levron et al. 2004). In freshwater parasitic crustaceans, *Microsporidium lamproglenae* Coste & Bouix, 1999, was found in the copepod *Lamproglena pulchella* Von Nordman, 1832, which is ectoparasitic on the cyprinid *Leuciscus leuciscus* (Linnaeus, 1758) (Coste and Bouix 1999). No microsporidians had been reported from marine parasitic crustaceans until Freeman et al. (2003) found a hyperparasitic microsporidian infecting the sea louse *Lepeophtheirus salmonis* (Køyer, 1937) on wild Atlantic salmon *Salmo salar* Linnaeus, 1758. This microsporidian could not be placed in the *Enterocytozoon* Lavergne, Ravisse & Modigliani, 1985, or *Nucleospora* Hendrick, Groff & Baxa, 1991, because the host species was not characteristic for these genera and the microsporidian was neither intranuclear nor found within intestinal enterocytes (Freeman et al. 2003).

Freeman and Sommerville (2009) examined the ultrastructure of the microsporidian they found infecting *L. salmonis* in 2003 and provided an updated molecular phylogenetic analysis. Using the combined data, they described *Desmozoon lepeophtherii* Freeman & Sommerville, 2009, as a new genus and species assigned to the Enterocytozoonidae, other genera and species which parasitise marine fishes and decapod crustaceans. Nylund et al. (2010) described Norwegian material as a new species, but Freeman and Sommerville (2011) regarded it as a junior synonym of *D. lepeophtherii*. A paper by Toguebaye et al. (2014) lists the microsporidian *Paranucleospora theridion* Nylund, Nylund, Watanabe, Arnesen & Karlsbakk, 2010, as a valid species found in *L. salmonis*; however, Jones et al. (2012) also considered it to be a junior synonym of *D. lepeophtherii*. Jones et al. (2012) recorded *D. lepeophtherii* in *L. salmonis* from Canada, expanding the known geographic range of this microsporidian. They found a second microsporidian in *L. salmonis*, *L. cuneifer* Kabata, 1974, and *L. parviventris* Wilson, 1905, all parasites of marine fishes from the Northeastern Pacific Ocean. Not only did this constitute a new species, i.e. *Facilispora margolisi* Jones, Prosperi-Porta & Kim, 2012, but also a new family, Facilisporidae (see Jones et al. 2012).

Desmozoon lepeophtherii undergoes two distinct cycles of development in salmon: (1) in the cytoplasm of cells from the skin, gill, heart, kidney and spleen and (2) in the nucleus of epidermal cells of skin and gills. The microsporidian was shown experimentally not to be transmitted directly from copepod to copepod (Freeman and Sommerville 2011), and it is still unclear exactly how transmission takes place in nature.

8.2.2 *Peritrichs on Branchiura*

8.2.2.1 Ciliates

Members of the phylum Ciliophora, generally referred to as ciliates, are a distinct, monophyletic group of protists with cilia at some stage of their life cycle (Lynn 2008). Ciliates were first observed more than three centuries ago by Van Leeuwenhoek, who is regarded as the founder of protozoology. Ciliates were visible as blooms or coloured waters in marine and freshwater habitats, probably thousands of years before Van Leeuwenhoek's discoveries (Lynn 2008). They were known as Infusoria throughout the nineteenth century, before the name was replaced in the early twentieth century with Ciliophora. More than 8000 ciliate species are known, with over 3000 symbiotic species, including the Oligohymenophorea, which is one of the most diverse classes within the phylum.

The life history of ciliates includes an asexual (vegetative) cycle during which growth and cell division (binary fission) occur and a sexual cycle in which exchange of genetic material takes place between conjugants (Lynn 2008; Peters et al. 2010). In some species, a resting cyst (cryptobiotic cycle) may form during periods of dryness and food shortage. Ciliates are heterotrophic, with a wide range of feeding habits, occupying diverse ecological niches. For example, bacterivorous ciliates are important in maintaining the quality of effluent from sewage treatment plants, as they reduce bacterial densities tenfold due to their feeding (Lynn 2008). Some ciliates are suspension feeders that use complex arrays of polykinetal cilia to create a current and filter particles out of the suspension (so-called upstream filter feeders) or create a current with the polykinetal array and filter particles with the separate linear ciliary array of a paroral membrane (downstream filter feeders). Examples of downstream filter feeders include the peritrich ciliates *Vorticella* Linnaeus, 1767, and *Epistylis* Ehrenberg, 1830, and they have a significant grazing impact on bacterial communities ingesting over 4000 bacterial cells per hour (Lynn 2008).

Ciliates belonging to the subclass Peritrichia (Ciliophora: Oligohymenophorea) are by far the most successful and abundant symbionts (or for this chapter hypersymbionts). Like a few other groups of primarily sessile ciliates (e.g. suctorians, chonotrichs), they have an ability to attach to solid substrates via a scopula. A free-swimming stage, the telotroch, in their life cycle enables them to disperse over suitable surfaces for attachment. A species of *Vorticella* was the first protist described by Van Leeuwenhoek (1674) and is the most specious genus of peritrichs with well over 100 species (Warren 1986). Free-living peritrichs are ubiquitous in aquatic habitats, but many species also live as epibionts on representatives of a variety of hosts such as sponges, cnidarians, ctenophores, rotifers, tardigrades, freshwater planarians, crustaceans, annelid worms, aquatic insects and insect larvae, molluscs amongst invertebrates and fishes, amphibian larvae and freshwater turtles amongst vertebrates (Dias et al. 2008). Peritrichs typically secrete a stalk for attachment to the substrate and also may form a protective lorica around the cell body. Aloricate and loricate peritrichs have been reported on every major group of crustaceans, i.e. cladocerans, ostracods, copepods, mysids, amphipods, isopods and on decapods from almost every place these hosts can be found (Lynn 2008). Many members of the aloricate genus *Epistylis* (Figs. 8.1, 8.2, 8.3, 8.4, and 8.5) are epibiotic and are the peritrichs most often found as hypersymbionts on crustaceans. Species of *Epistylis* have a noncontractile stalk (i.e. lacking the spasmoneme so characteristic of many peritrichs like *Vorticella* spp.) and form colonies of different sizes, with various patterns of branching.

8.2.2.2 Branchiura

Branchiurans (family Argulidae), commonly known as fish lice, are found in marine, freshwater and brackish habitats. They are ectoparasites that attach to the skin, fins,

Fig. 8.1 *Dolops ranarum* (Stuhlmann, 1981) covered with peritrichs

lining of the branchial chamber, gill filaments and lining of the oral cavity of hosts. They are generally small but are visible to the naked eye. Adult branchiurans are dorsoventrally flattened, with a trifoliate carapace and sexual distinct dimorphism. In the genus *Dolops* Audouin, 1837, the maxillulae are large, prominent hooks. In adults of *Argulus* Müller, 1785; *Chonopeltis* Thiele, 1900; and *Dipteropeltis* Calman, 1912, the maxillulae transform from the hook-like structures of the larvae to large, disc-shaped suckers (Van As and Van As 2001).

Van As and Viljoen (1984) found the colonial peritrich *Epistylis anastatica* (Engelmann, 1862) on *Dolops ranarum* (Stuhlmann, 1891) for the first time in South Africa on the Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), in natural ponds and rivers. This association was found frequently and in such high levels of infestation that ciliates were visible with the naked eye. Sutherland and Wittrock (1986) reported a similar occurrence on *Argulus appendiculosus* Wilson, 1907, with many peritrichous ciliates attached to the lateral and ventral body surfaces. Poly (1998) recorded species of *Argulus* in Illinois (USA) and observed species of peritrichs (*Epistylis* or *Opercularia* Goldfuss, 1820) on *A. americanus* Wilson, 1902, *A. mississippiensis* Wilson, 1916, *A. lepidostei* Kellicott, 1877 and *A. flavescens* Wilson, 1916. Green (2009) reported on the diversity of parasitic crustaceans in lakes Albert and Edward and observed species of *Epistylis* found on *D. ranarum* associated with the Sudan catfish *Bagrus docmak* (Forsskål, 1775), giraffe catfish *Auchenoglanis occidentalis* (Valenciennes, 1840), sharptooth catfish (also known as the North African catfish), *Clarias gariepinus* (Burchell, 1822) and Nile perch *Lates niloticus* (Linnaeus, 1758); on *Argulus*

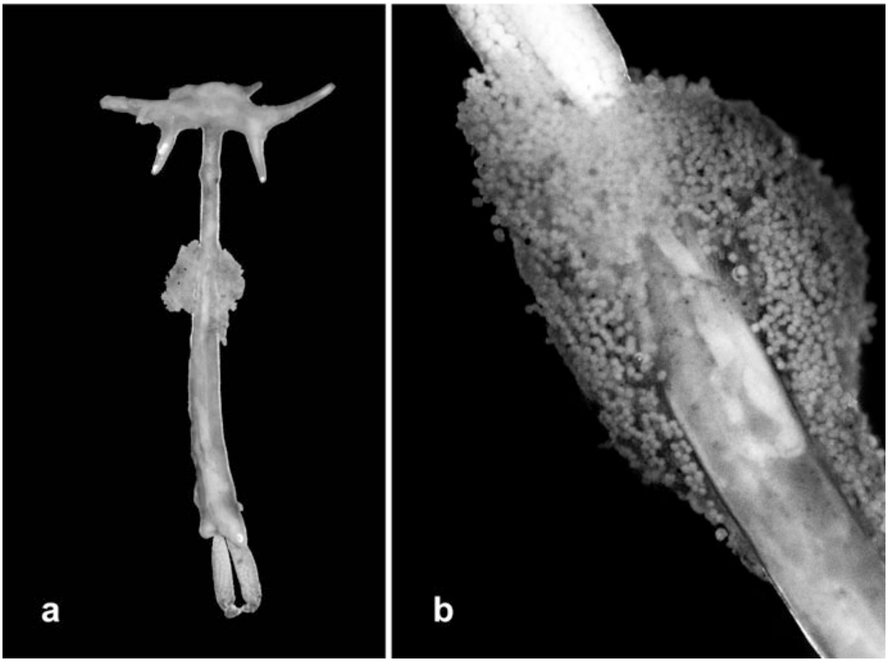

Fig. 8.2 (**a**) *Lernaea cyprinacea* Linnaeus, 1758 with collar of peritrichs around the thorax, (**b**) Enlargement of *Epistylis* Ehrenberg, 1830

cunningtoni Fryer, 1956, from *Labeo horie* Heckel, 1847, and *Lates niloticus* (Linnaeus, 1758); and on *A. rhipidiophorus* Monod, 1931, from *L. niloticus.* Van As and Van As (2015) collected more than 80 specimens of *D. ranarum* over a period of 16 years from 12 fish species in the Okavango system, Botswana, and found one female that was covered almost completely by a species of *Epistylis* (Fig. 8.1).

8.2.3 Peritrichs on Parasitic Copepoda

8.2.3.1 Copepoda

Huys and Boxshall (1991) hypothesised that all ten known orders of the subclass Copepoda had their origins in the marine hyperbenthic communities. Copepods are small, inconspicuous aquatic crustaceans at first glance but stand out by being very abundant (Boxshall 2005). Overall, copepods outnumber insects in terms of numbers of individuals in populations. Free-living species, such as *Calanus finmarchicus* (Gunnerus, 1770), dominate zooplankton communities in open, pelagic water columns in both marine and freshwater environments, which constitute the largest biomes on our planet (Boxshall 2005). More than 11,500 species are known, an

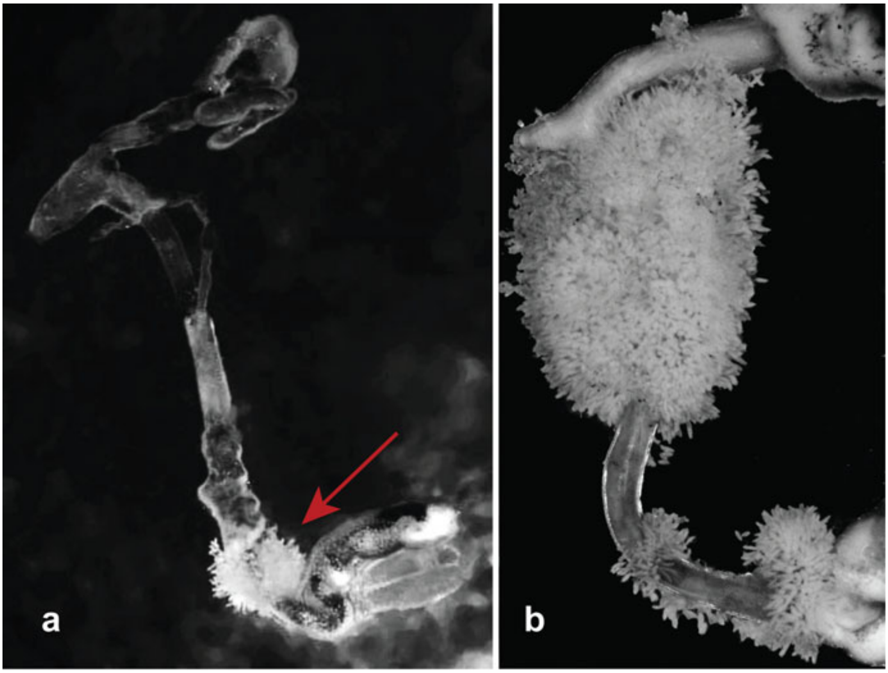

Fig. 8.3 (**a**) *Opistolernaea laterobranchialis laterobranchialis* (Fryer, 1959) with *Epistylis* Ehrenberg, 1830 attached to thorax above abdomen (arrow), (**b**) *Epistylis* ciliates covering large area of thorax

astonishing ~50% of which live in symbiotic associations. The higher classification of the Copepoda is in flux, with ten orders currently recognised by Huys and Boxshall (1991) based on morphological features; however Boxshall and Halsey (2004) regarded only nine of these as valid. The majority of parasitic representatives are found amongst the orders Cyclopoida and Siphonostomatoida with the latter being mostly marine species, with a few freshwater representatives. Cyclopoids are most abundant in freshwater and, apart from the free-living families, also include a total of 80 families that live in symbiotic associations with a wide range of host taxa. The three families of importance for this chapter are the Ergasilidae, Lernaeidae and Notodelphyidae.

8.2.3.2 Lernaeidae

This family comprises 131 species (in 17 genera), all parasites of freshwater fishes (Walter and Boxshall 2018). The genus *Lernaea* Linnaeus, 1758, with 57 known species, is characterised by a head with two to three (rarely four) pointed or swollen "horns," which are embedded in the host tissue. An elongate neck and thorax with

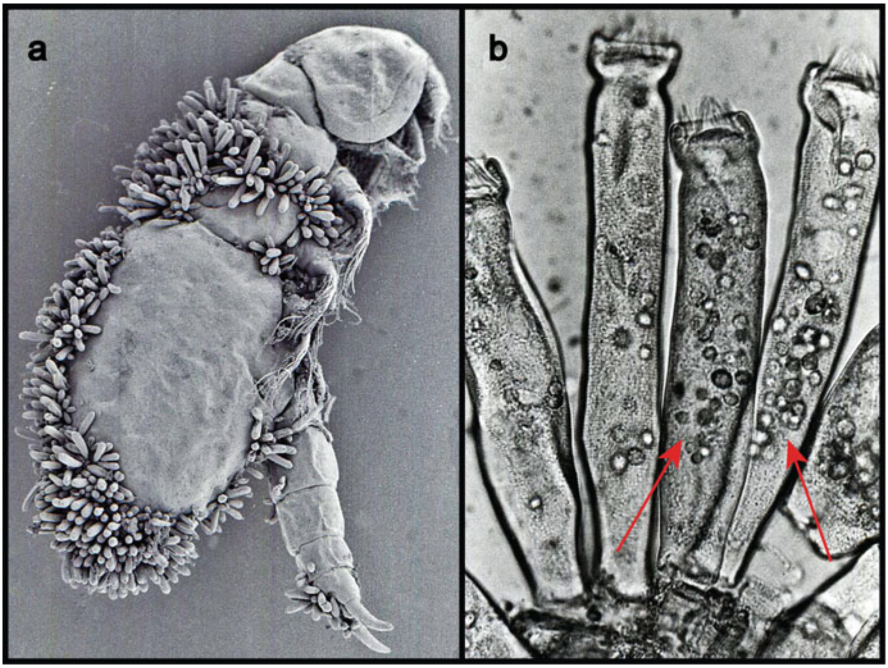

Fig. 8.4 (**a**) *Doropygus* Thorell, 1859 with *Epistylis* Ehrenberg, 1830 attached to carapace, (**b**) *Epistylis* sp. cytoplasm filled with zoochlorellae (arrows)

reduced swimming legs may thicken gradually towards the posterior end (Paperna 1996). The genus *Opistolernaea* Yin, 1960, is currently represented by four species. The head has four horns, with two posterior horns directed symmetrically posteriorly to form a 90° angle. A lateral outgrowth extends from the neck region, which may be located in close proximity to the head to become a functional part of the anchor complex (Paperna 1996). *Lamproglena* Von Nordmann, 1832, with 43 known species, has large mouthparts, of which the maxilliped has a terminal claw, elongate segments, reduced anterior thoracic appendages and no posterior legs. Sexual dimorphism is visible in all species of the family, with males retaining the cyclopoid form (Paperna 1996).

Epistylidids Attached to Lernaeids

A “necklace” of colonial peritrichs on lernaeids from freshwater fishes in Africa was mentioned and illustrated by Cunnington (1914) and Capart (1944). The ciliates were found mostly at the junction of the anterior third of the body with the more dilated posterior portion. Cunnington (1914) continued to observe that it seemed highly probably that the manner in which these parasitic Copepoda can be so densely encrusted by the ciliates is directly related to the peculiar fact that after fixing onto

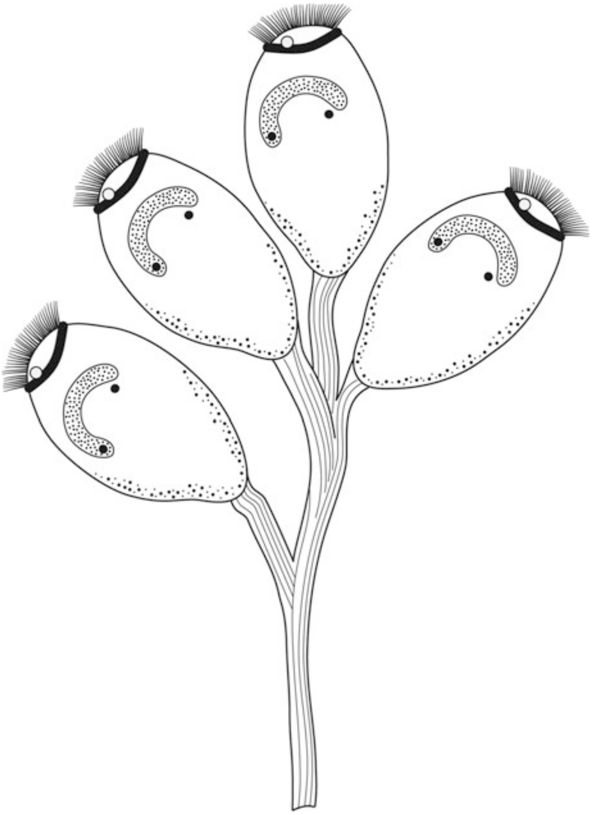

Fig. 8.5 *Epistylis* Ehrenberg, 1830 on *Amplexibranchius bryconis* Thatcher & Paredes, 1985. Images redrawn from Abdallah et al. (2011)

the host, the lernaeids appear to no longer undergo ecdysis. Fryer (1956) reported that such necklaces were present around the anterior end of *Lernaea bagri* Harding, 1950, near its point of entry into host fish in Lake Malawi. Amin (1981) reported on epibiotic species of *Epistylis* and *Rhabdostyla* Kent, 1880 (non-colonial relative of the former), from *L. cyprinacea* Linnaeus, 1758, infesting largemouth bass in Wisconsin rivers. Van As and Viljoen (1984) found a variety of hypersymbionts on *L. cyprinacea*, including *E. branchiophila* Perty, 1852, reported for the first time in South Africa as well as *E. cyprinaceae* Van As & Viljoen, 1984, and *E. magna* Van As & Viljoen, 1984. All the lernaeids from South Africa were collected from *O. mossambicus*. Sutherland and Wittrock (1986) found peritrich ciliates on *L. cyprinacea* (synonym *L. elegans*) on carp collected in the Little Sioux River (Iowa), without referring to the specific ciliate genus.

Epistylis epibarnimiana Van As & Viljoen, 1984, was recorded from the indigenous African *Lernaea barnimiana* (Hartman, 1870) attached to the skin of the Orange River mudfish, *Labeo capensis* (Smith, 1841), from South Africa by Van As and Viljoen (1984). The only other record of an *Epistylis* sp. collected from a lernaeid crustacean is a report by Silva-Souza and Rosim (2005), but they do not mention the specific lernaeid species (see Abdallah et al. 2011). Green (2009) found a necklace of peritrichs around the body of *L. barnimiana* in Lake Albert (from *Lates* *niloticus*) which he identified as "a remarkably large" (500 μm) species *Rhabdostyla elongata* Green, 1965.

Two individuals of *L. hardingi* Fryer, 1956, collected from five species of fish during surveys conducted in the Okavango system, Botswana, had a prominent necklace formed by a species of *Epistylis*. Other unpublished data (Aquatic Ecology Research Group, University of the Free State, UFS) from Lake Malawi revealed 10 of 16 lernaeids (63% infestation) harboured hypersymbionts belonging to the genus *Epistylis.* During surveys conducted in the Phongolo River, a total of 60 *L. cyprinacea* specimens were collected from *Oreochromis mossambicus*, of these anchor worms, 38 had collars of peritrichs (63% infestation) around the thorax (unpublished data, Water Research Group, North-West University) (Fig. 8.2a, b).

Fryer (1965) reported on the presence and location of epibiotic peritrichs on *Opistolernaea contorta* Fryer, 1965, and several specimens of *O. longa* (Harding, 1950) collected from *Lates niloticus*, which carried dense masses of stalked peritrichs. No further detail was provided, apart from a sketch indicating the position of the ciliates on *O. contorta*. During surveys conducted in the Okavango system, eight specimens of *O. laterobranchialis laterobranchialis* (Fryer, 1959) were collected from three fish species, and two of the lernaeids (29% infestation) had a ring of peritrichs attached just above the abdomen (Fig. 8.3a). Tilapias from a fish farm in the upper part of the Okavango system of Namibia had an 84% rate of infestation of *O. l. laterobranchialis*, and 64% (9/14) hosts were heavily covered by peritrich ciliates (Fig. 8.3b). In both cases, hypersymbionts were identified as a species of *Epistylis* (unpublished data, Aquatic Ecology Research Group, University of the Free State).

Fryer (1956) observed a necklace of peritrichs around the anterior part of the body of *Lamproglena clariae* Fryer, 1956. In the same paper, he described *L. nyasae* Fryer, 1956, which he later synonymised with *L. monodi* Capart, 1944 (Fryer 1959). During fish parasitological surveys in Botswana (1997–2013), *L. monodi* were collected from 12 cichlid species, *L. clariae* from *Clarias gariepinus* and *L. hepseti* Van As & Van As, 2007, from the African pike, *Hepsetus cuvieri* (Bloch, 1794), but the authors did not observe any ciliates on any of these *Lamproglena* species.

Vorticella sp. Attached to Lernaeids

Van As and Viljoen (1984) recorded two species of *Vorticella* from the alien anchor worm *Lernaea cyprinacea* Linnaeus, 1758, that were identified on the basis of morphological characters as *Vorticella convallaria* (Linnaeus, 1758) and *V. microstoma* Ehrenberg, 1830, from South Africa. Both species of *Vorticella* are normally free-living; therefore, this could be characterised as an opportunistic association if the identifications were proved valid.

8.2.3.3 Notodelphyidae

The copepod family Notodelphyidae is known world-wide as inhabiting the body cavities of ascidians, although distributional records are scanty. According to Wilson

(1932), at least 80% of the genera are in association with ascidians, and most notodelphyid species live a symbiotic existence in the branchial baskets of solitary ascidians, with a few species found encysted in the tunic or blood vessels of the host (Jones 1974). The subadult forms and males are free swimming; thus, the males remain unknown in half of the species. To date, very little is known of the life histories or ecology of notodelphyids, making the reference to Wilson (1932) still relevant today.

Epistylis sp. Attached to Notodelphyids

Species of both *Doropygus* Thorell, 1859, and *Gunenotophorus* Buchholz, 1869 (Copepoda), recorded from the branchial chamber of South African redbait (the tunicate *Pyura stolonifera* Heller, 1878) collected along the South African coastline in 1994–2006 were also found to harbour peritrichs (unpublished data, Aquatic Ecology Research Group, University of the Free State). One amphipod *Podocerus pyurae* Griffiths, 1975, was found along with two copepods, *Gunenotophorus blaizei* Kensley & Grindley, 1973, and a new species of *Doropygus*. Upon closer examination, clusters of *Epistylis* colonies were seen, forming a collar around the thoracic segments of the copepods (Fig. 8.4a). Other than this record, little information exists on these ectosymbionts of notodelphyid copepods. The only reported case is a note in the late 1950s by Illg (1958), in which he mentioned frequent encounters with epibiotic ciliates attached to North American notodelphyids, but no systematic or morphological descriptions of these ciliates were given.

The occurrence of the *Epistylis* species found on the two South African notodelphyids is the first confirmed record of this genus of colonial peritrichs on notodelphyid hosts. The ciliates were found on the dorsal ridge of the thorax, extending around the brood pouch to the ventral side, with only a few colonies found on the setae of the legs. Illg (1958) mentions setae as the site of attachment for ciliates he observed on notodelphyids, sometimes covering appendages densely. In most notodelphyid individuals on South African redbait, a large percentage of the copepod body was covered with ciliates. Forty-eight percent of the tunicates examined hosted notodelphyid copepods, and 30% of those copepods hosted species of *Epistylis* (see Molatoli and Van As 1995; Van As et al. 2002). These ciliates take the association one step further as they themselves harbour zoochlorellae (Fig. 8.4b) (see Sect. 8.5 on Babushkas).

8.2.3.4 Ergasilidae

The family Ergasilidae (Poecilostomatoida) comprises 29 valid genera, with the overwhelming majority found on freshwater fishes. Only the females are parasitic and are found on the gills of fish, whilst the males are free-living. A prolonged free-living larval development includes three to six nauplii stages and four to six copepodites and can last from 10 days to over a month (Paperna 1996).

Segmentation of the body is well-developed, and the morphology of the appendages (and the overall shape) is quite similar to free-living cyclopoid copepods. The second maxillae are large and elongate, resembling long arms terminating in slightly bent claws, which are used to attach to the gill filaments of fishes. The best known representative is the genus *Ergasilus* von Nordmann, 1832 containing 158 nominal species (Piasecki and Avenant-Oldewage 2008).

Epistylis sp. Attached to Ergasilids

Silva-Sousa and Rosim (2005) were the first to report on an *Epistylis* sp. collected from Brazil but without referring to the host species. Abdallah et al. (2011) found an *Epistylis* sp. (Fig 8.5) on *Amplexibranchius bryconis* Thatcher & Paredes, 1985 (Ergasilidae) parasitising the gills and nostrils of the streaked prochilod *Prochilodus lineatus* (Valenciennes, 1837), also from Brazil. Ninety percent of the copepods collected had ciliates attached to at least some parts of the body. Abdallah et al. (2011) found that in some cases the ciliates covered large portions of the copepod's body, as well as the egg sacs. A few years later, Azevedo et al. (2014) recorded an *Epistylis* sp. attached to *Ergasilus chelangulatus* Thatcher & Brasil-Sato, 2008, which occurs on the spotted pim, *Pimelodus maculatus* Lacepède, 1803, from Brazil. They found a 100% infestation of *E. chelangulatus* on the fish, and 20% of the copepods were infested by *Epistylis* sp. on some part of their bodies. Some of these copepods were heavily infested with more ciliates being found on the legs.

8.2.4 Monogenea on Parasitic Copepoda

In the case of the monogenean and parasitic isopods (section to follow), the term hyperparasite is used, as in these cases they derive a direct nutritional benefit from the parasitic crustaceans or the main host, which also can be a fish.

8.2.4.1 Udonellids

Species of the genus *Udonella* Johnson, 1835, are found on the carapace of caligids (Fig. 8.6) and sometimes on branchiurans that are parasitic on fishes (Okawachi et al. 2012). Until 1998, the taxonomic position of *Udonella* (Monogenea, or not) was more a matter of dispute than whether this monogenean was a hyperparasite or merely living in a commensal association on a parasitic crustacean (Littlewood et al. 1998). Since its original description in 1835, some of the morphological characters of the genus *Udonella* have placed its phylogenetic position in question. These worms were first regarded as leeches, then as monogeneans, before being placed in a separate class Udonelloidea, which was not widely accepted. Xylander (1988) and Rohde et al. (1989) concluded from ultrastructural evidence that these monogeneans

Fig. 8.6 *Udonella australis* Carvajal & Sepúlveda, 2002, on a caligid from the silver kob, *Argyrosomus inodorus* Griffiths & Heemstra, 1995, collected in Cape Town (Table Bay). Images © Dr Kevin Christison

should be included in the subphylum Neodermata. This was supported by Littlewood et al. (1998), as well as the hypothesis that they are most likely modified monopisthocotylean monogeneans.

Carvajal and Sepúlveda (2002) regarded *U. caligorum* Johnson, 1835, as a species complex owing to its geographical distribution and the morphological differences found between the different descriptions of this species. The frequent records of *U. caligorum* from different parts of the world may actually represent new species. Freeman and Ogawa (2010) questioned the usefulness of morphological data for differentiating species of *Udonella*, particularly *U. caligorum* that have been found on a variety of hosts and described from different localities. They also assert that the type of fish host and phylogeography are potentially important in identifying species of *Udonella*, especially if they are found only to infest host-specific copepods, for example, *U. fugu* Freeman & Ogawa, 2010, attaching to *Caligus fugu* (Yamaguti, 1936) found on wild grass puffer (*Takifugu* Abe, 1949). Recent studies suggest that species of *Udonella* can be used as a biological control agent of sea lice (see Sect. 8.4.1).

Species of *Udonella* lack hooks in all stages of development, whereas other representatives of the Monogenea have hooks in at least the larval stage. The absence of hooks in *Udonella* may be a consequence of their attachment to the copepod host, as the hard exoskeleton is probably not suitable for penetration by hooks (Littlewood et al. 1998). In the 1950s, Ivanov (1952) had already made a detailed light microscopic study of the attachment organ of *Udonella*. The sucker is terminal and an extension of the posterior part of the main body. Rohde and Watson (1995) studied the posterior suckers of symbiotic Platyhelminthes, including *U. caligorum*, with comparisons of temnocephalids, monogeneans and digeneans. They came to the conclusion that there is no defined stalk in udonellids and the suckers are indeed posterior extensions of the body, as illustrated by Ivanov (1952). The posterior surface is lined with basal lamina drawn out into microvilli attached to the adjacent tegument by a separate junction with gland ducts that open on the sucker.

Udonellids have been recorded from caligids and argulids, which are known to swim freely in water columns as adults to find new fish hosts (Freeman 2005). Udonellids have only been recorded from crustaceans (Table 8.1) that are parasitic on fishes and not from free-living copepods or other crustaceans. In general, monogeneans are considered to be amongst the most host-specific of fish parasites (Whittington et al. 2000). However, *Udonella caligorum* has been reported from numerous different fish hosts in the North Atlantic, thriving on host-specific copepods such as *Lepeophtheirus salmonis*, but it has also been found on generalist copepods such as *Caligus elongatus* Nordmann, 1832; thus it may be adapting and becoming less specialised (Freeman and Ogawa 2010). According to Byrnes and Rohde (1992), udonellids are more host-specific to the fish than to their crustacean parasites, suggesting there might be more than one species of *Udonella* in Australia, each being restricted to one genus of fish host. In Chile, *U. australis* Carvajal & Sepúlveda, 2002, have been found frequently on *C. rogercresseyi* Boxshall & Bravo, 2000, infesting the Patagonian blenny but were absent from the same caligid found on cultured salmonids (Marín et al. 2002), suggesting that the species of fish host is also important.

8.2.5 Tantulocardia on Parasitic Copepoda

8.2.5.1 Siphonostomatoida

This diverse order includes nearly 75% of the species of copepods that are parasites of fish (1050 from marine fishes and a few species from freshwater fishes), as well as some 500 species found associated with invertebrate hosts (Huys and Boxshall 1991). They are characterised by the particular form of mandibles and the formation of an oral cone from the labrum, as well as the medially fused paragnaths. Seventeen families are characterised by mandibles that have lost the palp and the array of teeth located subdistally on the margin of the mandibular stylet. Nine families (including Asterocheridae) are characterised by the retention of the basic cyclopoid-shaped body. The rest are characterised by a modified body which is dorsoventrally flattened (two families) and ten families (including Nicothoidae) that have more or less swollen or globular bodies with ill-defined segmentation (Boxshall and Halsey 2004).

Parasitic copepods found on other parasitic crustaceans are relatively scarce. More than 136 species of Nicothoidae are known, with the majority recorded from

Table 8.1 List of known *Udonella* Johnson, 1835 species, copepod and fish hosts, locality and references

Udonella sp.	Copepod host	Fish host, locality	Reference
Udonella australis Carvajal & Sepúlveda 2002	*Caligus rogercresseyi* Boxshall & Bravo, 2000	*Eleginops maclovinus* (Cuvier, 1830), Chile	Carvajal and Sepúlveda (2002)
Udonella caligorum Johnston, 1835	*Caligus elongatus* Von Nordmann, 1832	*Gadus morhua* Linnaeus, 1758, Scotland	Kabata (1973)
	Lepeophtheirus pravipes Wilson, 1912	*Gadus morhua* Linnaeus, 1758, Russia	Kornakova and Timofeeva (1981)
	Lepeophtheirus mugiloidis Villalba, 1986	*Mugiloides chilensis* (Molina, 1782), Chile	Carvajal and Sepúlveda 2002)
		Sebastes capensis (Gmelin,1789), Chile	González and Acuña (1998)
	Caligus curtus Müller, 1785	*Gadus morhua* Linnaeus, 1758, Norway	Van der Land (1967)
	Caligus flexispina Lewis, 1964 *Lepeophtheirus mugiloidis* Villalba, 1986	*Eleginops maclovinus* (Cuvier, 1830), Chile	Carvajal et al. (1998)
	Caligus sp.	*Mugil cephalus* Linnaeus, 1758, South Africa	Grobler et al. (2003)
Udonella fugu Freeman & Ogawa, 2010	*Pseudocaligus fugu* Yamaguti, 1936	*Takifugu rubripes* (Temminck & Schlegel, 1850), *T. niphobles* (Jordan & Snyder, 1901), Japan	Freeman and Ogawa (2010)
		Takifugu niphobles Jordan & Snyder, 1901), Japan	Okawachi et al. (2012)
Udonella murmanica Karnakova & Timofeeva, 1981	*Caligus curtus* Müller, 1785	*Gadus morhua* Linnaeus, 1758, Russian Coast	Kornakova and Timofeeva (1981)
Udonella myliobati (Guberlet, 1936)	*Trebius latifurcatus* Wilson, 1921	*Myliobatis californica* Gill, 1865, USA (California)	Freeman and Ogawa (2010)
	Caligus epidermicus Hewitt, 1971	*Acanthopagrus australis* (Günther, 1859), Australia	Aiken'Ova and Lester (1996)
	Lepeophtheirus natalensis Kensley & Grindley, 1973	*Carcharias taurus* Rafinesque, 1810, South Africa	Olivier et al. (2000)

(continued)

Table 8.1 (continued)

Udonella sp.	Copepod host	Fish host, locality	Reference
[a]*Udonella ophiodontis* Kay, 1945	*Lepeophtheirus* von Nordmann, 1832 sp.	*Ophiodon elongates* Girard, 1854, USA (Washington)	Freeman and Ogawa (2010)
	Lepeophtheirus pravipes Wilson, 1912	*Ophiodon elongates* Girard, 1854, USA (Washington)	Ching and Leighton (1993)
	Lepeophtheirus hospitalis Frasser, 1920	*Platichthys stellatus* (Pallas, 1787), USA (Washington)	
Udonella papillifera van der Land, 1967	*Ceratocolax euthynni* Vervoort, 1965	*Euthynnus alleteratus* (Rafinesque, 1810), Ivory Coast (Côte d'Ivoire)	Van der Land (1967)

[a] Van der Land (1967) and Aiken'Ova and Lester (1996) regarded this species to be a junior synonym of *U. caligorum,* however, Freeman and Ogawa (2010) listed it as a valid species

crustacean hosts (Boxshall and Halsey 2004). *Pseuonicothoe procircularis* (Carton, 1967) and *Paranicothoe cladocera* Carton, 1970, may parasitise bopyrid isopods (found on *Pseudione affinis* (Sars, 1882) and *Orbione natalensis* Bourdon, 1972, respectively), which infect the branchial cavity of pandalid and penaeid shrimps. There is, however, some doubt as to whether the copepod parasitises the decapod host or hyperparasitises the epicaridean isopod (Boxshall and Lincoln 1983; Humes and Boxshall 1993).

8.2.5.2 Tantulocarida

Tantulocaridans are highly specialised obligate ectoparasites of meiobenthic crustaceans. They resemble copepods, except for the fact that the thoracic legs are absent. These tiny animals (80–400 μm) are gonochoric and sexually dimorphic, with a complex life cycle that includes alternating sexual and parthenogenetic stages (Kolbasov et al. 2008). Adult stages of both sexes are free-swimming and do not feed. Feeding takes place whilst the larva is attached to a host with the oral disc, using the stylet to make an opening in the host's cuticle through which nutrients are absorbed (Ohtsuka and Boxshall 1998).

Hypertantulus siphonicola Ohtsuka and Boxshall, 1998 (Basipodellidae), was reported from the first endopodal segment of the antennae of siphonostomatoid hosts, i.e. *Asteropontoides* Stock, 1975 (Asterocheridae), from western Japan (Fig. 8.7a–d). The precise relationship between the asterocherid Copepoda and their hosts is mostly unknown, and these copepods have, by convention, been referred to as "associated," by Ohtsuka and Boxshall (1998), even though the siphonostome mouthparts suggest a direct feeding relationship. The relationship between *H. siphonicola* and the asterocherid host represents a case of hyperassociation, and according to Ohtsuka and Boxshall (1998), it seems likely that this was the first case of hyperparasitism in the Tantulocarida. In view of the relatively low levels of host specificity exhibited by some tantulocaridans parasitic on copepods, it is considered likely that

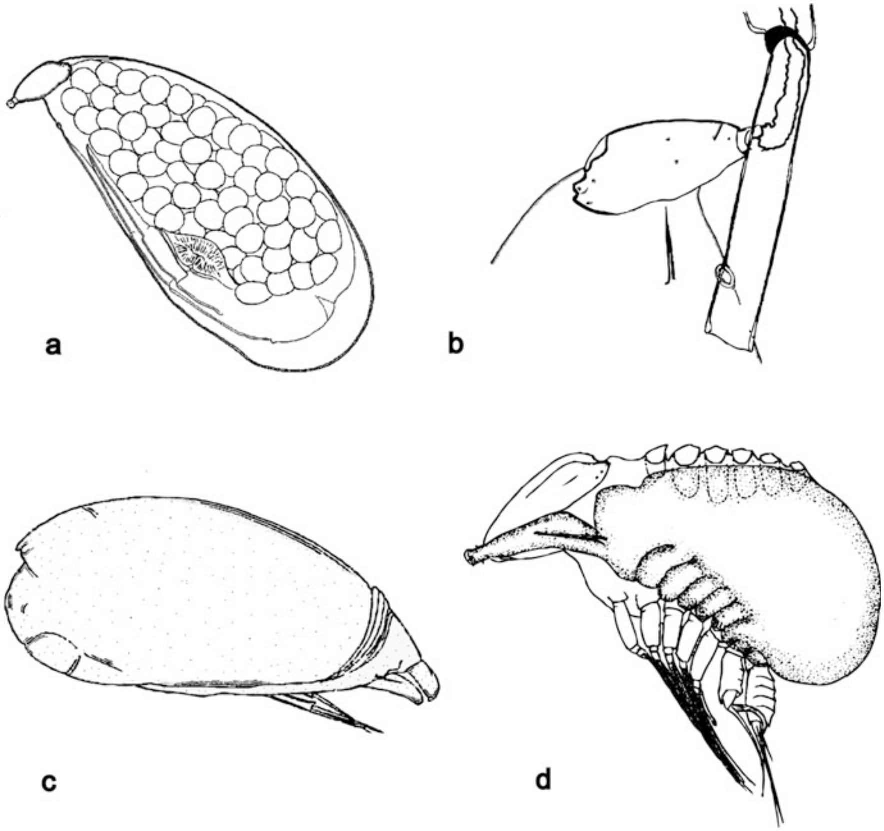

Fig. 8.7 *Hypertantulus siphonicola* Ohtsuka & Boxshall, 1998, (**a**) sexual female, with expanded trunk sac of preceding tantulus larva, (**b**) anterior end of tantulus larva, with female attached to antenna of host, (**c**) lateral view of female dissected out of trunk, (**d**) metamorphosing male in expanded tantulus, lateral view of early stage with expanding trunk sac of preceding tantulus larva. Images redrawn from Ohtsuka and Boxshall (1998)

tantulocaridans also should be able to utilise representatives of other groups of associated copepods as hosts, such as the poecilostomatoids (Ohtsuka and Boxshall 1998).

8.2.6 Hyperparasitic Isopoda on Parasitic Crustacea

8.2.6.1 Isopoda

Epicarideans (Bopyroidea and Cryptoniscoidea) are parasites of other crustaceans, including free-living forms as well as hyperparasites on parasitic barnacles (rhizocephalans) and parasitic isopods (bopyrids) (Freeman 2005). All epicarideans are sexually dimorphic, with large females having more modified features than the dwarf males. In the case of Bopyroidea, three families are recognised, namely, Bopyridae, Entoniscidae and Ionidae (Boyko et al. 2013). Both bopyrids and ionids are ectoparasitic macroparasites of decapod hosts, whilst entoniscids are endoparasitic in the visceral cavity of decapods such as anomuran, brachyuran and shrimp hosts (Williams and Boyko 2012). Cryptoniscoidea are protandric sequential hermaphrodites, exhibiting a life cycle similar to that of bopyrids; however, the males of cryptoniscoids retain the cryptoniscus larval form. Egg-bearing females lose their typical isopod appearance and become sac-like. Cryptoniscoidea contains nine families (Asconiscidae, Cabiropidae, Crinoniscidae, Cryptoniscidae, Cyproniscidae, Dajidae, Entophilidae, Hemioniscidae and Podasconidae) composed of endoparasitic species associated with a diverse assemblage of crustacean hosts and includes some species that are hyperparasitic (Williams and Boyko 2012; Boyko 2013, 2015; Boyko et al. 2013). The main difference between bopyrids (ectoparasitic) and rhizocephalans (endoparasitic with an externa) is that the latter have a direct life cycle and bopyrids require an intermediate host (Boyko and Williams 2009); however, both use decapods as definitive hosts.

8.2.6.2 Hyperparasitic Isopoda: Cabiropidae

Members of the Cabiropidae (*Cabirops* Kossmann, 1884) (Fig. 8.8a–d) are hyperparasites found on bopyrid hosts (found freely in the marsupium of shrimps or crabs; see Sassaman 1985, Boyko 2013). The females have lost all traces of segmentation (Fig. 8.8b–d) and have a distinctive developmental pattern from cryptoniscus to adult, as illustrated by Boyko (2013). According to Williams and Boyko (2012), bopyrids do not pose any medical threat to humans, but their presence in the branchial chamber of the shrimp host negatively impacts its commercial market value. One *Cabirops* species has been examined as a possible biological control method (see Sect. 8.4.2). Table 8.2 is a summary of the known and partially described *Cabirops* species found in or on other parasitic Isopoda.

8.2.7 Hyperparasitic Isopoda in and on Parasitic Barnacles (Cirripedia)

8.2.7.1 Rhizocephala

All rhizocephalan barnacles are highly specialised endoparasites of other crustaceans, disturbing the moulting cycle and growth of their hosts, causing parasitic castration, modifying the host's secondary sexual characteristics and behaviour and negatively affecting the overall metabolism of the host (McDermott 2009). They

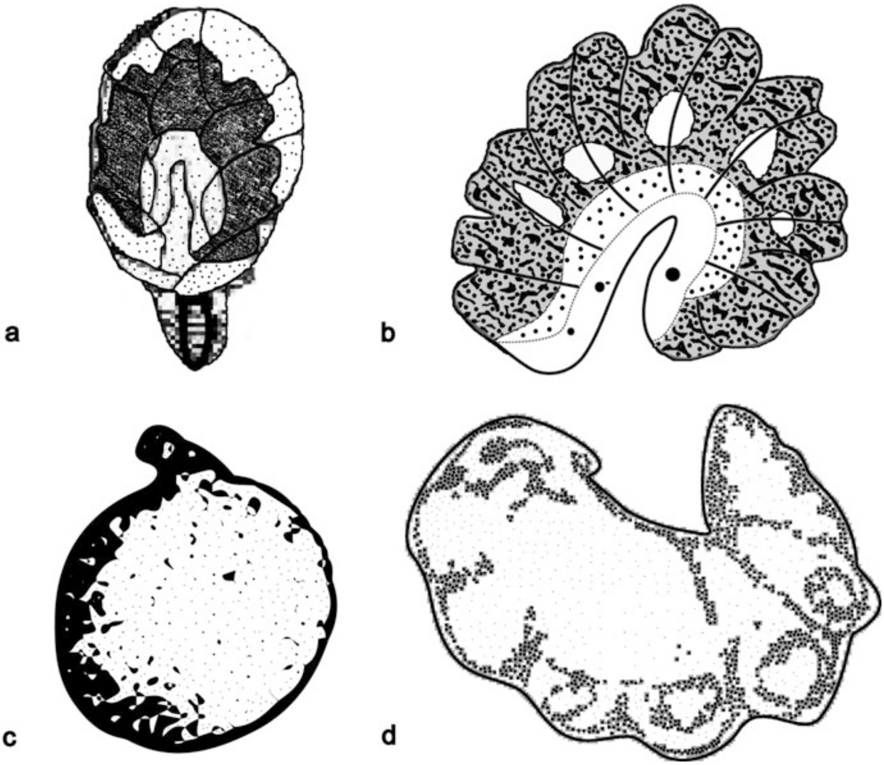

Fig. 8.8 (**a**) *Cabirops perezi* Carayon, 1942, stage 3 female in marsupium of bopyrid host, (**b**) *Cabirops perezi* stage 3 female, (**c**) *Cabirops orbionei* Bourdon, 1972 stage 1 female, (**d**) *Cabirops bombyliophila* Williams & Boyko, 2004 female ventral view. Images (a)–(c) redrawn from Boyko (2013); image (d) redrawn from Williams and Boyko (2012)

share little similarity with other Cirripedia or, indeed, other crustacean adults, as there are neither appendages nor segmentation and the host is always another crustacean, in most instances an anomuran or brachyuran crab (Webber et al. 2010). Unlike bopyrid isopods, intermediate hosts are not involved in their life cycles (Boyko and Williams 2009). These parasites develop an extensive, fine, root-like system of tissue within the host's haemocoel that serves to extract nutrients from the host's body. This stage in the parasite's life cycle (the interna) shows no external manifestations until the host's exoskeleton is ruptured and the parasite protrudes as a consolidated, rounded or irregular, tumour-like structure known as the externa, containing the female reproductive organs (Boyko and Williams 2009; McDermott 2009). Despite their bizarre appearance, rhizocephalans are related to the nonparasitic barnacles, which they resemble by having short-lived planktonic nauplii and/or cypris larvae (Webber et al. 2010).

Table 8.2 List of *Cabirops* Kossmann, 1884, hyperparasitic Isopoda species found on bopyrid hosts, locality and decapod host

Hyperparasite	Bopyrid host	Locality, decapod host
Cabirops sp. Giard & Bonnier, 1888	*Probopyrus ascendens* (Semper, 1880) or *Probopyrus borrie* (Giard & Bonnier, 1888)	Indonesia, *Macrobrachium lar* (Fabricius, 1798) or *Macrobrachium australe* (Guérin-Méneville, 1838)
Cabirops sp. Stebbing, 1910	*Trapezicepon amicorum* (Giard & Bonnier, 1888)	Amirante Islands, *Actumnus tomentosus* Dana, 1852
Cabirops sp. Romano, 1953	*Bopyrina ocellata* (Czerniavsky, 1868)	Italy, *Hippolyte inermis* Leach, 1816
Cabirops sp. Bourdon, 1967	*Scyracepon levis* Barnard, 1940	South Africa, *Rochinia hertwigi* (Doflein, 1904)
Cabirops sp. Haig & Ball, 1988	*Athelges* sp. Gerstaecker, 1862	Indonesia, *Trizopagurus strigatus* (Herbst, 1804)
Cabirops sp. A. Boyko & Williams, 2004	*Cancricepon choprae* (Nierstrasz & Brender à Brandis, 1925)	Bahamas, *Panopeus boekie* Rathbun, 1915
Cabirops sp. B. Boyko & Williams, 2004	*Pseudionella deflexa* Bourdon, 1979	Bahamas, *Pagurus brevidactylus* (Stimpson, 1859)
Cabirops bombyliophyla Williams & Boyko, 2004	*Schizobopyrina bombyliaster* Williams & Boyko, 2004	Tonga, Pacific Ocean, *Gnathophyllum americanum* Guérin-Méneville, 1855
Cabirops codreanui Bourdon, 1967	*Bopyrissa diogeni* (Popov, 1929)	France, *Diogenes pugilator* (Roux, 1829)
Cabirops fraissei (Nierstrasz & Brender á Brandis, 1925)	*Cancricepon choprae* (Nierstrasz & Brender á Brandis, 1925)	Curaçao, *Domecia hispida* Eydoux & Souleyet, 1842
	Cancricepon choprae (Nierstrasz & Brender á Brandis, 1925)	Mexico, *Rhithropanopeus harrisii* (Gould, 1841)
	Cancricepon choprae (Nierstrasz & Brender á Brandis, 1925)	Bahamas, *Panopeus boekei* Rathbun, 1915
Cabirops ibizae Bourdon, 1967	*Asymmetrione foresti* (Bourdon, 1969)	Baleares, Mediterranean *Paguristes oculatus* (Fabricius, 1775)
Cabirops lernaeodiscoides (Kossmann, 1872)	*Probopyrus ascendens* (Semper, 1880)	Philippines, *Macrobrachium lar* (Fabricius, 1798)

(continued)

Table 8.2 (continued)

Hyperparasite	Bopyrid host	Locality, decapod host
Cabirops lobiformis Lemos de Castro, 1970	*Probopyrus* Giard & Bonnier, 1888 sp.	Brazil, *Palaemon pandaliformis* (Stimpson, 1871)
Cabirops marsupialis Caroli, 1953	*Gyge branchialis* Cornalia & Panceri, 1861	Italy, *Upogebia litoralis* (Risso, 1816)
Cabirops montereyensis Sassaman, 1985	*Aporobopyrus muguensis* Shiino, 1964	USA (California), *Pachycheles rudis* Stimpson, 1858 *Pachycheles pubescens* Holmes, 1900
Cabirops orbionei Bourdon, 1972	*Orbione halipori* Nierstrasx & Brender à Brandis, 1923	South Africa *Haliporoides triarthus* Stebbing, 1914
Cabirops perezi Carayon, 1942	*Bopyrissa fraissei* (Carayon, 1943)	Spain, France, *Clibanarius erythropus* (Latreille, 1818)
Cabirops pseudioni Lemos de Castro, 1970	*Progebiophilis upogebiae* (Hay, 1971)	Brazil, *Upogebia omissa* Gomes Corrêra, 1968
Cabirops reverberii Restivo, 1971	*Acrobelione reverberii* (Restivo, 1970)	Italy, *Necallianassa truncata* (Giard & Bonnier, 1890)
[a]*Cabirops tenuis* (Nierstrasz & Brender á Brandis, 1925)	Unknown	Indonesia, Host unknown
Cabirops tuberculatus Shiino, 1942	*Scyracepon oceanicum* Shiino, 1942	Palao, *Eriphia scabricula* Dana, 1852

Compiled from Sassaman (1985), Boyko and Williams (2004), Williams and Boyko (2004), McDermott et al. (2010) and Boyko (2013)

[a] Boyko (2013) regarded this species as congeneric to the type species of *Cabirops* and transferred it from *Paradajus*, he also assumed the host to be a bopyrid isopod found in Indonesia, but the decapod host remains unknown

8.2.7.2 Hyperparasitic Isopoda: Cryptoniscidae

Members of the family Cryptoniscidae are almost exclusively parasites of rhizocephalan barnacles that attach to decapods and sometimes directly to decapod hosts (Freeman 2005; Peresan and Roccatagliata 2005; McDermott et al. 2010; Boyko 2015). Table 8.3 provides more information on the isopods and their rhizocephalan and decapod hosts.

Most of the descriptions of *Liriopsis* Schultze in Müller, 1859 (Fig. 8.9a–c), are incomplete, rare or poorly documented. According to Peresan and Roccatagliata (2005), the differences between *L. pygmaea* (Rathke, 1843) and *L. monophthalmus*

Table 8.3 List of hyperparasitic Isopoda species found in Rhizocephala attached to Decapoda hosts and locality, compiled from McDermott et al. (2010) and Boyko (2013, 2015)

Hyperparasitic Isopoda	Rhizocephalan host	Locality, decapod host
Cryptoniscus paguri Fraise, 1878	*Septosaccus rodriguezi* (Fraisse, 1876)	Corsica, *Clibanarius erythropus* (Latreille, 1818)
Cryptoniscus planariodes Müller, 1871	*Pagarus purpureus* (Dana, 1852)	Brazil, *Clibanarius* Dana, 1852 sp.
Danalia sp. Øksnebjerg, 2000	*Sacculina zariquieyi* Boschma, 1947	Turkey, *Monodaeus couchii* (Couch, 1851)
Danalia curvata (Fraisse, 1878)	*Drepanorchis neglecta* (Fraisse, 1877)	Italy, *Inachus communissimus* Rizza, 1839
Danalia dohrnii Giard, 1877	*Sacculina carcini* Thompson, 1836	Italy, *Pachygrapsus marmoratus* (Fabricius, 1787)
Danalia gregaria Caullery, 1908	*Sacculina gonoplaxae* Guérin-Ganvet, 1911	Italy, *Goneplax rhomboides* (Linnaeus, 1758)
Danalia inopinata Harant, 1925	*Sacculina gerbei* Giard in Bonnier, 1887	France, *Pilumnus hirtellus* (Linnaeus, 1758)
Danalia larvaeformis (Giard, 1974)	*Sacculina carcini* Thompson, 1836	France, *Carcinus maenas* (Linnaeus, 1758)
Danalia longicollis (Kossmann, 1880)	*Sacculina* Thompson, 1836 sp.	Red Sea, *Leptodius exaratus* (Milne Edward, 1834)
Danalia pellucida Giard, 1877	*Sacculina inflate* Leukart, 1859	France, *Cancer pagurus* Linnaeus, 1758
Danalia ypsilon Smith, 1906	*Triangulus galatheae* (Norman & Scott, 1906)	France, Galatheid hosts Spain, *Galathea dispersa* Bate, 1859
Hemioniscus pagurophilus Williams & Boyko, 2006	*Tomlinsonia mclaughlinae* Williams & Boyko, 2006	Philippines, *Calcinus gaimardii* (Milne Edwards, 1848)
Liriopsis monophthlamus Fraisse, 1878	*Peltogaster curvata* Kossmann, 1874	Italy, *Pagarus excavatus* (Herbst, 1791)
Liriopsis pygmaea Rathke, 1843	*Peltogaster paguri* Rathke, 1842	France, Norway, *Pagarus bernhardus* (Linnaeus, 1758)
	Peltogaster paguri Rathke, 1842	United Kingdom, *Pagarus cuanensis* Bell, 1846

(continued)

Table 8.3 (continued)

Hyperparasitic Isopoda	Rhizocephalan host	Locality, decapod host
	Peltogaster paguri Rathke, 1842	USA (Alaska, Washington), *Pagarus hirsutiusculus* (Dana, 1851)
	Peltogaster paguri Rathke, 1842	USA (Maine), *Pagarus pubescens* Krøyer, 1828
	Peltogasterella gracilis (Boschma, 1927)	USA (Washington), *Pagarus ochotensis* Brandt, 1851
	Peltogaster paguri Rathke, 1842	USA (Washington), *Orthopagurus schmitti* (Stevens, 1925)
	Peltogaster paguri Rathke, 1842	Northern Atlantic, *Anapagurus laevis* (Bell, 1846)
	Septosaccus rodriguezi (Fraisse, 1876)	France, *Diogenes pugilator* (Roux, 1829)
Perezina gregaria Nierstrasz & Brender á Brandis, 1929	*Sacculina carcini* Thompson, 1836	Italy, *Pisa armata* (Latreile, 1802)

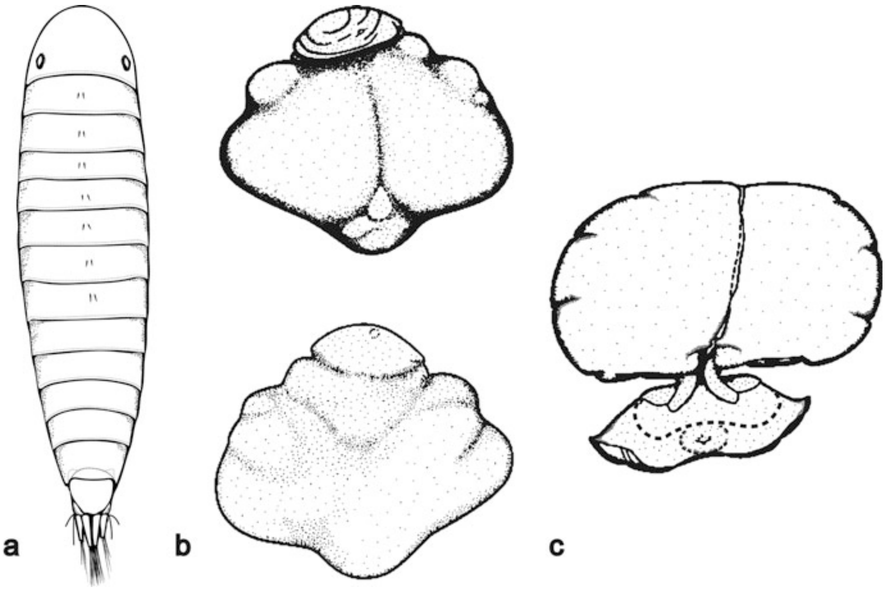

Fig. 8.9 *Liriopsis pygmaea* Rathke, 1843 (**a**) cryptoniscus larva, (**b**) habitus of two early subadult females, (**c**) ventral habitus of adult female. Images redrawn from Peresan and Roccatagliata (2005)

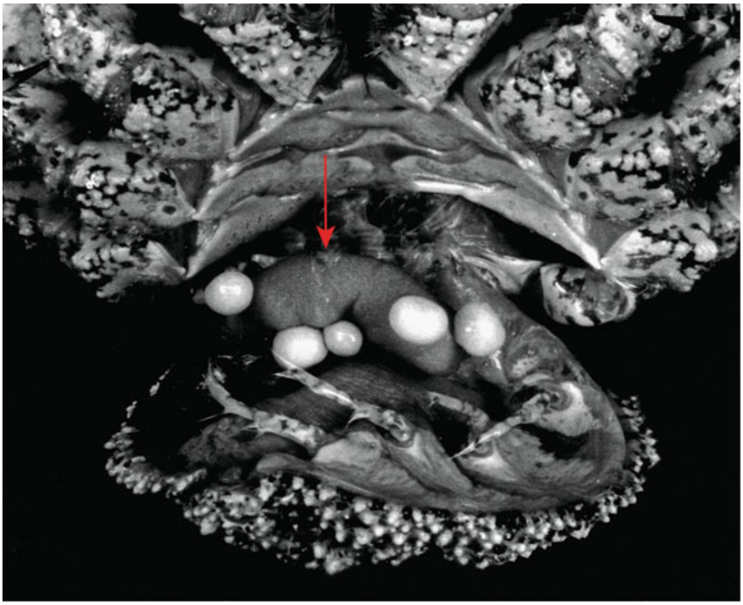

Fig. 8.10 *Paralomis granulosa* (Hombron & Jacquinot, 1846) parasitised by *Briarosaccus callosus* Boschma, 1930 (arrow), hyperparasitised by six late subadult females of *Liriopsis pygmaea* Rathke, 1843. Images from Lovrich et al. (2004)

(Fraisse, 1878) remain obscure. *Liriopsis pygmaea* has been reported mainly from *Peltogaster paguri* Rathke, 1842, but also from *Septosaccus cuenoti* Duboscq, 1912, and *P. gracilis* Boschma, 1927 (all rhizocephalans), found on hermit crabs, whilst *L. monophthalmus* was found only in the Mediterranean on *P. curvata* Kossmann, 1874 (McDermott et al. 2010). Pohle (1992a) reported that the rhizocephalan *Briarosaccus callosus* Boschma, 1930, carrying a cryptoniscinid isopod infected the porcupine crab *Neolithodes grimaldii* (Milne-Edwards and Bouvier, 1894) and the stone crab *Paralomis bouvieri* Hansen, 1908, both from Canadian Atlantic waters (Pohle 1992b). The hyperparasites were collected from the same rhizocephalan host, but the barnacles occurred on different but sympatric hosts, leading Pohle (1992b) to the conclusion that the hyperparasites belonged to the same species. However, no identification of the species was provided. Warrenchuck and Shirley (2000) found *L. pygmaea* for the first time in southern Alaska on 36% of the individuals of *P. paguri* and *Peltogastrella gracilis* that were found on the hairy hermit crab *Pagurus hirsutiusculus* (Dana, 1851). Lovrich et al. (2004) presented the first comprehensive data on the biology of *L. pygmaea* collected from Argentina. Peresan and Roccatagliata (2005) found a species of *Liriopsis*, provisionally identified as *L. pygmaea* (Fig. 8.10), on *B. callosus* parasitising the false king crab *Paralomis granulosa* (Hombron & Jacquinot, 1846). They also provided information on its life cycle (epicardium, cryptoniscus larvae, and three female stages) and additional morphological information. Another reference to rhizocephalans infested

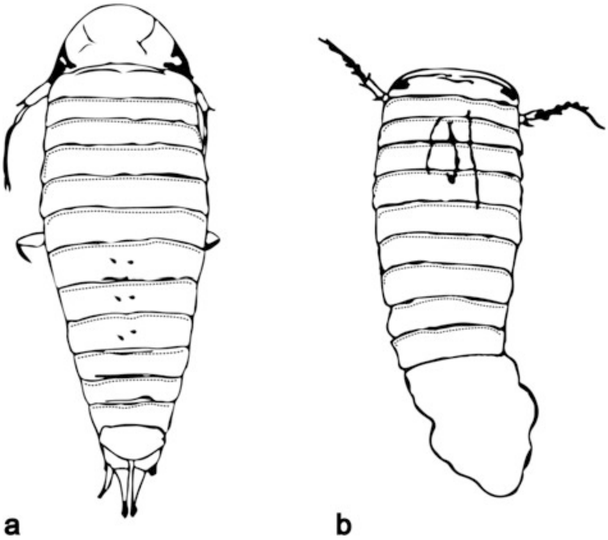

Fig. 8.11 *Hemioniscus pagurophilus* Williams & Boyko, 2006. (**a**) male, (**b**) immature female. Images redrawn from Williams and Boyko (2006)

by cryptoniscids is that of Webber et al. (2010), who reported on the examination of museum material collected from New Zealand; however, the rhizocephalan host is no longer identifiable in the final stages of the infection (Øksnebjerg 2000), which means that some of the parasitic barnacles that Webber et al. (2010) examined could not be identified to species level.

Cryptoniscus planarioides Müller, 1871, and *Liriopsis monophthalmus* have not been recorded with confidence since their original descriptions, and according to McDermott et al. (2010), nothing is known of their biology. Males (Fig. 8.11a) and immature females (Fig. 8.11b) of *Hemioniscus pagurophilus* Williams & Boyko, 2006, were found in the mantle cavity of rhizocephalans attached to the shell of the mollusc *Cantharus* Röding, 1798 (see Williams and Boyko 2006).

Boyko (2015) revised the Cryptoniscidae genera *Danalia* Giard, 1887 (Fig. 8.12a), and *Avada* Boyko, 2015, some species of which are hyperparasites of rhizocephalans, whilst others are directly parasitic on crab hosts. According to Boyko (2015), *Danalia* was established for isopods that parasitise rhizocephalans and that differ from the *Liriopsis* found in *Peltogaster* Rathke, 1842. The genus *Avada* includes three species, *A. kedavra* Boyko, 2015, *A. porcellanae* (Kossmann, 1872) and *A. eldredgei* Boyko, 2015, but it seems that only *A. kedavra* (Fig. 8.12b) and a single female of an *Avada* sp. were found in succulinid hosts, whilst the other two species parasitise crab hosts (Boyko 2015).

Boyko (2013) confirmed that the monotypic genus *Perezina* Nierstrasz & Brender á Brandis, 1929 (Fig. 8.12c), belonged to the family Cabiropidae and not to the Cryptoniscidae. Only mature, non-ovigerous females of *P. gregaria* Nierstrasz & Brender á Brandis, 1929, are known. *Perezina* is a replacement name for the name

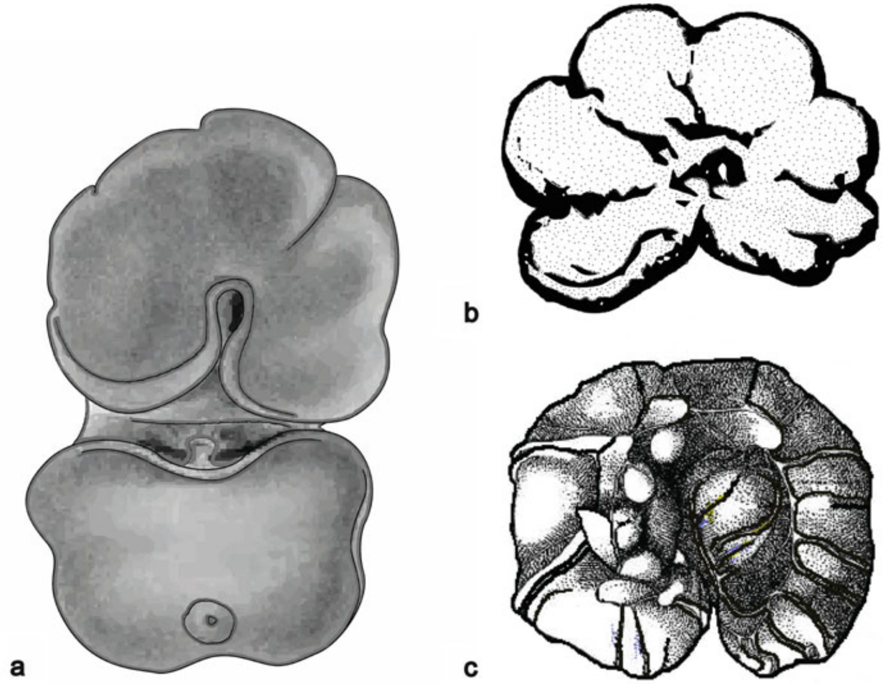

Fig. 8.12 (**a**) *Danalia curvata* (Fraisse, 1878) female (*upper*) on rhizocephalan host (*lower*), (**b**) *Avada kedavra* Boyko, 2015 adult female lateral view, and (**c**) *Perezina gregaria* (Nierstrasz & Brender à Brandis, 1929) stage 4 female. Images (a)–(b) redrawn from Boyko (2015); image (c) redrawn from Boyko (2013)

of the original genus, *Perezia*, because it is a junior homonym of a microsporidian that once was classified under the zoological code, even though it is now placed in the fungi under the botanical code (Boyko 2013). The material was found loose in the brooding chamber of the mantle cavity of the rhizocephalan host (*Sacculina carcini* Thompson, 1836), rather than in the marsupium of the bopyrid isopod (*Pisa armata* Latreille, 1802) (Boyko 2013).

8.3 Effect of Hypersymbionts and Hyperparasites on Hosts

8.3.1 Microsporidians

Microsporidians have been observed in pre-adult and adult stages of both male and female copepods (Freeman et al. 2003; Freeman and Sommerville 2011; Jones et al. 2012). The number of *Lepeophtheirus salmonis* infected by the microsporidians varied between 1% and 10%, with an average of 5% of adult females having microsporidian infections (Freeman and Sommerville 2011). When the microsporidian was present in adult females, a similar proportion of adult male lice from the same population were also infected (Freeman et al. 2003; Freeman and Sommerville 2011). Jones et al. (2012) found that only *L. salmonis* collected from Atlantic salmon were infected with *Desmozoon lepeophtherii*, with a prevalence of 15% in copepods from Washington State and 1.5% in those from British Columbia. Parasitised individuals appeared opaque at the sites of infection, which were observed throughout the body, and heavily infected female lice were often observed with malformed or disproportionately extruded egg strings (Freeman and Sommerville 2011).

Microsporidians have been implicated as a possible primary agent of proliferative gill disease amongst Atlantic salmon in Norway (Nylund et al. 2010). The patent "Microbiological control of sea lice" UK patent GB2371053, international patent PCT/GB02/00134, included microsporidians, amongst other candidates, for use in alternative control strategies for sea lice (Freeman and Sommerville 2011). It is interesting that microsporidians have been recognised as opportunistic pathogens in humans and this has led to an increased interest in the molecular biology of these pathogens (Vossbrinck et al. 2004). The interest grew tremendously following the discovery that a number of microsporidian species are the cause of persistent diarrhoea and systemic diseases in AIDS patients. Eight genera (currently 14 species) have been found to infect humans (Didier and Weiss 2006). This highlights the fact that as new information on microsporidians emerges, whether it is identification as an organism responsible for a zoonotic disease in humans or a hyperparasite in parasitic crustaceans, there are still many gaps to be filled.

8.3.2 Peritrichs

Peritrichous colonisers would be attracted by a hydrophilic carapace, whilst they would be repelled by hydrophobic surfaces. According to Viljoen and Van As (1983), a prerequisite for settlement by peritrichs could be the hydrophilic nature of surfaces, a suitable chemical composition and the presence of protrusions or a roughness of the surface. They came to the conclusion that these factors may explain the distinctiveness of peritrichs found associated directly with fish hosts, in comparison to those found on other and inanimate hosts. Settlement of epibionts on a raised or elevated basibiont will result in a hydrodynamically favourable position for the epibiont. According to Harder (2008), an additional increase in flow dynamics ensures a better supply of nutrients and more efficient removal of excretory products for the epibionts (hypersymbionts). Harder (2008) is also of the opinion that the predominantly advantageous association of epibionts with host organisms indicates that the mere presence of a surface is often not the only criterion for successful colonisation. According to him there is clear experimental evidence for physical settlement cues, such as surface roughness and wettability; environmental conditions in direct proximity to the surface (e.g. irradiation and microhydrodynamics); as well as biogenic chemical signals emanating from the basibiont (parasitic crustacean host) or other epibionts (e.g. the hypersymbionts or hyperparasites) already present on the host surface (Harder 2008).

Epibionts (*Vorticella* or *Epistylis*) may have evolved adaptations of their life cycles to the moulting cycle of the host such as synchronisation of reproduction and formation of mobile stages (telotrochs), which then are able to reinfest the basibionts (Branchiura or parasitic copepods), with the host's ecdysis. Peritrichs exhibit some degree of site-specificity on different crustacean hosts. The reasons for the specific location of attachment are diverse and related to the host habits. For example, water currents formed by the hosts that carry food particles are exploited by their epibionts (Fernandez-Leborans 2009). This will be the case for hypersymbionts that use parasitic crustaceans as a substrate because the flow of any current is obtained via movement of the final host, i.e. fish or free-living crustacean. In the case of the crustacean parasites that attach to a fish host, the crustacean may represent an "island of hard substrate" to which it may be difficult for the peritrich to attach directly. A few examples exist of ciliates that attach directly to external uninjured fish skin, such as *Heteropolaria colisarum* Foissner & Schubert, 1977. These ciliates have a special root-like base of the stalk; thus they penetrate below the mucus on the skin and anchor in the soft tissue of the fish host (Foissner et al. 1985).

Bozkurt and Genc (2009) found *Epistylis* on free-living plankton, with a greater burden on copepods than on Cladocera and Rotifera. Saler and Dörücü (2005) found *Epistylis* attached to *Cyclops vicinus* Ulyanin, 1875, on all of its body parts. This was not the case for the species of *Epistylis* and *Vorticella* recorded from the branchiuran and copepod representatives, except in the case of one *D. ranarum* specimen (Van As and Van As 2015). According to Pritchett and Sanders (2007), the abundance of *Epistylis* found could be related to low water quality, high content of organic matter and inadequate handling. Certain biological aspects and behaviours of the basibiont may be advantageous for its epibionts. Basibionts of the genus *Pomacea* Linnaeus, 1758, can select microhabitats with favourable characteristics, transporting the epibionts to more oxygenated places, away from sources of pollution, or even modifying the conditions of the environment (Dias et al. 2008).

In general, epibionts can compete with their basibionts for available nutrients (Fernandez-Leborans et al. 2006). According to Fryer (1956), the nutrition of ciliates attached to lernaeids seems largely dependent on the extravasated blood and other fluids seeping from the wound in the skin of the fish host caused by the parasitic crustacean. The prerequisite for settlement of the peritrich may also facilitate the settlement of organic material, as well as the growth of algae and bacterial layers (Viljoen and Van As 1983). This hypothesis can be supported by the association of epistylidids with the lesions they cause when attaching directly to a fish host, leading to red sore disease due to secondary infections by *Aeromonas hydrophila* (Chester, 1901) (see Basson and Van As 2006; Colorni 2008). Species of *Epistylis* associated with other parasitic crustaceans, such as branchiurans and lernaeids, are different because both hosts feed directly on the blood of the fish host. A possible benefit to free-living basibionts is the camouflage (Harder 2008) provided by a dense covering of epibionts, which for the fish louse and parasitic copepods might not be true. In free-living basibionts, the presence of epibionts might actually make the basibiont even more visible for predation (Harder 2008). This also might be the case in the instance of a hypersymbiont-parasitic crustacean-fish association.

Xu and Burns (1991) noted that *E. daphniae* Faure-Fremiet, 1905, that settle on free-living adult copepods can live relatively longer since the host no longer moults. Bozkurt and Genc (2009) found *Epistylis* only on adult copepods and cladocerans, which is also true for the majority of *Epistylis* colonies found on parasitic crustaceans referred to in this chapter. In lernaeids, it’s only the females that are completely parasitic (Fryer 1968; Paperna 1996), and some of the infested individuals found had egg sacs, confirming peritrichs attached to adult hosts in which no further ecdysis would take place. On one hand, Sherman and Schaner (1965) mentioned that the lack of *Epistylis* colonies on younger, free-living copepodite stages could be due to moulting, which effectively removes the epibionts. On the other hand, adult copepods have a larger body surface; thus, they would be expected to be preferred by epibionts. The latter is probably also true for the hypersymbionts found on parasitic crustaceans.

According to Xu and Burns (1991), the effect of peritrich infestations on fitness parameters of the host is not known; thus, they tested the hypotheses that *Epistylis* lowers the fitness of the host through effects on survival, growth rates and reproduction. This study was on peritrichs associated with free-living calanoids, but it also could apply to peritrichs hypersymbiotic on parasitic crustaceans. Xu and Burns (1991) found that adult calanoids were easily infested and 66% of juvenile copepodites were rapidly reinfested after moulting under experimental conditions. It seems as if moulting stimulates peritrichs to change from their sedentary, trophic stage to a motile, dispersive telotroch. No obvious lesions were detected and the ciliates often attached to the same area as before ecdysis. Xu and Burns (1991) also found that ciliates behaved as commensals on calanoids in a food-rich environment but had the potential to increase the mortality rate of the host through competition when food was limited. This alternative could not exist in associations of ciliates as hypersymbionts of parasitic crustaceans because the ciliates are filter feeders, whilst the crustacean hosts feed on the blood or mucus of the fish host.

8.3.3 Udonellids

Aiken’Ova and Lester (1996) found more udonellids on female caligids than on males. Male copepods have a shorter life span than females; hence, there is insufficient time after deposition for the eggs to develop. This means that not only will females live longer than the males but are also are more likely than males to become infested with udonellids prior to maturity. They also stated that the factors that limit udonellid numbers are unknown, but once established on a copepod that has completed its final moult, udonellids probably increase in number until the copepod dies. Udonellids develop through their entire life cycle (Fig. 8.13) of eggs, juvenile stages and adult stages whilst attached on the copepod host (Carvajal et al. 2001).

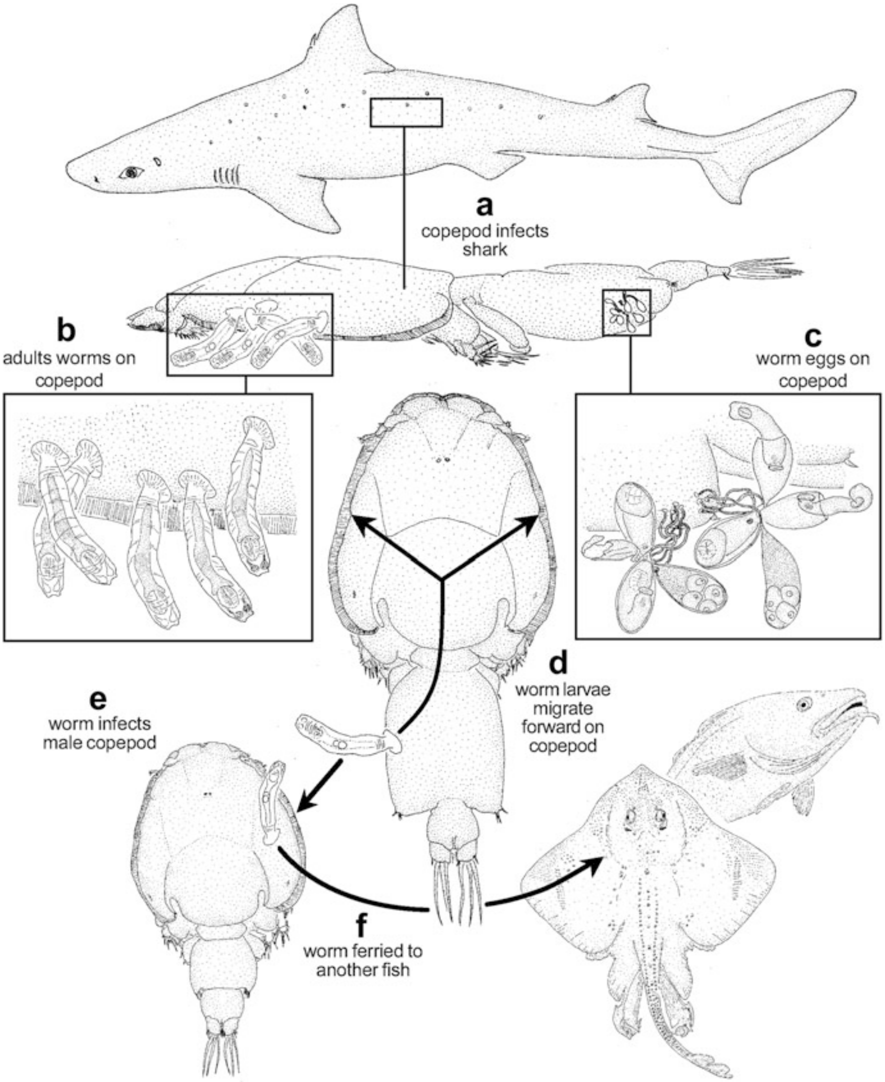

Fig. 8.13 The hypothetical life cycle of *Udonella caligorum* (Udonellidae), reproduced with permission from Benz and Bullard (2004). (**a**) Copepods infect fishes and in turn serve as platforms for udonellids; (**b**) adult udonellids usually attach to the cephalothorax (lateral regions) of adult female copepods; (**c**) udonellid eggs can typically be found on the posterior region of the copepod body; (**d**) once larvae have hatched, they migrate anteriorly on the copepod where maturation will occur; (**e**) spread of udonellids could occur through transference during copepod copulation (infect male copepod); (**f**) udonellids are further spread to new fish hosts when the copepod switches hosts. Image from Benz and Bullard (2004)

Transfer of worms to other hosts may take place during contact between copepods whilst on the fish host.

According to Sporton (1946) members of *Udonella* are detritus feeders, taking in mucus and gill epithelium of the fish that is "kicked" back by copepods. Freeman (2005) stated that the presence of udonellids may be more pathogenic to the fish than to the caligids. Olivier et al. (2000) believe that *U. myliobati* (Guberlet, 1936) feed directly on the epithelial cells of the skin of sharks as they are epithelial browsers. Carvajal et al. (2001) confirmed that *Udonella* survives on mucus secreted by the skin of the fish host and not the caligids to which they attach. It is now widely accepted that *Udonella* specimens feed directly on the mucus of the fish host (Freeman and Ogawa 2010). According to Freeman (2005), this hyperparasitic relationship may have evolved to enable udonellids to avoid an immune response from the fish host. All known species are obligate parasites of fish, found exclusively and commonly on caligid copepods and argulids parasitising marine fishes. The udonellids undoubtedly are totally dependent on the parasitic crustacean hosts for continued survival (Freeman and Ogawa 2010).

The commensal relationship between udonellids and their crustacean hosts is supported by observations from two studies. Marín et al. (2002) concluded that a species of *Udonella* uses *Caligus rogercresseyi* Boxshall & Bravo, 2000, as a means of transport, a breeding site and a substrate to which they can attach whilst feeding on mucus from the skin of the fish host. Carvajal et al. (2001) analysed the histology of the site at which the flatworm attaches to the copepod and found that it showed no trace of the alteration of tissue that would be expected if there were a parasitic relationship between the two.

Kabata (1973) found an average of 5.8 individuals of *Udonella caligorum* per individual *C. elongatus*. The highest infestation of udonellids on copepods (111 juvenile stages and 9 adults on a single host) was found by Minchin and Jackson (1993) in *U. caligorum* on *Lepeophtheirus salmonis*, and Aiken'Ova and Lester (1996) found an average of 38.7 individuals of *U. caligorum* on each individual of *C. elongatus*. Olivier et al. (2000) found *U. myliobati* for the first time along the South Africa coast, with an average of 14.3 worms per infested copepod (*L. natalensis* Kensley & Grindley, 1973). Grobler et al. (2003) reported only two adult worms, but many filamentous eggs and non-ciliated worms, on a species of *Caligus* (South Africa) attached to the flathead grey mullet *Mugil cephalus* Linnaeus, 1758. According to Marín et al. (2007), *U. australis* is the only species occurring in the Southern Hemisphere; therefore, it seems that those found by Olivier et al. (2000) and Grobler et al. (2003) might have been misidentified. Okawachi et al. (2012) found *U. fugu* on *Caligus fugu* (previously *Pseudocaligus fugu*) from Japan, with an infestation of 4.9 females and 2.5 males, respectively. On one adult female of *C. fugu*, they collected a maximum number of 66 worms. Aiken'Ova and Lester (1996) found *U. myliobati* at an infestation of 66%, mostly on the dorsal shield of *C. rogercresseyi*, and with a prevalence of 10% on female fish lice compared to 3% on males. Marín et al. (2007) noted that the large number of udonellids on host copepods found by Kabata (1973), Minchin and Jackson (1993) and Marín et al. (2002) may indicate that these worms have developed life cycle strategies and dispersal capacities to compensate for the absence of a free-living larval stage.

8.3.4 *Tantulocarida*

No information is available on the potential effect of tantulocarids on their hosts (see Ohtsuka and Boxshall 1998).

8.3.5 *Parasitic Isopoda*

Parasitic isopods may also affect the morphology and perhaps also the behaviour of hosts, in addition to potential impacts on their reproduction. Owens (1993) examined 224,000 penaeid prawns and collected 1208 bopyrids and found that up to four females and seven cryptonisci could infect one bopyrid isopod. The impact of bopyrids on the reproductive capacity of their hosts is less pronounced than infection by rhizocephalans, which often completely or partially sterilise the host (Boyko and Williams 2009). According to Boyko and Williams (2009), some bopyrids do not cause "reproductive death" of their host; however, Owens (1993) found that *Cabirops orbionei* Bourdon, 1972, usually sterilised bopyrids that it hyperparasitised (see Sect. 8.4.2 below on biological control that elaborates on the effect of *Cabirops* on the host).

Rhizocephalans always have the drastic impact of parasitically castrating the host and may even modify its behaviour (Boyko and Williams 2009). These parasitic barnacles "hijack" the reproductive system of the decapod host, and the crab is "tricked" into caring for the externa as if it were its own brood. Crabs normally moult after they release their eggs, but infected crabs are also "tricked" into not moulting their exoskeleton as long as the rhizocephalan stays attached.

Otto and MacIntosh (1996) reported a maximum prevalence of 15% of *Briarosaccus callosus* on the Antarctic crab *Paralomis spinosissima* Birstein & Vinogradov, 1972, around the South Georgia Islands. In turn, 26% of the rhizocephalans were infested by an isopod hyperparasite. According to Lovrich et al. (2004), they most likely only recorded the hyperparasites that were attached to the outer surface of the externae and therefore underestimated the actual prevalence of the hyperparasite. Lovrich et al. (2004) found that the prevalence of the hyperparasite *Liriopsis pygmaea* on *B. callosus* was moderately high (36.5%) despite the low, prevalence of the rhizocephalan on its host. All of the externae that had female *L. pygmaea* attached to their outer wall were non-ovigerous. This suggests a detrimental effect of *L. pygmaea* on the egg production of the rhizocephalan. Lovrich et al. (2004) found that the isopod *L. monophthalmus* has a life span of approximately 12 weeks and recorded externae of *B. callosus* with up to 69 annuli that indicate the number of moults that the rhizocephalan has undergone. This indicates that the potential life span of *B. callosus* is much longer than that of *L. pygmaea*, and taking into account the prevalence of *L. pygmaea*, it is possible that nearly all of the individuals in the population of *B. callosus* were hyperparasitised one or more times throughout their life span (Lovrich et al. 2004). Kuris (1974) even used the term hypercastrator to describe the impact of *Liriopsis* on the primary castrator, the parasitic barnacle. McDermott et al. (2010) emphasised that the presence of *Liriopsis* and *Cryptoniscus* Müller, 1864, on the rhizocephalans may weaken them and perhaps allow additional rhizocephalans to establish themselves on the same decapod host, owing to the natural competitive abilities of the healthy parasite being compromised. *Hemioniscus pagurophilus* found on parasitic Cirripedia also sterilise the parasitic cirripede and, in doing so, assist the hermit crab (on which the parasitic barnacles attach) by preventing weakening of its shell by the parasitic barnacles (Williams and Boyko 2006). According to Boyko (2015), any host parasitised by a species of *Avada* probably suffers reproductive death by sterilisation.

8.4 Biological Control

8.4.1 Udonellids as Biological Control of Sea Lice

Sea lice (species of *Lepeophtheirus* and *Caligus*) are natural parasites of both salmon and sea trout and are commonly found on wild salmonids. Over the past two decades, there has been increasing evidence that lice dispersing from salmon farms can increase the abundance of sea lice in adjacent bays and estuaries, which adversely impacts wild, migratory, salmonid stocks. It has clearly been shown that epizootic sea lice have been recorded from a wide range of bays, sea lochs and fjords in fish farming areas throughout Ireland, Scotland and Norway over the past 20 years (Whelan 2010).

Caligus rogercresseyi has been recognised as a pest of farmed salmonids in southern Chile owing to the economic losses it causes to the industry. Biological control was the strategy chosen by Marín et al. (2002) to evaluate the feasibility of controlling these copepods. Biological control is currently being used for sea lice in the Northern Hemisphere but not in Chilean waters.

Preliminary results published by Carvajal et al. (1998) revealed that udonellids could cause mechanical damage to copepod eggs, which would affect fecundity, survival and other reproductive factors in populations of copepods. They proposed that udonellids could be considered as a potential biological control agent if these effects can be proven to occur in *Caligus* present on salmonids. Marín et al. (2002) found that more female caligids were infested with *Udonella* specimens attached to the genital complex and egg sacs. Also, they found udonellids frequently on copepods collected from Chilean rock cod, but they were absent on caligids from cultured salmonids. Carvajal et al. (1998) hypothesised that the udonellids themselves cannot elicit a mucus reaction from the skin of the fish host owing to their attachment to the cuticle of the parasitic copepod. It is the caligid that stimulates secretion of mucus that can serve as food for *Udonella* (Carvajal et al. 2001), when it feeds by pressing its tubular mouth onto the skin of the fish and scraping tissue by sucking with its oral apparatus as observed by Boxshall (1990). Carvajal et al. (2001) also found that caligids occurring on salmonids were never associated with the monogeneans. They concluded from this that salmon mucus may not be adequate as food for *Udonella*. These results suggest that udonellids will not be suitable agents for biological control for sea lice on farmed salmonids because they are not found naturally on salmonids, and infestation by *Udonella* did not reduce either fecundity or survival of the free-living stages of the caligid copepods (Marín et al. 2002).

According to Marín et al. (2007), dispersal of udonellids between copepods of different species seems to be restricted to content between copepods on the same fish, in which case the probability of encounters would increase in proportion to the number of copepods per fish. The number of known *Udonella* species that are recognised is likely to increase if the parasitic crustacean hosts are found to have genetic differences and host specificity is taken into account. *Lepeophtheirus salmonis* is the primary sea louse of concern in the Northern Hemisphere, and *C. rogercresseyi* has become a significant concern in Chile (Bravo 2003). In Japan, *Caligus fugu* has become a serious pest for cultured tiger puffer fish, and Freeman (2005) suggested that *U. fugu* has even more impact on the fish host than the caligids; therefore, Okawachi et al. (2012) concluded that more attention should be paid to the ecology of these hyperparasitic worms.

8.4.2 Cabiropsids as Biological Control for Bopyrids

The hyperparasitic bopyrid *Cabirops orbionei* was originally described by Bourdon (1972) from a single male found on *Orbione natalensis* Carton, 1970, that was parasitic on the knife shrimp *Haliporoides triarthrus* Stebbing, 1914, from South Africa. Owens (1993) reported *C. orbionei* from Orbioninae (bopyrids) infecting penaeid prawns and found that hyperparasitised bopyrids were mostly fully sterilised (no eggs or epicaridia) by the cabiropsids. Some bopyrids were only partially sterilised, with reduced numbers of eggs or epicaridia in their marsupia. He estimated a loss of more than five million dollars per year in the prawn fishery along the Gulf of Carpentaria (Australia) owing to sterilisation of the prawn hosts by bopyrids. This prompted the study into *C. orbionei* to be used as biocontrol for bopyrids.

Species of *Epipenaeon* Nobili, 1906, have been found to be infected by *Cabirops* in the Persian Gulf, Australia, South Africa and the Red Sea. The prevalence of the bopyrids were very high (up to 70%) at certain times of the year if the population was not infected by a cabiropsid. By contrast, the prevalence was lower in populations that included *Cabirops*. According to Owens (1993), this provides direct evidence that the hyperparasite limits reproductive success of the bopyrids parasitic on decapods and, hence, supports a strategy of using cabiropsids as biocontrol agents. The most commonly hyperparasitised prawn in the study by Owens (1993) was *Penaeus esculentus* Haswell, 1879 (brown tiger prawn), followed by *P. semisulcatus* Daan, 1844 (giant tiger prawn), *P. longistylus* Kubo, 1943 (redspot king prawn), and *P. latisulcatus* Kishinouye, 1896 (western king prawn). *Metapenaeus endeavouri* (Schmitt, 1926) (endeavour prawn) was not infected at all. *Epipenaeon ingens*

Nobili, 1906, was 4–5 times more heavily infested with *Cabirops* than other species of bopyrids. Prevalence of *C. orbionei* rose to a maximum in prawns with carapaces up to 34–36 mm long and dropped slowly with increase in size beyond this. It is not uncommon to use parasitic Isopoda as biological indicators in disturbed habitats (Penha-Lopes et al. 2011), and they may make hosts even more vulnerable to environmental toxins (Williamson et al. 2009), thereby increasing their usefulness.

8.5 The Babushkas

Babushka is the name for a set of wooden Russian dolls (matryoshka) with one fitting inside the other. The author is of the opinion that this is an appropriate and interesting way to explain the occurrence of hyper-hypersymbionts found in or on other hypersymbionts attached to parasitic crustaceans.

8.5.1 Zoochlorellae and the Rest

The hypersymbionts of notodelphyids have taken their association to the next level, as the peritrichs themselves harbour zoochlorellae (Fig. 8.4b). Zoochlorellae were found in individuals of *Epistylis* sp. occurring on parasitic copepods that were found inside the branchial area of the ascidian red bait that inhabited the infratidal zone along the South African coastline. This occurrence is almost similar to an Afrikaans song with the following lyrics: “There is a hole in the ground and the green grass is growing around the hole, in the hole is a tree, on the tree there is a branch which has a birds nest on it, the bird has a wing, which has feathers on it, between the feathers is a tick and on the tick there is bacteria” and so it goes on.

Symbiotic algae have been observed in the cytoplasm of *E. chlorelligerum* Shen, 1980, and *E. lalinensis* Qi, Shi, Liu & Hu, 2009, both recorded from freshwater habitats in China, as well as from *E. riograndensis* Utz, Farias, Freitas & de Araújo, 2014 collected from an artificial lake in a Brazilian botanical garden (Utz et al. 2014). Some peritrichs are known specifically to harbour *Chlorella* symbionts. Photosynthesis by the cytoplasmic zoochlorellae in *Ophrydium versatile* (Müller, 1786) is very efficient at low light levels and along with filter feeding by the ciliates and produces carbon that is sufficient to maintain the growth rate of the colony (Lynn 2008). *Chlorella* Beijerinck, 1890, symbionts in *Paramecium* O.F. Müller, 1773, were found to enhance the growth rate, maximum population density and survival of ciliates (Lynn 2008). Gu et al. (2002) found that *Chlorella* cells can be digested by *P. bursaria* (Ehrenberg) Focker, 1836, and this is particularly enhanced in the dark. Perhaps darkness increases the mortality of the *Chlorella*, which cannot then “control” their vacuolar environment (Lynn 2008). *Chlorella*-type symbionts have also been observed in *Frontonia* Ehrenberg, 1838 (Ciliophora, Hymenostomatida), and species of *Vorticella* (see Lynn 2008). The abundance of these ciliates, coupled with the photosynthetic activity of their symbionts, can make them significant contributors to the primary production of some waters at times (Lynn 2008). This might just be the case with the zoochlorellae found in the *Epistylis* attached to the carapace of *Doropygus* that lives inside the branchial sacs of red bait.

8.5.2 The Other Babushka

Freeman and Ogawa (2010) reported the presence of an unidentified species of *Trichodina* Ehrenberg, 1830, on the body surface of *Udonella fugu* as well as in its intestinal contents. They assumed that the trichodinid was parasitic on the grass puffer, and it was consumed opportunistically by udonellids as they fed on fish mucus. The presence of the trichodinid in the intestine of the udonellid together with epithelial cells of the puffer supports the suggestion that these monogeneans do feed on the fish, as has been reported by Olivier et al. (2000), Carvajal et al. (2001) and Freeman and Ogawa (2010).

8.6 Concluding Remarks

In a chapter such as this one, there might be a few even more “dramatic” associations of hypersymbionts and hyperparasites that occur in or on parasitic crustaceans. The main question is still “What is the influence of the hypersymbionts or hyperparasites on the parasitic crustaceans?” The majority of the examples of symbiotic associations covered in this chapter involve organisms that use parasitic crustaceans merely as a place for attachment and a mechanism to “move around” in the aquatic habitat. With a few exceptions, the most extreme effects and influences are caused by the parasitic crustacean on the primary host and not so much by the hypersymbionts on or in the parasitic crustaceans. The exceptions might include microsporidians that cause malformations or opacity in sea lice or the hypercastration effect of *L. pygmaea* on rhizocephalans, which reduces their production of eggs. Using hyperparasites as a method of biological control is a fairly new concept and still in the experimental stage. In the meantime, the presence of sea lice is a major concern in mariculture and needs much more attention. Understanding (and appreciating) the association of an animal (hypersymbiont or hyperparasite) found on or in another animal (parasitic crustaceans) attached to another animal (fish or decapod host) requires that we understand that all of these role players form part of the total biodiversity and ecosystems found in oceans, lakes and river systems.

Maybe the lyrics of the Afrikaans song referred to above (see Sect. 8.5.1) can change to: “There are major habitats in our oceans, lakes and river systems, with green grass and aquatic plants growing around and in our watery habitats, in the ocean, lakes or rivers there is a fish, a shrimp or a crab (choose your favourite), on the fish, shrimp or crab there is an appendage, on the appendage is a scale or cuticle, on the skin or cuticle is a parasitic crustacean, on the parasitic crustacean there is a hypersymbiont or parasite, and on or in these symbionts or parasites there are zoochlorellae or trichodinids and so the song goes on," and we have not even mentioned the bacteria.

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Chapter 9
Unravelling the Evolutions of the Rhizocephala: A Case Study for Molecular-Based Phylogeny in the Parasitic Crustacea

Jens T. Høeg, David John Rees, Pamela C. Jensen, and Henrik Glenner

Abstract We use Rhizocephala to illustrate the problems inherent in estimating the phylogeny of parasitic crustaceans. The adult rhizocephalan parasite has such a reduced morphology that little else than the presence of a moulted cuticle relegates them to Arthropoda. Therefore, until the advent of molecular phylogenetic analysis relegation of the Rhizocephala to taxon relied exclusively on larval characters. The reduced adult morphology also entailed that very few characters were available for intrinsic rhizocephalan systematics and virtually none that could be compared with any outgroup. Thus, rhizocephalan taxonomy relied only on analysis within the group and, with few exceptions, was not based on any phylogenetic principles. The advent of DNA methods in phylogeny confirmed, with high confidence, rhizocephalans as cirripedes and nested them within the taxon as the sister group to Thoracica. This result was supported by SEM studies of the cypris larvae. Additional molecular phylogenetic studies yielded detailed insight into rhizocephalan relationships, culminating in the phylogeny presented here, which includes species from all but one family. Contrary to traditional hypotheses, the new phylogeny shows that infection of

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the host using a kentrogon stage represents the plesiomorphic condition, while rhizocephalans (Akentrogonida) without this stage are advanced. In this analysis, both Kentrogonida and the species-rich Sacculinidae are paraphyletic. In addition, recent hypotheses on family-level relationships in Akentrogonida, based on larval structure and the sexual system, were largely confirmed. This shows that when accurately analysed in a strict homology regime, morphological characters can be powerful partners to molecular data in elucidating rhizocephalan phylogeny.

9.1 Introduction

Parasites often present considerable problems in animal systematics and phylogenetics. The obvious reason for this is that the parasitic mode of life most often is accompanied by a simplified morphology. This can greatly impede both comparisons of the parasites with their putative nonparasitic relatives and polarisation of character evolution, a prerequisite to establishing evolutionary scenarios. Furthermore, the simplified morphology will, by itself, limit the character set available for systematic purposes, even if the resulting taxonomy is not based on a phylogenetic analysis.

In Crustacea, parasitic forms typically have obscured segmentation, and appendages and other body parts can be lacking altogether (Rohde 2005). This situation is nowhere more so than in parasitic barnacles (Cirripedia: Rhizocephala), which are highly modified parasites of other crustaceans. In fact, by morphology alone, the adult rhizocephalan parasite (Figs. 9.1, 9.2, 9.3 and 9.4) cannot be recognised as a crustacean, and they are, therefore, an excellent taxon to demonstrate the importance of alternative characters in elucidating systematics and evolutionary pathways. Larval characters offer the best morphological evidence as to the systematic position of rhizocephalans, but they are difficult to use for any attempts at their intrinsic systematics (Thompson 1836; Høeg 1992a; Jensen et al. 1994a, b; Høeg and Møller 2006). Solid insight into intrinsic rhizocephalan evolution had to await the advent of techniques to sample molecular characters. When molecular techniques were applied, it became apparent that a number of phylogenetic suggestions based on critical analysis of larval development could be verified (Spears et al. 1994; Glenner and Hebsgaard 2006; Glenner et al. 2010). The Rhizocephala, therefore, represent a prime example of how critical analysis of morphology and molecular phylogeny can go hand in hand to arrive at a deeper insight into the evolution of a taxon (Glenner et al. 2010). This chapter is in part presented as a historical narrative, but we do not intend to give a fully fledged account on the history of rhizocephalan research. The historical narrative is only used when it serves to illuminate important biological features. We are principally concerned with higher-level systematic issues in Rhizocephala, and, therefore, we do not review the few molecular studies concerned mainly with species-level taxonomy (e.g. Yoshida et al. 2011).

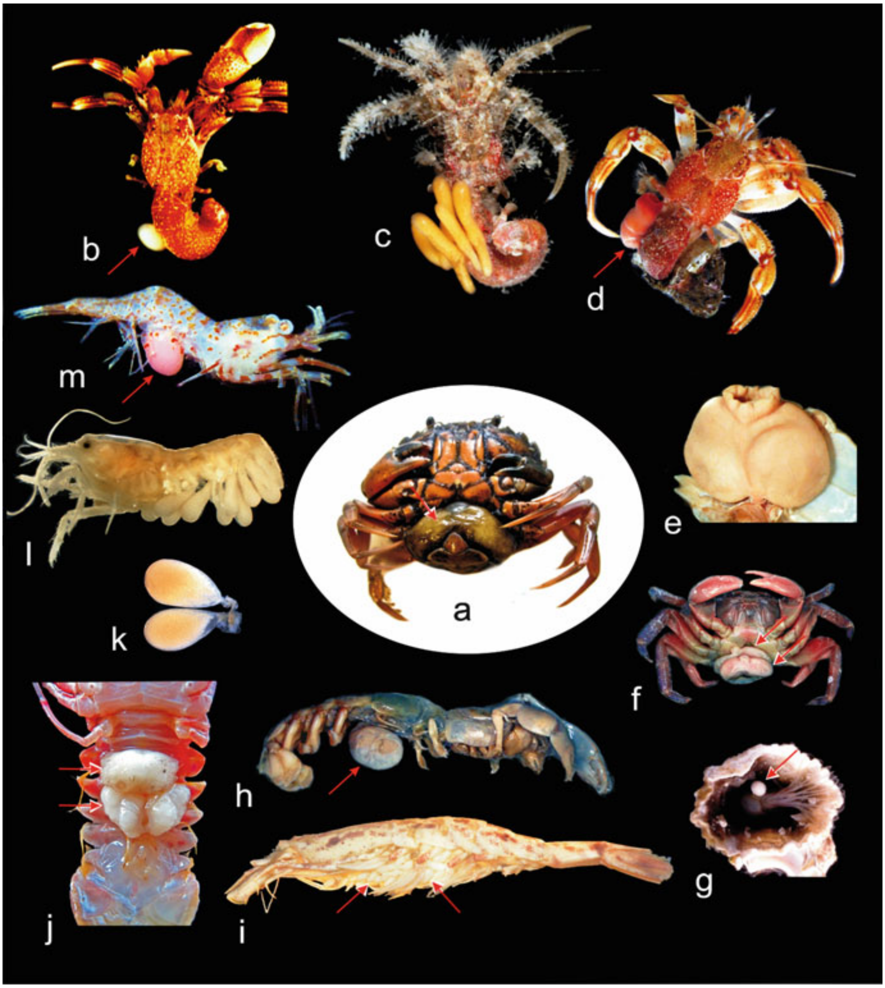

Fig. 9.1 Rhizocephalan diversity in the orders Kentrogonida (**a, c–f, h, j**) and Akentrogonida (**b, g, i, k–m**). The shape of the external reproductive body (externa) varies considerably. The numerous externae in (**c**) and (**l**) belong to the same parasite individual and are internally connected (colonial externae); but the double externae in (**f**) and (**j**) may represent two individual parasites. (**a**) *Sacculina carcini* Thompson, 1836; (**b**) *Clistosaccus paguri* Lilljeborg, 1861; (**c**) *Peltogasterella sulcata* (Lilljeborg, 1859); (**d**) *Peltogaster paguri* Rathke, 1842; (**e**) *Heterosaccus dollfusi* Boschma, 1960; (**f**) *Sacculina confragosa* Boschma, 1933; (**g**) *Chthamalophilus delagei* Bocquet-Védrine, 1957; (**h**) *Parthenopea subterranea* Kossmann, 1874; (**i**) *Mycetomorpha vancouverensis* Potts, 1912; (**j**) *Lernaeodiscus ingolfi* Boschma, 1928; (**k**) *Thylacoplethus isaevae* Rybakov & Shukalyuk, 2004; (**l**) *Thylacoplethus* Coutière, 1902 sp.; (**m**) *Sylon hippolytes* Sars, 1870

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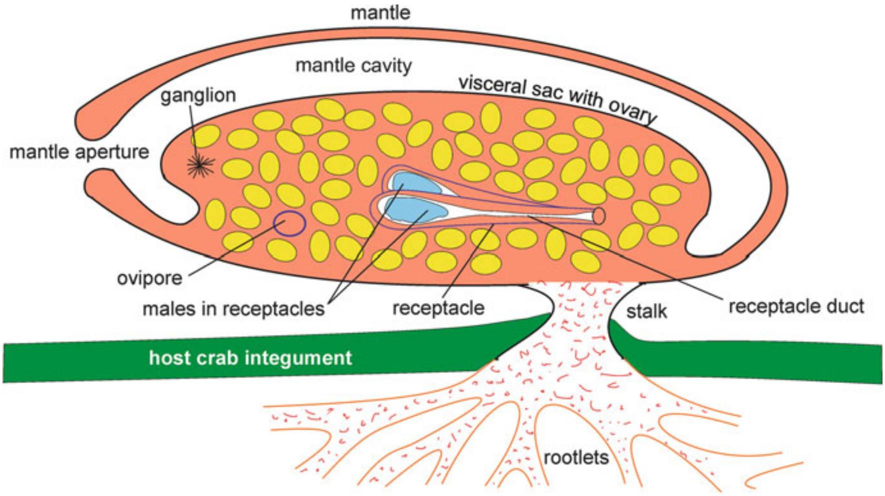

Fig. 9.2 Diagram of a (kentrogonid) rhizocephalan. The externa is unsegmented and lacks appendages and an alimentary canal. The visceral sac contains a small ganglion, a large ovary and a pair of receptacles, each hosting a single dwarf male. Eggs are released through a pair of glandular ovipores and fertilised by sperm exiting through the receptacle ducts. Embryos are brooded in the mantle cavity until released as free-swimming larvae

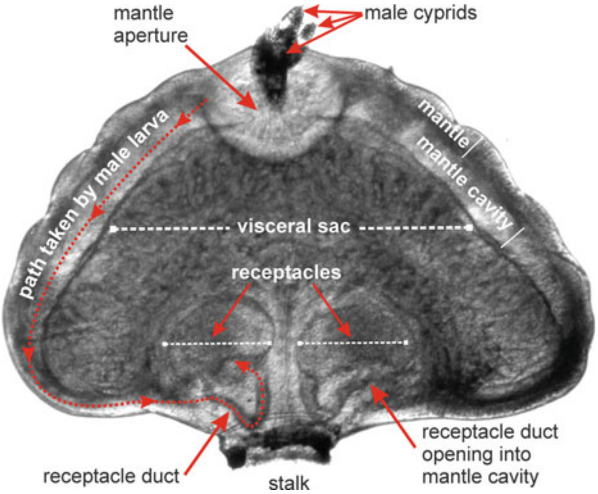

Fig. 9.3 Virginal externa of *Lernaeodiscus porcellanae* Müller, 1862 (Kentrogonida). Male cyprids settled in the mantle aperture and metamorphose into trichogon larvae that invade the receptacles (dotted line). Once males are received, the female parasite can live for up to 2 years, producing a brood every 2–3 weeks, all fertilised by cyclic spermatogenesis in the two originally implanted males

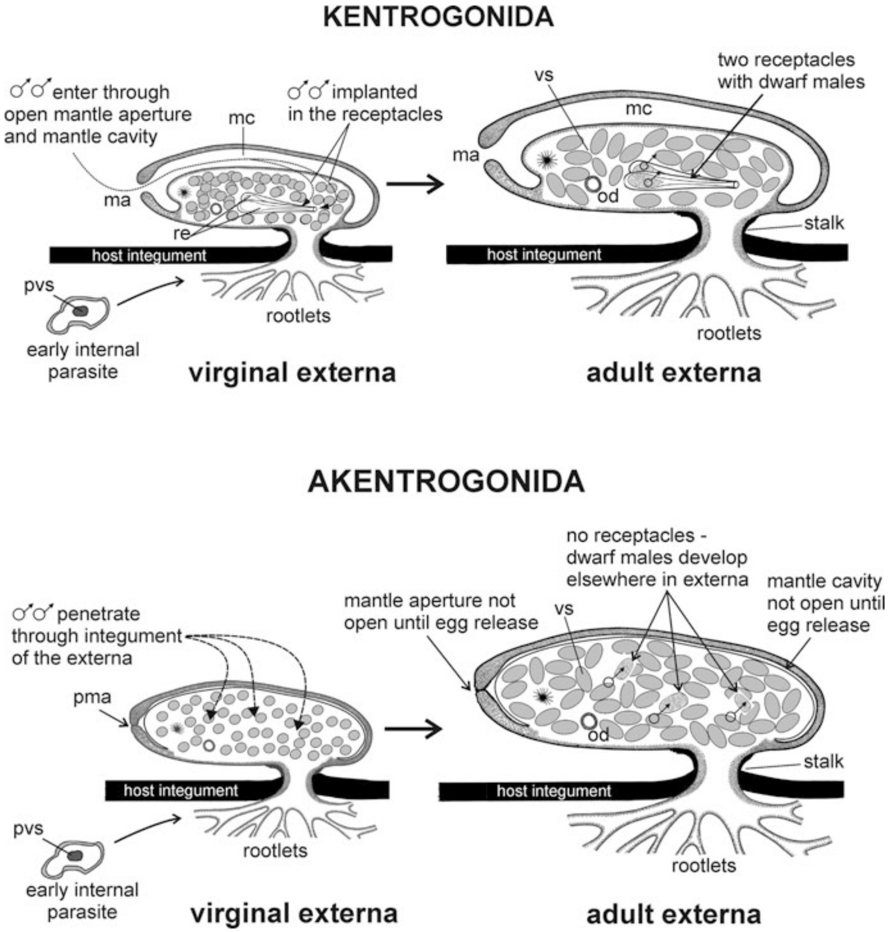

Fig. 9.4 Externa development in Kentrogonida and Akentrogonida. The female parasite develops from a bladder-shaped internal stage. It eventually emerges as an external brood sac (externa) connected to system of rootlets inside the host. The virginal female parasite acquires males either through an open mantle aperture (Kentrogonida) or directly through the integument (Akentrogonida). Kentrogonid females host a single male in each of their two receptacles. Akentrogonida, except *Clistosaccus* Lilljeborg 1860, lack receptacles and can host a variable number of males elsewhere in the body. Further explanation in text. Labels: *ma* mantle aperture, *mc* mantle cavity, *od* oviduct, *pma* prospective mantle aperture, *pvs* primordial visceral sac, *re* receptacle, *vs* visceral sac with ovary

9.2 Material and Methods

This chapter is partly based on two previous phylogenetic analyses (Glenner and Hebsgaard 2006; Glenner et al. 2010) and a new, more extensive analysis (Figs. 9.5 and 9.6). New evidence indicates that the species here listed as *Sacculina confragosa*

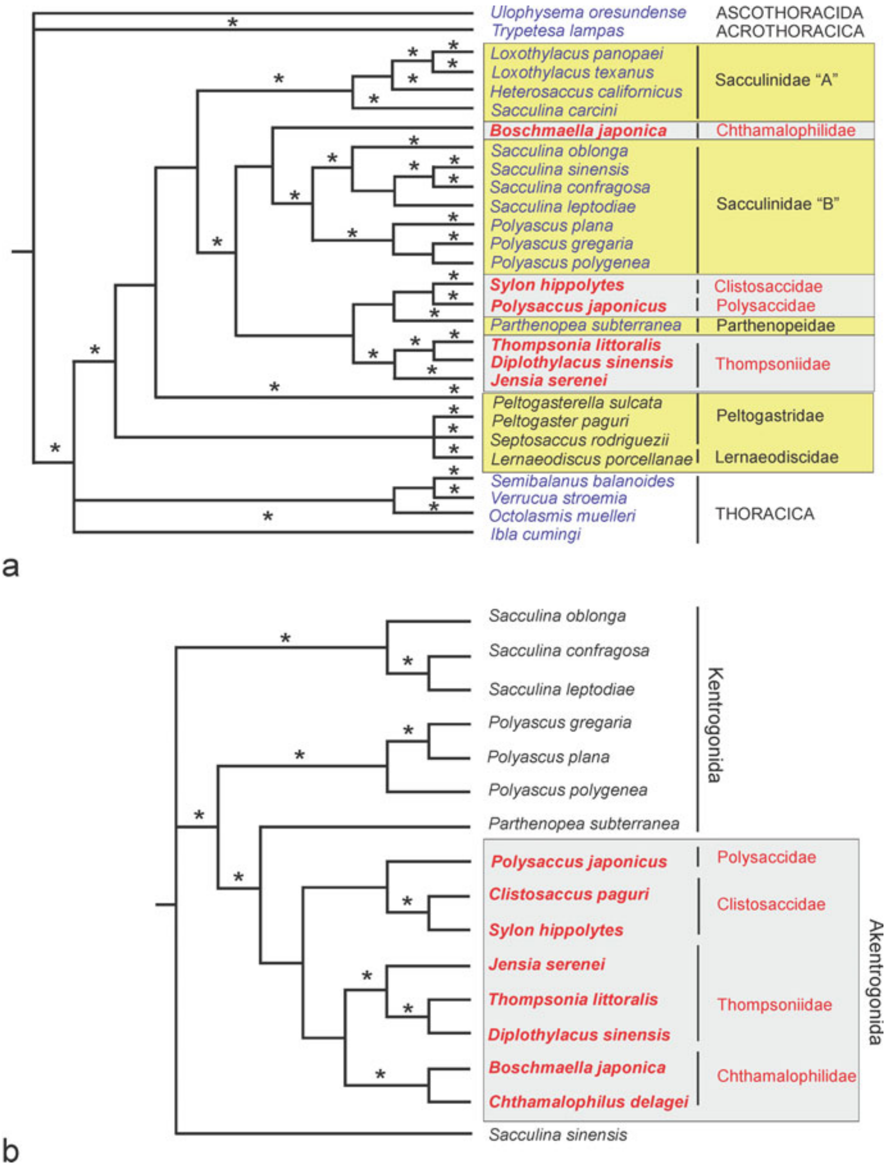

Fig. 9.5 Rhizocephalan phylogeny. (**a**) From Glenner and Hebsgaard (2006); outgroups blue; both Kentrogonida (black) and Akentrogonida (red) are polyphyletic; Sacculinidae also polyphyletic, forming two separate clades ("A" and "B"); (**b**) phylogeny of Akentrogonida from Glenner et al. (2010), including more species than A; outgroups were kentrogonid taxa (black); Akentrogonida (red) now monophyletic, but with low support. Branches with * have a posterior probability >95

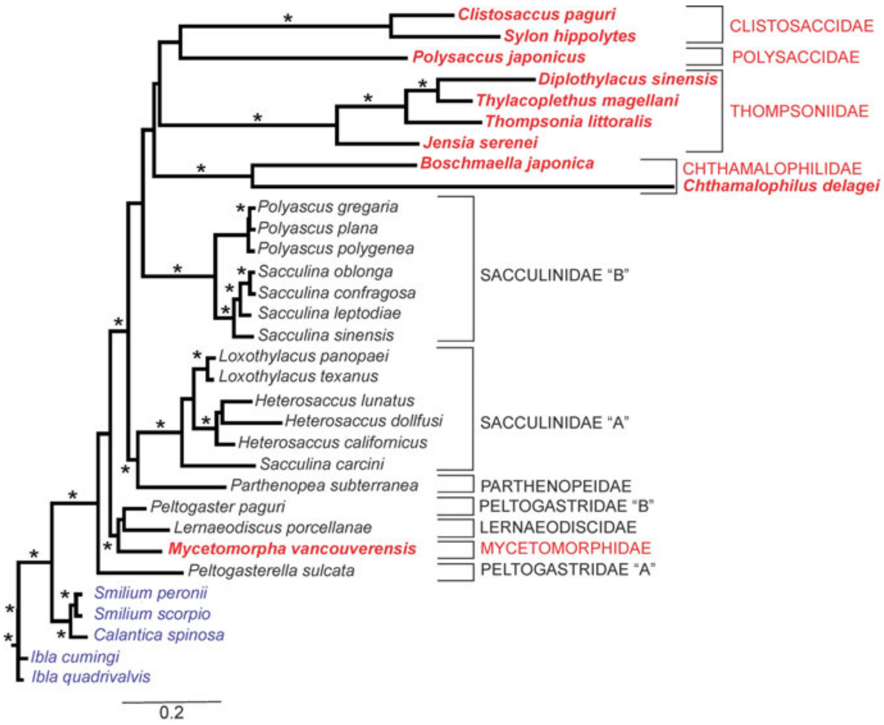

Fig. 9.6 Rhizocephalan phylogeny from the present analysis. Outgroups were thoracican cirripedes (blue). Akentrogonida (red) is not monophyletic, since *Mycetomorpha* (not included in analyses in Fig. 9.5a, b) is placed among kentrogonid species. All remaining akentrogonid families form a monophyletic clade. All akentrogonid families also monophyletic. The kentrogonid families Sacculinidae and Peltogastridae are polyphyletic. Branches with * have a posterior probability >95

Bochsma, 1933, is in fact *Sacculina yatsui* Boschma, 1936, but this possible misidentification has no impact on the conclusions reached here. For the present analysis, genomic DNA was extracted from two individuals of *Mycetomorpha vancouverensis* Potts, 1912, parasitising the caridean shrimp and *Neocrangon communis* Rathbun, 1899 (collected from Alaskan waters, 2012), and subsequently amplified and sequenced for mitochondrial 16S (534 bp) and nuclear 18S (1757 bp) and 28S (682 bp) genes. The full dataset comprised 31 additional cirripede taxa, including the most available and identified rhizocephalan 18S sequences from GenBank, representing both Kentrogonida and Akentrogonida sensu Høeg and Rybakov (1992). A few species analysed by Hiller et al. (2015) are not included here, because our analysis was run prior to that publication. Sequences were aligned using ClustalW, implemented in eBioX 1.5.1 (http://www.ebioinformatics.org/ebiox/), and the best-fit models of sequence evolution were determined for each gene using JModeltest v.2.1.4 (Darriba et al. 2012). Best-fit models were GTR+I+G for 18S and 28S and TVM+I+G for 16S; the more parameter-rich GTR+I+G model was implemented in subsequent Bayesian analyses for all data since MrBayes (v.3.2.1) does not currently support the TVM model. Bayesian analysis (10 million generations) was performed on the resulting multigene dataset. The maximum clade credibility tree (MCC; the tree with the largest product of posterior clade probabilities) was selected from the posterior tree distribution (after removal of 25% burn-in) using the programme TreeAnnotator v.1.8.0 (available as part of the BEAST package, Drummond et al. 2012). The phylogeny from this analysis is presented in Fig. 9.6, and GenBank accession details for all taxa are shown in Table 9.1.

Table 9.1 GenBank accession numbers for the genes of the taxa included in the phylogenetic analysis

Taxon	16S	18S	28S
Boschmaella japonica Deichmann & Høeg, 1990	FJ481951	AY265369	GU190701
Chthamalophilus delagei Bocquet-Védrine, 1957	–	GU190696	GU190710
Clistosaccus paguri Lilljeborg, 1861	–	GU190697	GU190709
Diplothylacus sinensis (Keppen, 1877)	–	DQ826568	–
Heterosaccus californicus Boschma, 1933	AY520756	AY520657	AY520623
Heterosaccus dollfusi Boschma, 1960	FJ481949	EU082413	EU082333
Heterosaccus lunatus Phillips, 1978	FJ481947	EU082414	EU082334
Ibla cumingi Darwin, 1851	–	U89493	EU082332
Ibla quadrivalvis (Cuvier, 1817)	AY520755	AY520655	AY520621
Lernaeodiscus porcellanae Müller, 1862	–	DQ826569	–
Loxothylacus panopaei (Gissler, 1884)	FJ481956	AY265364	–
Loxothylacus texanus Boschma, 1933	–	L26517	–
Mycetomorpha vancouverensis Potts, 1912	MH974513	MH974514	MH974515
Parthenopea subterranea Kossmann, 1874	–	DQ826566	FJ790317
Peltogaster paguri Rathke, 1842	FJ481958	EU082415	EU082335
Peltogasterella sulcata (Lilljeborg, 1859)	FJ481955	DQ826572	EU082336
Polyascus gregaria (Okada & Miyashita, 1935)	JN616263	AY265363	GU190705
Polyascus plana (Boschma, 1933)	FJ481954	AY265368	GU190698
Polyascus polygenea (Lützen & Takahashi, 1997)	–	AY265362	GU190704
Polysaccus japonicus Høeg & Lützen, 1993	–	DQ826565	GU190708
Jensia serenei (Lützen & Du, 1999)	–	DQ826567	GU190702
Sacculina carcini Thompson, 1836	FJ481957	AY265366	AY520622
Sacculina confragosa Boschma, 1933	–	AY265361	GU190706
Sacculina leptodiae Guérin-Ganivet, 1911	FJ481952	AY265365	–
Sacculina oblonga Lützen & Yamaguchi, 1999	FJ481953	AY265367	GU190699
Sacculina sinensis Boschma, 1933	–	AY265360	GU190707
Smilium peronii Gray, 1825	–	EU082386	EU082305
Smilium scorpio (Aurivillius, 1892)	–	AB751197	–
Smilium spinosa (Quoy & Gaimard, 1834)	AY428051	EU082384	EU082303
Sylon hippolytes Sars, 1870	–	DQ826564	GU190700
Thompsonia littoralis Lützen & Jespersen, 1990	–	DQ826573	–
Thylacoplethus magellani Høeg & Lützen, 1993	–	FJ751889	–

9.3 What Are Rhizocephalans?

The 288+ species of Rhizocephala are parasites of other crustaceans, principally decapods, but a few species also occur on other Malacostraca and on balanomorphan barnacles (Fig. 9.1, Table 9.2; Høeg and Lützen 1985, 1995). The adult parasite always consists of an external part (externa) that is connected by a narrow stalk to a ramified system of nutrient-absorbing rootlets (interna) inside the host (Fig. 9.2). There is no segmentation, no appendages, no alimentary canal and no sensory or excretory organs, so neither external morphology nor internal organs offer any clue to the position of these parasites within Metazoa, except that the presence of a moulted cuticle suggests that they are arthropods (Høeg 1992b). The internal system of rootlets, also clothed in a very thin cuticle, serves to absorb nutrients and most likely also to exercise the elaborate host control that is a key feature in rhizocephalan parasitism (Bresciani and Høeg 2001). Almost all rhizocephalans sterilise their hosts either partially or completely, the only exception being species of the small family Chthamalophilidae. Furthermore, rhizocephalans also manipulate their hosts into accepting the parasite externa as "self", so it is left unharmed. Finally, many rhizocephalans feminise male hosts structurally, behaviourally and physiologically. In the Kentrogonida, the externa is always located on the abdomen (Fig. 9.1), and the combined effects of host control have the result that both infested males and females care for the parasite as they would for their own offspring (Ritchie and Høeg 1981).

Table 9.2 List of suborders and families in Rhizocephala

Taxon	M/ P	Type of metamorphosis	# genera	Hosts
Order Akentrogonida	P			
Chthamalophilidae	M	Akentrogonid (?)	3	Balanomorpha
Clistosaccidae	M	Akentrogonid	2	Anomura, Caridea
Duplorbidae	M?	Akentrogonid (?)	3	Isopoda, Cumacea
Mycetomorphidae	M*	Akentrogonid (?)	1	Caridea
Pirusaccus incertae sedis		Akentrogonid (?)	1	Anomura
Polysaccidae	M*	Akentrogonid (?)	1	Callianassidae
Thompsoniidae	M	Akentrogonid	4	Brachyura, Anomura, Caridea, Stomatopoda
Order Kentrogonida	P			
Lernaeodiscidae	M*	Kentrogonid	4	Anomura
Parthenopeidae	M*	Kentrogonid (?)	1	Callianassidae
Peltogastridae	P	Kentrogonid	14	Anomura, Caridea[a]
Sacculinidae	P	Kentrogonid	7	Mostly Brachyura; also Anomura and Thalassinidea

[a] Only *Trachelosaccus* Boschma, 1928, which may well warrant a separate family

M/P indicates whether the taxon is monophyletic or poly/paraphyletic in the present analysis (see Fig. 9.6); * indicates that the taxon is monotypic or in this analysis represented only by a single species. Metamorphosis of "kentrogonid" or "akentrogonid" type is either confirmed for at least one species or, when marked by (?) inferred from indirect morphological data or phylogenetic position

In summary, a rhizocephalised host is essentially a crab phenotype controlled by a parasite genotype, with largely unknown but potentially very important impacts on the host population (Høeg 1995; O'Brien 1999; Kuris et al. 2008).

Compared to the advanced level of host control, the rhizocephalan externa has an exceedingly simple structure and principally contains the reproductive organs (Høeg 1992b). A large ovary fills the so-called visceral sac that is normally suspended in a spacious mantle cavity (Fig. 9.2). A very small ganglion may also be present and strands of muscle traverse both the visceral sac and the mantle. The male organs can be situated in the visceral sac, in the mantle or even as free bodies in the mantle cavity (Høeg and Lützen 1995) and are now known to be separate dwarf male organisms (Høeg 1991; Høeg and Lützen 1995).

The shape of the externa offers some clues to species-level systematics but also reflects its position on the host animal (Fig. 9.1). Some have elongated shapes suited to their position on the left side of the abdomen in hermit crab hosts (Fig. 9.1b–d), while others have broad and somewhat flattened shapes to fit beneath the reflexed abdomen of Brachyura. Several species of the kentrogonid genus *Lernaeodiscus* Müller, 1862, have externae with several marginal lobes, containing extensions of the brood chamber, but a somewhat similar shape also characterises externae (Fig. 9.1i) of the akentrogonid *Mycetomorpha* Potts, 1912.

9.4 The Position of the Rhizocephala in the Animal Kingdom

Despite their reduced morphology, the current position of Rhizocephala in animal systematics was suggested almost two centuries ago. It was Thompson (1830) who first found that thoracican barnacles brood nauplii in their mantle cavity, and he used this trait to affiliate them to the Crustacea (Høeg and Møller 2006; Martin et al. 2014; Damkier 2016). Shortly thereafter, Thompson (1836) also found nauplii in the "classical" rhizocephalan, *Sacculina carcini* Thompson, 1836, and realised that nauplii of species in both the thoracican *Balanus* Da Costa, 1778, and the rhizocephalan *Sacculina* Thompson, 1836, have fronto-lateral horns (Martin et al. 2014). With this insight, Thompson (1836) included rhizocephalans in cirripedes and demonstrated that Cirripedia is characterised by the unique presence of naupliar fronto-lateral horns, a character that is now considered an autapomorphy for this taxon (Høeg 1992a; Høeg et al. 2009; Damkier 2016). Thompson's (1830, 1836) findings took some time to become accepted (Damkier 2016), but by the middle of the eighteenth century, both the crustacean nature of cirripedes and the cirripede nature of rhizocephalans had become universally accepted. In parallel with Burmeister (1834), Thompson (1830, 1835) also described the cyprid, the terminal larval stage in barnacles. The first sighting of cyprids in rhizocephalans may have been by Lilljeborg (1860), who found a cyprid attached to the mantle aperture of small-sized externae of *Peltogaster paguri* Rathke, 1842 (see also Fig. 9.3). Mistakenly, he believed that the cyprid was a remnant from the original infection of the host, because it was assumed that infection occurs where the adult parasite is later found. It was Delage (1884), who in his seminal monograph, demonstrated that infecting cyprids of *S. carcini* settle in a location quite distant from where the parasite later emerges, and that the parasite subsequently develops by means of an internal migratory stage (Høeg 1995; Høeg and Lützen 1995). The cyprids found at the mantle aperture by Lilljeborg (1860) were in fact male cyprids attached to virginal female parasites. The realisation that rhizocephalans have a dioecious sexual system had to wait almost a century for the benchmark research of Ichikawa and Yanagimachi (1957, 1958, 1960) and Yanagimachi (1961a, b).

9.5 Present Rhizocephalan Systematics

The present family-level taxonomy of the Rhizocephala is summarised in Table 9.2. The superorder is divided into two orders: Akentrogonida and Kentrogonida (Martin and Davis 2001), and the status of these is discussed below. Until recently, rhizocephalan taxonomy was based on crude characters associated with the externa and without any reference whatsoever to character evolution or phylogeny. This explains why all non-monotypic families of the order Kentrogonida are para- or polyphyletic in light of the analysis presented herein. Prior to the use of molecular characters, the aforementioned problems with adult morphological characters almost prevented any phylogenetic approach to rhizocephalan systematics (Høeg and Lützen 1995; Øksnebjerg 2000). However, building on the ideas of Glenner and Høeg (1994) that larval metamorphosis in Akentrogonida is highly derived, Høeg and Rybakov (1992) revised the families of this order, and the taxa created or amended by them are presently shown to be monophyletic.

9.6 The Classic Rhizocephalan Life Cycle

"Classic" textbook rhizocephalans are those that belong to the order Kentrogonida (Høeg and Lützen 1995; Brusca and Brusca 2002; Ruppert et al. 2004). This order comprises the majority of the 288 rhizocephalan species, with Sacculinidae being by far the largest family (Table 9.2). In principle, all kentrogonid females have the same morphology and pass through very similar life cycles (for details, see Høeg and Lützen 1995). The adult parasite is female, and its externa is always situated on the abdomen of the decapod host. The externa has two specialised pockets, termed male receptacles, located in the visceral sac and communicating with the mantle cavity (Fig. 9.4). Each receptacle hosts a highly reduced dwarf male that cyclically produces sperm each time the female is ready to release a new batch of eggs into the mantle cavity. As in other barnacles, the eggs pass out through two glandular oviducts (colleteric glands), and fertilisation and brooding of embryos take place in the mantle cavity. The larvae are normally released as lecithotrophic nauplii, although some species release them as fully functional cypris larvae (Høeg 1995). Thus, in terms of reproductive biology, the rhizocephalan externa functions as, and is probably homologous with, the capitulum of a thoracican barnacle. Many of the latter are also dioecious with dwarf males present at various stages of reduction (Yusa et al. 2012; Lin et al. 2015). The main difference is the unique presence of receptacles, where the two dwarf males are nursed and nourished by the female externa and kept for her entire lifetime (Høeg and Lützen 1995). No such specialised structures occur elsewhere in Cirripedia (Spremberg et al. 2012; Lin et al. 2015).

The Kentrogonida are dioecious with genetic sex determination (GSD), and the larvae are sexually dimorphic (Yanagimachi 1961a, b; Walker 1985; Glenner et al. 1989; Høeg 1995). Female cyprids attach on the surface of new host animals, where they metamorphose into a kentrogon stage that, by means of a hollow stylet, penetrates through the host integument and injects a so-called vermigon (Fig. 9.7; Glenner and Høeg 1995; Glenner et al. 2000; Høeg et al. 2012). The vermigon larva is slug-shaped, without any segmentation, and indisputably the most highly reduced stage known in Arthropoda, but it is nevertheless enveloped in an exceedingly thin cuticle and contains four distinct types of cells including an epithelium (Glenner 2001). Therefore, the stage injected into the host by the rhizocephalan kentrogon is a true instar and not just a mass of undifferentiated cells as was originally believed (Delage 1884; Høeg 1985a). Once inside the host, the vermigon travels through the hemocoel from the site of infection (e.g. on the appendages or gills) to the abdomen, where it grows until a small, juvenile externa finally emerges (Fig. 9.4). This virginal parasite must now receive male cyprids that settle at the small mantle aperture (Fig. 9.3) and thereafter metamorphose into trichogon larvae, which are male equivalents of vermigons (Høeg and Lützen 1995). Two trichogons migrate into

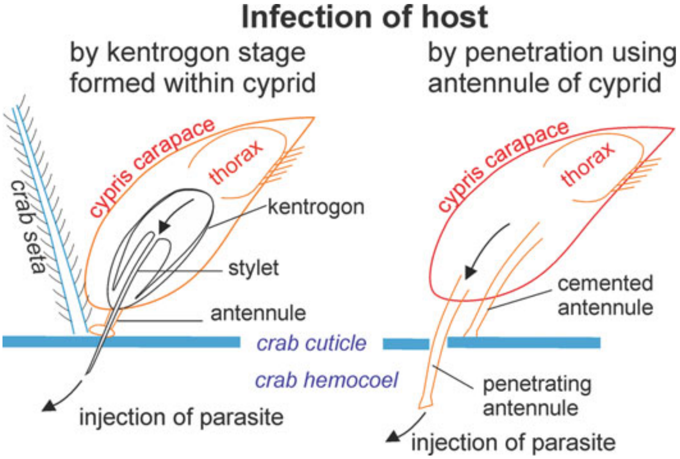

Fig. 9.7 Modes of host infection. In kentrogonid species the cyprid forms a kentrogon, which penetrate into the host using a hollow stylet. Akentrogonid species form no kentrogon, and the cyprid penetrates by itself using an antennule. Host structures blue, cypris structures red, kentrogon black

the receptacles, where they mature into sperm-producing males (Høeg 1987). Thereafter, the female parasite grows quickly to sexual maturity (Fig. 9.4).

Within Kentrogonida there is little variation in the described morphology and life cycle, with one remarkable exception. Some species have female parasites that consist of several externae connected to the same system of rootlets (Fig. 9.1c). In these colonial forms, each individual externa has its own pair of receptacles. Thus, the number of males per individual female parasite is accordingly twice the number of externae and thus much higher than the two males present per female in species with only a single externa. The evolution and selective advantage of such a multi-male system pose some very interesting questions (Yamaguchi et al. 2014).

9.7 Akentrogonida and Variations in Morphology and Life Cycle

The principal diagnostic character for the order Akentrogonida is that the female cyprid infects the host all by itself without passing through a kentrogon stage. Furthermore, species of Akentrogonida deviate in morphology and life cycle, both from kentrogonid species and among themselves. Finally, species of Akentrogonida are not confined to decapod hosts but also parasitise peracarids, stomatopods and even balanomorphan cirripedes (Fig. 9.1). The reproductive organs in Akentrogonida are particularly variable. Just as in the Kentrogonida, all akentrogonid species are now believed to have separate sexes, but the juvenile externa never possesses a mantle aperture that could allow a male larva to enter (Høeg and Lützen 1995). Instead, where investigated, the male cyprid uses one of its antennules to penetrate through the externa integument and inject itself into the female tissue (Fig. 9.4). Once injected, the male can begin spermatogenesis in various places such as the mantle, the ovary or even as a free-floating body within the mantle cavity. Except for a single species, *Clistosaccus paguri* Lilljeborg, 1861, there is never a specialised structure (receptacle) to receive the male (Høeg 1982). Furthermore, where studied, the female cyprid infects its host by antennular penetration just as in males (Fig. 9.7). Host infection and male implantation without formation of kentrogons or trichogons are now believed to occur in all species of Akentrogonida (hence the name), but have been experimentally verified only for species in Clistosaccidae and Thompsoniidae. There is also strong, but indirect, evidence that male implantation by antennular penetration occurs in Mycetomorphidae (Høeg 1990; Høeg and Rybakov 1996a; Lützen et al. 1996).

The morphological difference to kentrogonids is perhaps most evident in Thompsoniidae (Fig. 9.1c), where all species have colonial externae. The female thompsoniid consists of numerous ball or club-shaped externae that can be situated anywhere on the body, including the appendages (Høeg and Lützen 1993, 1995). In contrast to Kentrogonida, the externae of most akentrogonids reproduce only once and then perish. However, in Thompsoniidae, the lost externae are replaced by production of new ones from the root system, just as in kentrogonids with colonial externa such as *Peltogasterella* Lilljeborg, 1860 (Høeg and Lützen 1995; Glenner et al. 2003). Only species of Duplorbidae and Chthamalophilidae seem to have longer lived externae that can produce a series of broods as in most kentrogonid species.

9.8 How to Analyse Rhizocephalan Phylogeny?

The variation displayed within Akentrogonida begs the question as to whether Rhizocephala is a monophyletic taxon or a polyphyletic assemblage of cirripedes that evolved convergently into advanced parasites, as suggested by Rubiliani (1984). Whether monophyletic or not, there is also a need to resolve the intrinsic phylogeny of the rhizocephalan species. The existing higher-level taxonomy, based on gross morphology of the externae, is next to useless for a modern phylogenetic systematic approach and is often diagnostically unreliable, even at species level (Øksnebjerg 2000). The most reliable morphological character sets are derived from the ultrastructure of the cypris larvae and fine details of the male organs, but such data have only been obtained for a minority of species (Glenner et al. 1989; Høeg and Lützen 1995; Yoshida et al. 2011). Most rhizocephalan systematics are based on generalised similarities without claim to represent phylogenetic relationships, except for recent contributions using DNA data (e.g. Glenner et al. 2003; Glenner and Hebsgaard 2006; Yoshida et al. 2011; Hiller et al. 2015). Due to this paucity of morphological characters, there have also been very few hypotheses on rhizocephalan phylogeny. By far the most influential theory was developed by Bocquet-Védrine (1961, 1972), who argued that the akentrogonid family Chthamalophilidae represented the most "primitive" member of the taxon. *Chthamalophilus delagei* Bocquet-Védrine 1958, infesting balanomorphan barnacles (Fig. 9.1g), was argued to be an ectoparasite with a self-fertilising hermaphroditic system and no real root system inside the host. With no internal stage believed to be present, *C. delagei* was therefore argued to lack any kentrogon stage, although this was never experimentally verified. Based on this explanation, *C. delagei* was considered basal in Rhizocephala, with Kentrogonida representing an advanced lineage. The hypothesis was also adopted in the influential review by Newman et al. (1969) and was even presented as a cladogram by Bocquet-Védrine and Bourdon (1984).

9.9 Phylogenetic Hypotheses Based on Larvae and Ontogeny

The hypothesis of Bocquet-Védrine (1961), linking infection by a kentrogon with the presence of an internal stage, was first challenged by Høeg (1990) and elaborated into a provisional phylogenetic scheme by Glenner and Høeg (1994). They argued for the monophyly of all Rhizocephala based on apomorphic similarities in the development following host infection. The infecting larva always develops into an epithelium-enclosed bladder containing a so-called "nucleus" which is the primordial visceral sac containing the ovary (Fig. 9.4). Furthermore, they analysed in detail the variation in host infection (Delage 1884; Høeg 1985a, 1990) and emphasised that the type of kentrogon found in the family Sacculinidae could well have evolved into the antennular penetration system known from Clistosaccidae and Thompsoniidae (Fig. 9.7). Finally, Glenner and Høeg (1994) argued that metamorphosis by means of a female kentrogon and a male trichogon is comparable to the events in other barnacles, whereas a metamorphosis without such intermediate stages, as seen in akentrogonids, has no equivalent at all. This led to the hypothesis that rhizocephalans with cypris antennular penetration (the de facto akentrogonids) form a monophyletic taxon that evolved from a sacculinid-like ancestor, thus rendering Kentrogonida paraphyletic (Glenner and Høeg 1994).

In parallel with this, scanning electron microscopy (SEM) characters from cyprids began to provide limited insight into rhizocephalan relationships. The cyprids of *Clistosaccus* Lilljeborg 1860 and *Sylon* Sars, 1870, species (then placed in separate families) are nearly identical, especially in the sensory organs in the antennules and the carapace (Glenner et al. 1989; Jensen et al. 1994b), and this led Høeg and Rybakov (1992) to place the two genera in a single family, Clistosaccidae.

Another special case within the Akentrogonida was the monogeneric Mycetomorphidae, comprising two species with an externa morphology (Figs. 9.1 and 9.9) unlike any seen elsewhere in the Rhizocephala (Potts 1912; Høeg and Rybakov 1996a, b). However, the cypris larvae of *M. vancouverensis* are remarkably similar to those of the Kentrogonida, especially in antennular morphology (Fig. 9.8). *Mycetomorpha* was therefore hypothesised as being a transitory form between Kentrogonida and Akentrogonida (Glenner et al. 1989; Høeg and Rybakov 1996b, 2007).

As part of a revision of the family Thompsoniidae, Høeg and Lützen (1993) analysed the phylogeny of the entire order Akentrogonida down to genus level. They used Kentrogonida as the outgroup and a data matrix based largely on the characters of the externa. Finally, for Rhizocephala as a whole, Jensen et al. (1994a) used cypris sensory organs (lattice organs) to argue that Rhizocephala and Thoracica were formal sister groups, with Acrothoracica diverging at the base of the cirripede phylogenetic tree.

9.10 The Advent of Molecular Methodology

Not surprisingly, barnacles were one of the first crustacean taxa to which molecular phylogenetic methods were applied. Spears et al. (1994) analysed a few species from all three cirripede superorders, the burrowing barnacles (Acrothoracica), the parasitic barnacles (Rhizocephala) and the stalked and acorn barnacles (Thoracica), and also included a species of the parasitic Ascothoracida. Collectively, Grygier (1987) had

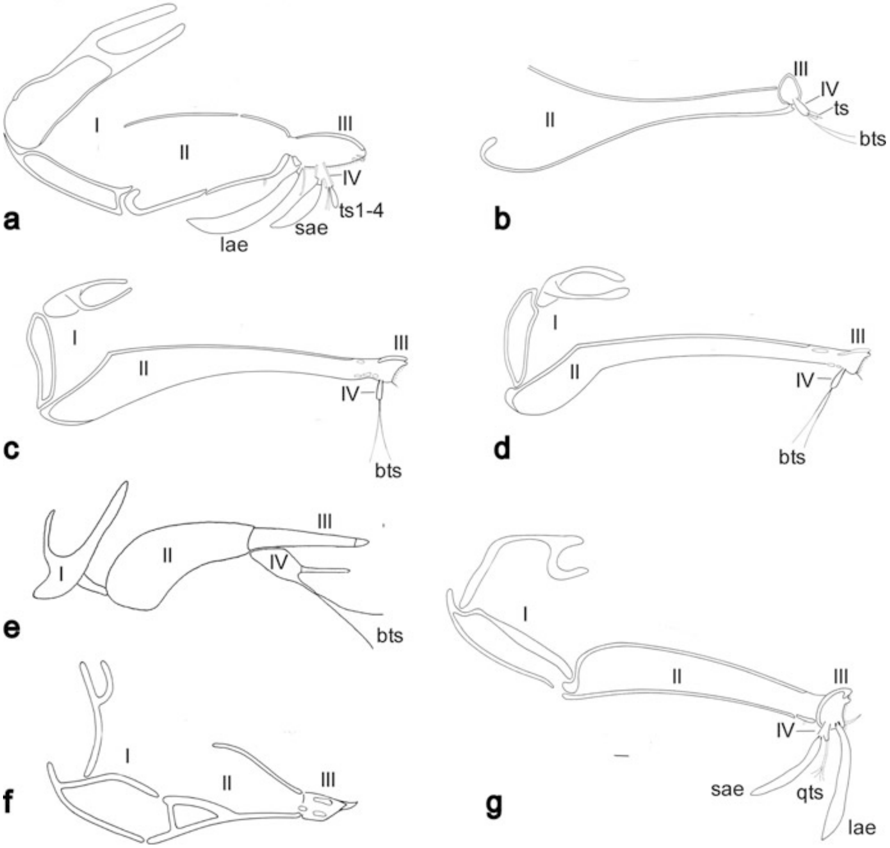

Fig. 9.8 Cypris larvae and rhizocephalan systematics. (**a**) *Sacculina carcini*, (**b**) *Thompsonia* sp., (**c**) *Sylon hippolytes*, (**d**) *Clistosaccus paguri*, (**e**) *Polysaccus japonicus*, (**f**) *Chthamalophilus delagei*, (**g**) *Mycetomorpha vancouverensis*. In Kentrogonida (**a**), the cypris antennules carry two aesthetasc setae (lae, sae) sited on the third (III) and fourth (IV) segments. A similar pattern occurs in the akentrogonid species *Mycetomorpha vancouverensis* (**g**). In other Akentrogonida, the cyprid antennules have fewer setae and they never carry aesthetascs (**b–f**). The aesthetasc pattern in *Mycetomorpha* (**g**) and the near identical antennules in *Sylon* (**c**) and *Clistosaccus* (**d**) dovetail with the molecular phylogenetic analyses shown in Figs. 9.5 and 9.6 (see text). Lables: *I–IV* antennular segments 1–4, *bts* bifid terminal setae on segment 4, *lae* large aesthetasc on segment III, *qts* quadrifid terminal seta on segment 4, *sae* small aesthetasc on segment IV, *ts* terminal setae

recently united these taxa and Facetotecta into the class Thecostraca. His cladistic analysis was based on larval characters because the Facetotecta are known only from larval forms (y-nauplii and y-cyprids, see Martin et al. 2014). The Spears et al. (1994) study, based on 18S RNA data, supported the almost simultaneous claim of Jensen et al. (1994a, b) that Rhizocephala is the sister group to thoracican barnacles. All subsequent analyses, with much greater taxon sampling and much improved sequence data and analytical methods, have confirmed this Rhizocephala-Thoracica

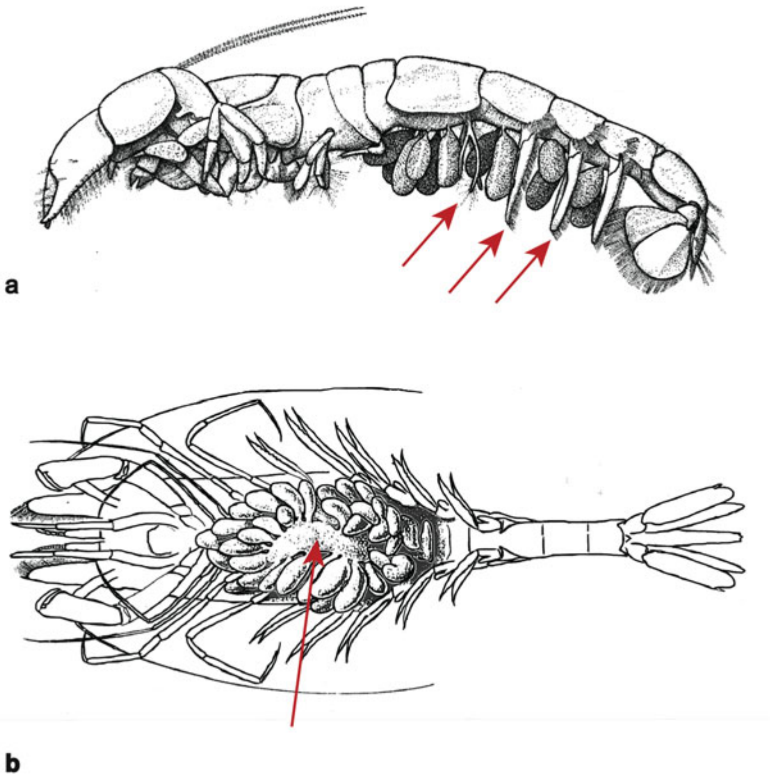

Fig. 9.9 Two enigmatic rhizocephalan genera. (**a**) *Polysaccus mediterraneus*, (**b**) *Mycetomorpha vancouverensis. Polysaccus* shows similarities both with Thompsoniidae (colonial externae, arrows) and Kentrogonida (cypris morphology in one of the two species). *Mycetomorpha*, previously of very uncertain position, is presently placed within the "Kentrogonida". It deviates much from kentrogonids in the sexual system but shows close similarity in cypris morphology

relationship (e.g. Pérez-Losada et al. 2008, 2012). However, the taxon sampling in Spears et al. (1994) was very limited and did not include any akentrogonid species. Thus both rhizocephalan monophyly and the intrinsic phylogeny of the taxon remained unanswered questions.

9.11 DNA-Based Phylogenies

The first DNA-based analysis on intrinsic rhizocephalan phylogeny was by Glenner et al. (2003), where mitochondrial and nuclear genes were used on species of Sacculinidae. They erected the monophyletic genus *Polyascus* Glenner et al., 2003, to comprise species with colonial externa that were formerly placed in

Sacculina. Following this study, Glenner and Hebsgaard (2006) performed the first DNA analysis with a broad sampling of taxa in both Kentrogonida and Akentrogonida (Fig. 9.5a). Their results, based on 18S RNA, confirmed several of the hypotheses of Høeg (1992a) and Glenner and Høeg (1994). They concluded that Rhizocephala is a monophyletic taxon, while all akentrogonid species were deeply nested within a paraphyletic Kentrogonida, in a pattern that also rendered Sacculinidae paraphyletic (Fig. 9.5a). As the only akentrogonid taxon, *Boshmaella japonica* Deichmann & Høeg, 1990, was placed outside Akentrogonida in the statistical analyses, but inside in the parsimony analysis. The support values for *B. japonica* were in both cases low, so Glenner and Hebsgaard (2006) suggested that Akentrogonida should preliminarily be considered as monophyletic, while the final phylogenetic position of *B. japonica* awaited future studies. *Boshmaella japonica*, however, is morphologically very similar to *Chthamalophilus delagei*, and it was in all analyses placed deep within Kentrogonida. The Glenner and Hebsgaard (2006) analysis therefore failed to support Bocquet-Védrine's (1961) assertion that Chthamalophilidae is an ancestral lineage within Rhizocephala. The position of akentrogonid forms within Sacculinidae was in full agreement with the hypothesis of Glenner and Høeg (1994) concerning the evolution of antennular penetration from a *Sacculina*-type kentrogon. In the Glenner and Hebsgaard (2006) tree, the paraphyletic Sacculinidae fell into two groups. One formed a monophyletic taxon comprising *Heterosaccus* Smith, 1906; *Loxothylacus* Boschma, 1928; and the "classical" species *Sacculina carcini*. The other was comprised of species from both "*Sacculina*" and the colonial genus *Polyascus*. The species-rich "*Sacculina*" is therefore para- or polyphyletic, and the full taxonomic consequences of this have yet to be played out.

9.12 Family Phylogeny Addressed

The analysis of Glenner and Hebsgaard (2006) left some key questions unanswered, mainly due to the relatively limited taxon sampling in Akentrogonida. The claim of Bocquet-Védrine (1961) of the primitive nature of the Akentrogonida was based solely on the chthamalophilid species, *Chthamalophilus delagei*. Unique among rhizocephalans, this species lacks a ramified rootlet system and has instead a large bladder-shaped expansion at the base of the stalk (Høeg 1992b). Based on this character, and observations on the very early development of the externa, Bocquet-Védrine (1961) considered *C. delagei* to be an ectoparasite, since the "bladder" was not supposed to penetrate the epithelium of the host barnacle. This notwithstanding, she later described a true rootlet system in the very similar species *Boschmaella balani* Bocquet-Védrine, 1967, and included both in the same family. Høeg et al. (1990) as well as Bresciani and Høeg (2001) used histology and transmission electron microscopy (TEM) on both these parasites. They demonstrated that the bladder-shaped "root" of *C. delagei* does indeed penetrate the host integument, but there was still a need to include this species in a phylogenetic analysis to effectively refute the original hypothesis (Bocquet-Védrine 1961, 1972; Newman et al. 1969; Bocquet-Védrine and Bourdon 1984). Moreover, Glenner and Hebsgaard (2006) analysed only one clistosaccid species, *Sylon hippolytes* Sars, 1870, and hence could make no statement on the relationship between this species and *Clistosaccus paguri*, which Rybakov and Høeg (1992) had placed in the same family based on putative synapomorphies in the cypris larvae.

Glenner et al. (2010) focused their analysis on the stated, unsolved questions within Akentrogonida, using kentrogonid species as the outgroup. Their conclusion was that *Boschmaella* Bocquet-Védrine, 1968, and *Chthamalophilus* Bocquet-Védrine, 1957, form a monophyletic Chthamalophilidae and *Clistosaccus* and *Sylon* a monophyletic Clistosaccidae and that both these families are nested within a monophyletic Akentrogonida (Fig. 9.5b). Thompsoniidae, represented by three of its four genera, was also monophyletic as previously hypothesised in the morphological cladistic analysis of Høeg and Lützen (1993). Accordingly, the claim of Bocquet-Védrine (1961) can finally be dismissed. Within Clistosaccidae, both *Clistosaccus* and *Sylon* are monotypic, and the adult parasites differ both biologically and morphologically (Lützen 1981; Høeg 1982). *Sylon hippolytes* Sars, 1870, infests caridean shrimps, while *Clistosaccus paguri* infests hermit crabs (Fig. 9.1). In *S. hippolytes*, the spermatogenesis of the male material injected by the cypris proceeds among the ovarian lobules, while *C. paguri*, sole among akentrogonids, has a single receptacle to receive the male (Høeg and Lützen 1995). In contrast to the absence of obvious similarities in externae morphology, the cypris larvae of *S. hippolytes* and *C. paguri* (Fig. 9.8) are nearly identical in terms of general shape, antennular morphology and the sensory lattice organs of the carapace, which in cirripedes often carry important phylogenetic information (Glenner et al. 1989; Jensen et al. 1994a, b). Cyprids of *C. paguri* and *S. hippolytes* can, in fact, only be separated by small but distinct differences in the setation pattern on the carapace. Thus, the study of Glenner et al. (2010) confirmed the value of cypris characters in rhizocephalan taxonomy.

9.13 The Present Phylogenetic Analysis

The present analysis of rhizocephalan phylogeny (Fig. 9.6) is the most comprehensive to date, with a broad taxon sampling in both Akentrogonida and the Kentrogonida and employing multiple genetic markers. It also includes the elusive *Mycetomorpha vancouverensis* (Mycetomorphidae), which was suggested by Glenner et al. (1989) and Høeg and Rybakov (1992, 1996a, b, 2007) as a morphological intermediate between kentrogonid and akentrogonid parasites. Therefore, all hitherto described rhizocephalan families, other than Duplorbidae, are represented in the tree by one or several species (Table 9.2, Fig. 9.6).

Disregarding *Mycetomorpha* (see below), the new tree structure (Fig. 9.6) is rather similar to the trees in Glenner and Hebsgaard (2006) and Glenner et al. (2010) (see Fig. 9.5a, b). All the akentrogonidan families remain monophyletic, but the clade comprising Chthamalophilidae, Clistosaccidae, Polysaccidae and Thompsoniidae (henceforward "Akentrogonida") has weak support. Nonetheless, it is clear that none of these akentrogonids sit near the base of the rhizocephalan tree. The weak support is primarily due to the unstable position of *Boschmaella* and *Chthamalophilus*; a better support of the "Akentrogonida" clade is obtained if these taxa are excluded (results not shown).

Within "Kentrogonida", both Peltogastridae and Sacculinidae are polyphyletic, the latter forming two separate clades ("A" and "B"). The pattern in Sacculinidae resembles Fig. 9.5a, with Sacculinidae "B" as sister group to a large clade of akentrogonid species. The polyphyly of both Sacculinidae and the genus *Sacculina* is hardly surprising. Most rhizocephalan species and genera were described as the result of a lifelong effort by the late Hildebrand Boschma from the Naturalis Museum in Leiden (Øksnebjerg 2000). This tremendous effort was unfortunately based only on very crude 20 μm celloidin sections and in many cases on only single specimens, some of which exist only as slides, while others have become lost or been separated from their identifying data. Moreover, sacculinids that showed distinct morphological deviation from the classical *Sacculina carcini* were assigned to separate genera, while the genus *Sacculina* remained a "catch all" taxon for the remaining species. In our analysis, the sacculinid genera *Heterosaccus* and *Loxothylacus* Boschma 1928 are both monophyletic, in agreement with the analysis based on DNA and cypris morphology in Glenner et al. (2008b). Both genera were erected using externa morphology, only (see Øksnebjerg 2000), so it is rather comforting to see them confirmed by wholly independent datasets. Obviously, much taxonomic work at both morphological and molecular levels is needed to construct a sound phylogeny for the more than 180 species of sacculinids.

9.14 Colonial Externae in Rhizocephalans

The situation where a female parasite has several, internally connected externae is here called colonial externae. Such externae normally reproduce only once and are thereafter lost, being replaced by a new generation of externae that are often more numerous in number (Høeg and Lützen 1995). From the phylogeny in Fig. 9.6, we conclude that species with colonial externae have evolved independently several times. All species of *Peltogasterella* Krüger, 1912; *Polyascus*; *Polysaccus* Høeg & Lützen, 1993; and Thompsoniidae are colonial. However, homoplasy in this character is even more frequent, because several other species not included here also possess colonial externae. The peltogastrid genera *Cyphosaccus* Reinhard, 1958, and *Boschmaia* Reinhard, 1958, are a particularly interesting case, where the sexual system is also in need of a close study (Høeg 1991). It would be interesting to investigate both the ontogeny and the adaptive value of colonial externae further too. We surmise that the low level of differentiation in the infecting vermigon larva facilitated this type of development (Glenner 2001). Other parasitic crustaceans do not show a comparable situation, and in other arthropods it is known only in the form of "polyembryony" in parasitoid hymenopterans (Beckage et al. 1990).

An important consequence of colonialism is that each female parasite hosts many males and must replace these when externae are regenerated. This is opposed to the few males present in rhizocephalan species with a single externa. Therefore, evolution of colonial externae may in part have been driven by selection pressures associated with the sexual system (Yamaguchi et al. 2014). An extreme consequence is seen in the thompsoniid *Diplothylacus* Høeg & Lützen, 1993. Here, the few externae that receive male cyprids first are wholly converted to house and provide for the males. These males supply sperm via the rootlet system to the remaining egg-producing externae (Jespersen and Lützen 1992). In other rhizocephalans, externae that fail to receive males will not grow and are cast from the host (Høeg and Lützen 1995).

9.15 The Elusive Mycetomorphidae

The monogeneric akentrogonid family Mycetomorphidae has two species. Most morphological details derive from *Mycetomorpha vancouverensis*, but the close similarity between the two species leaves little doubt that the genus is monophyletic. *Mycetomorpha* is one of the most enigmatic forms in all Rhizocephala. This is in part due to some obvious autapomorphies in its externa morphology (Figs. 9.1i and 9.9) but also because the sexual system and the cypris larvae seem to combine characters from both Akentrogonida and Kentrogonida. Therefore, *Mycetomorpha* has recently been speculated to occupy a basal position in Akentrogonida (Høeg and Rybakov 1996a, 2007). Both species of *Mycetomorpha* are always solitary on their hosts, which are North Pacific caridean shrimp. They have very rarely been sampled, and all previous information derives from Potts (1912), Reinhard and Evans (1951) and Høeg and Rybakov (1996a, b).

The *Mycetomorpha* externa has an unusual flattened shape fringed with marginal lobes (Figs. 9.1i and 9.9). Only externae in some Lernaeodiscidae species have a somewhat similar shape. The mantle aperture, open only in the adult, is canal shaped. The male organs are numerous bodies in the mantle tissue, and there is strong, indirect evidence they are injected through the integument by cypris antennular penetration, just as has been directly observed in clistosaccids and thompsoniids (Reinhard and Evans 1951; Høeg and Rybakov 1996a). Høeg (1991) suggested that the male organs in *Mycetomorpha* are homologous to those of Chthamalophilidae. However, the spermatogenic bodies in chthamalophilids are evaginated into the mantle cavity, where they float free as "spermatogenic islands", and the male cells are surrounded by a female epithelium and cuticle (Høeg et al. 1990). In contrast, the spermatogenic bodies in *Mycetomorpha* remain in the mantle until sperm release, and they are surrounded by an epithelium and cuticle that belongs to the male itself (Høeg and Rybakov 1996a), so there is no obvious homology to the chthamalophilid islands. The cypris larvae of *Mycetomorpha* exhibit a surprising similarity to those of the kentrogonid species, especially in the antennules, where they have a pattern of aesthetascs identical to that of kentrogonid species (Fig. 9.8). In other akentrogonids, such aesthetascs are lacking altogether, and the antennular setation is much simplified (Høeg and Rybakov 1996b; Glenner et al. 1989, 2010).

9.16 *Mycetomorpha* and Akentrogonid Monophyly

The phylogeny in Fig. 9.6 does not place *Mycetomorpha* with the other “Akentrogonida”. Instead it is, with high support, situated lower in the tree as sister group to the kentrogonid species *Peltogaster paguri* and *Lernaeodiscus porcellanae* Müler, 1862, and this entails that that Akentrogonida sensu Høeg and Rybakov (1992) is diphyletic. Furthermore, if *Mycetomorpha* employs antennular penetration to implant males into the juvenile female, this mechanism has evolved at least twice, viz. in *Mycetomorpha* and in the stem line to the remaining “Akentrogonida” (Chthamalophilidae, Clistosaccidae, Thompsoniidae and Polysaccidae). The precise mechanism of antennular penetration is not known, but Høeg (1985b) suggested it to be some kind of chemical mechanism, which makes its evolution also in the *Mycetomorpha* lineage even more interesting. On the other hand, the phylogeny in Fig. 9.6 indicates that loss of antennular aesthetascs in rhizocephalan cyprids is a synapomorphy for an “akentrogonid” clade without *Mycetomorpha* (Fig. 9.8).

The caridean hosts of *Mycetomorpha* are somewhat surprising, considering that almost all basal kentrogonid forms (Peltogastridae and Lernaeodiscidae) are parasites of Anomura. However, one very poorly known peltogastrid species, *Trachelosaccus hymenodorae* Sars, 1879, also infest caridean shrimp (Høeg and Lützen 1985).

9.17 Remaining Taxa and Future Sampling

9.17.1 Kentrogonid Families

Our analysis included species from all existing families of Kentrogonida, but some are still very poorly represented. Many more species must be sampled for molecular analysis from Sacculinidae, not least from *Sacculina* itself. Several species of Sacculinidae spend all their life (even as larva) in freshwater. They are the only truly freshwater cirripedes, and tracing their evolution would be particularly interesting. The monophyly of the Lernaeodiscidae must be tested by inclusion of several additional species of its four genera. Many peltogastrid genera are also missing, including the poorly known species of *Cyphosaccus*, *Boschmaia* and *Trachelosaccus* Boschma, 1928, whose sexual systems are suspected to present interesting features (see Høeg and Lützen 1985; Høeg 1991).

9.17.2 Parthenopeidae

This family contains only *Parthenopea* Kossman, 1874, with two species (Lützen et al. 2009), and our unpublished data shows the existence of at least three additional ones. The genus was, until recently, placed in Peltogastridae, although it clearly deviates in many respects from other members of this taxon. This caused Rybakov and Høeg (2013) to erect the new family Parthenopeidae for the genus. This move is supported by the molecular-based phylogenies, all of which place *Parthenopea* away from the paraphyletic assemblage of Peltogastridae and instead as a close relative to sacculinid species (Figs. 9.5 and 9.6). The cyprids of *Parthenopea* are peculiar in having paired compound eyes, while these structures are otherwise absent in rhizocephalans other than some species of Thompsoniidae (Glenner and Hebsgaard 2006; Rybakov and Høeg 2013). Presence of compound eyes is a ground pattern feature of both Cirripedia and Thecostraca, being found in cyprids of Acrothoracica and Thoracica and also in the cypris-like larvae of Ascothoracida and Facetotecta (Fig. 9.10). In Rhizocephala, their presence only in *Parthenopea* and some thompsoniids, both nested deep in the phylogeny (Fig. 9.8c), indicates that evolution of this type of eye was subject to homoplasy. Compound eyes are image forming, even if the number of ommatidia is very low in cyprids (Hallberg and Elofsson 1983). It is interesting that they are found in cirripede species from a wide variety of habitats and highly diverse settlement substrata (including parasitic forms); however, there are unfortunately no studies of compound eyes function in cyprids (Martin et al. 2014).

The position of *Parthenopea* also highlights another larval feature. Nauplii of Peltogastridae and Lernaeodiscidae are always surrounded by a hollow cuticular flotation collar, while this structure is lacking from all sacculinid nauplii (Collis and Walker 1994; Høeg et al. 2004). From the presence of a similar collar in nauplii of

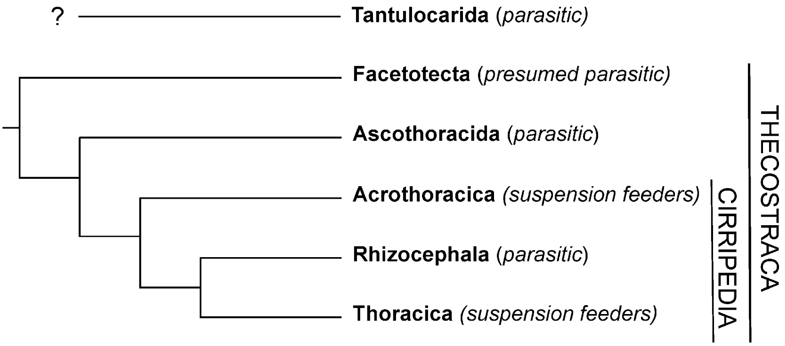

Fig. 9.10 The phylogeny of Crustacea Thecostraca based on molecular evidence (Pérez-Losada et al. 2009). Taxa known or presumed (Facetotecta) to be parasitic have evolved separately three times. An advanced metamorphosis involving a slug-shaped stage without appendages and segmentation has evolved separately in Facetotecta (ypsigon larva) and Rhizocephala (vermigon and trichogon larvae). The position of the parasitic Tantulocarida remains uncertain

Parthenopea (Rybakov and Høeg 2013), we suggest that it evolved in the rhizocephalan stem line but was then lost at least twice, viz. in the lineages leading to the two sacculinid clades. All Akentrogonida sensu Høeg and Rybakov (1992) hatch and are released as cyprids, so the character cannot be scored for these forms.

9.17.3 Duplorbidae

This family, missing from our analysis, contains five species in three genera infesting isopods (including parasitic forms) and cumaceans. They always occur as multiple externae per host, but it is uncertain whether this represents true, internally connected colonial externae. The only in depth morphological descriptions were given by Rybakov and Høeg (1992) and Høeg and Rybakov (1996b). Duplorbids are very rarely sampled, or at least rarely reported, but it can be stated with high confidence that they form a monophyletic taxon together with Chthamalophilidae. Both families have a mantle aperture in the form of a mesenteric canal. Furthermore, the male organ forms spermatogenic islands that are evaginated from the mantle to float free in the mantle cavity (Høeg 1991, 1992b; Rybakov and Høeg 1992). However, several obvious apomorphies also indicate that the three genera contained in Chthamalophilidae are monophyletic. These include that the spermatogenic islands split into secondary islands that subsequently enter spermatogenesis (Bocquet-Védrine 1961; Høeg et al. 1990), while spermatogenesis proceeds in the original undivided island in species of Duplorbidae. In addition, chthamalophilid cyprids lack a thorax and can only move by walking on the antennules, while duplorbid cyprids have both a thorax and natatory thoracopods (Glenner et al. 1989; Høeg and Rybakov 1996b). By themselves, the duplorbid species present few, if any, putative apomorphies (aside from infesting peracarids), and they might be a paraphyletic assemblage allied to a monophyletic Chthamalophilidae.

9.17.4 Polysaccidae

This family contains one genus with two species, both with colonial externae (Fig. 9.9). Cyprids of *Polysaccus japonicus* Høeg & Lützen, 1993, have a unique antennular structure, which clearly is adapted for the antennular penetration mechanism known to exist in clistosaccids and thompsoniids (Fig. 9.8). The position of *P. japonicus* in our tree (Fig. 9.6) is therefore fully consistent with this larval trait. The phylogenetic status of the other species, *Polysaccus mediterraneus* Caroli, 1929, is debatable because its cypris larvae very much resemble those of Kentrogonida (Høeg and Rybakov 2007). Both the presence of colonial externae and their specific shape are potential synapomorphies between thompsoniids and polysaccids, but due to low support of some nodes in our tree (Fig. 9.6), we cannot yet decide on this issue.

9.17.5 *Pirusaccus*

This monotypic genus is, at present, the only rhizocephalan not assigned to a family. *Pirusaccus* Lützen, 1985, differs conspicuously from other "akentrogonids" with colonial externae (Polysaccidae, Thompsoniidae) by having the male organs organised as spermatogenic islands in a mantle cavity. This peculiar type of male organ is therefore a putative synapomorphy for a clade comprising Duplorbidae and Chthamalophilidae. *Pirusaccus* is a deep-sea form sampled only once, and nothing is known about the larvae (Lützen 1985). Similar to the cases of *Mycetomorpha* and *Parthenopea*, *Pirusaccus* illustrates how species with a unique combination of characters (e.g. club-shaped colonial externae and spermatogenetic islands) may yield potentially important insight into character evolution in rhizocephalan barnacles.

9.18 Evolution of Parasitism in Thecostraca and Cirripedia

Within Thecostraca, parasitism is found in several taxa, and this begs the question whether some of these parasitic forms have a common origin. Due to the morphological reductions seen in most thecostracan parasites (Høeg et al. 2009), this problem can only be solved using molecular phylogenetic techniques.

9.18.1 *Thoracican Parasitism*

Within Thoracica there are several forms with a parasitic or semiparasitic mode of life (Høeg et al. 2005; Y. Yusa personal communication), but radical morphological specialisation for parasitism is known only from *Rhizolepas* Day, 1939, infesting annelids, and *Anelasma* Darwin, 1852, parasitising lantern sharks. *Anelasma* has a remarkable transitory morphology between a setose feeding, pedunculated barnacle and a parasitic form. Like some epibiotic pedunculated barnacles, *Anelasma* lacks shell plates altogether and is in traditional systematics placed close to these forms. However, based on DNA data, Rees et al. (2014) recently showed that it is a close relative of *Capitulum mitella* Linneaus, 1758, an upper intertidal barnacle found on rocky shores, and with which *Anelasma* has no gross physical similarity whatsoever. *Anelasma* retains thoracopodal cirri and an alimentary canal, but neither is functional. Instead, nourishment is obtained from the host by a system of rootlets that penetrate into the shark tissue in a manner that parallels that of rhizocephalans (Ommundsen et al. 2016). *Anelasma* is therefore a remarkable transitory form between setose feeding and parasitism (Rees et al. 2014). Divergence from the *Capitulum* lineage appears to have happened more than 120 million years ago but evolution into parasitism was in all probability quite recent.

9.18.2 Facetotecta, Ascothoracida and Rhizocephala

Within Thecostraca, three major clades (Facetotecta, Ascothoracida and Cirripedia: Rhizocephala) are known or believed to be obligatorily parasitic (Høeg et al. 2009). Ascothoracida are parasitic in echinoderms and cnidarians and Rhizocephala in crustaceans, while Facetotecta are known only as larval stages (y-nauplii and y-cyprids). Recently, Glenner et al. (2008a) found that facetotectan y-cyprids metamorphose into a slug-shaped stage, the ypsigon, which in many respects resembles the rhizocephalan vermigon. With adult Facetotecta and their suspected hosts being completely unknown, it was a real possibility that facetotectan and rhizocephalan parasitism had a common origin. However, Pérez-Losada et al. (2009) demonstrated that Facetotecta is the sister group to an Ascothoracida + Cirripedia clade, while Rhizocephala is nested within the latter (Fig. 9.10). Moreover, Høeg et al. (2009) found many apomorphies in cypris structure that support a monophyletic Cirripedia, confirming the result of Thompson (1836) based on nauplii only. Thus, molecular phylogenetics was instrumental in showing that parasitism in facetotectans, ascothoracidans and rhizocephalans, as well as the remarkable similarity between the ypsigon and vermigon stages arose independently.

9.19 Tantulocarida

Tantulocarida presents another enigma. Being parasites of various crustaceans, tantulocarid species have a remarkably complex life cycle, and their infecting larval stage (called *tantulus*) has at least some superficial similarity to a rhizocephalan kentrogon, such as the presence of a stylet (Boxshall and Lincoln 1987). Recently, Petrunina et al. (2014) used molecular data to argue that tantulocarids may be nested within Thecostraca, but their excellent TEM data also shows that the kentrogon and the tantulus do not exhibit any convincing homologies. More morphological information on the life cycle and the mechanism of host infection is needed, but it is likely that tantulocarids represent yet another case of highly specialised parasitism within either Thecostraca or a clade comprising thecostracans and tantulocarids.

9.20 Families of the Rhizocephala

The latest major revisions of the Rhizocephala were by Høeg and Rybakov (1992), Boyko and Harvey (2000), Øksnebjerg (2000), and Rybakov and Høeg (2013). Below we survey the existing families. Many of the taxa are para- or polyphyletic in the present analysis (Fig. 9.6), but we refrain from further revisionary steps until more species have been analysed.

ORDER AKENTROGONIDA HÄFELE, 1911

Diagnosis in Høeg and Rybakov (1992). Polyphyletic.

Family Chthamalophilidae Bocquet-Védrine, 1961

Type genus: *Chthamalophilus* Bocquet-Védrine, 1957
Diagnosis in Høeg and Rybakov (1992). Monophyletic.
Genera: *Bocquetia* Pawlik, 1987; *Boschmaella* Bocquet-Védrine, 1968; *Chthamalophilus* Bocquet-Védrine, 1957

Family Clistosaccidae Boschma, 1928

Type genus: *Clistosaccus* Lilljeborg 1860
Diagnosis in Høeg and Rybakov (1992). Monophyletic.
Genera: *Clistosaccus* Lilljeborg 1860, *Sylon* Sars, 1870 (both monotypic, but our unpublished molecular data suggests that *Sylon* may be comprised of several distinct species)

Family Duplorbidae Høeg & Rybakov, 1992

Type genus: *Duplorbis* Smith, 1906
Diagnosis in Høeg and Rybakov (1992). Monophyly not yet tested by molecular data.
Genera: *Arcturosaccus* Rybakov & Høeg, 1992; *Cryptogaster* Bocquet-Védrine & Bourdon, 1984; *Duplorbis* Smith, 1906

Family Mycetomorphidae Høeg & Rybakov, 1992

Type genus: *Mycetomorpha* Potts, 1912
Diagnosis in Høeg and Rybakov (1992). Monophyletic.
Genera: *Mycetomorpha* Potts, 1912
Remarks. Although formally placed in the Akentrogonida, this family with only two species is shown by the present analysis to be nested within the paraphyletic assemblage of kentrogonidan Rhizocephala.

Family Polysaccidae Lützen & Takahashi, 1996

Type genus: *Polysaccus* Høeg & Lützen, 1993
Diagnosis in Lützen and Takahashi (1996). Monophyly of the two described species dubious, but not yet tested (see Høeg and Rybakov 2007).
Genera: *Polysaccus* Høeg & Lützen, 1993

Family Thompsoniidae Høeg & Rybakov, 1992

Type genus: *Thompsonia* Kossmann, 1872
Diagnosis in Høeg and Rybakov (1992). Monophyletic.
Genera: *Diplothylacus* Høeg & Lützen, 1993; *Jensia* Boyko & Williams in Hiller et al., 2015; *Thompsonia* Kossmann, 1872; *Thylacoplethus* Coutière, 1902. Note that Hiller et al. (2015) corrected the genus *Pottsia* to *Jensia*, because the former name was preoccupied.

ORDER KENTROGONIDA DELAGE, 1884

Diagnosis in Høeg and Rybakov (1992). Polyphyletic.

Family Lernaeodiscidae Boschma, 1928

Type species: *Lernaeodiscus* Müller, 1862
Diagnosis in Høeg and Lützen (1985). Monophyly uncertain, as only one species analysed here.
Genera: *Lernaeodiscus* Müller, 1862; *Septodiscus* Van Baal, 1937; *Triangulopsis* Guérin-Ganivet, 1911; *Triangulus* Smith, 1906

Family Parthenopeidae Rybakov & Høeg, 2013

Type genus: *Parthenopea* Kossmann, 1874
Diagnosis in Rybakov and Høeg (2013). Monophyletic.
Genera: *Parthenopea* Kossmann, 1874

Family Peltogastridae Lilljeborg, 1860

Type genus: *Peltogaster* Rathke, 1842
Diagnosis in Høeg and Lützen (1985). Polyphyletic.
Genera: *Angulosaccus* Reinhard, 1944; *Boschmaia* Reinhard, 1958; *Briarosaccus* Boschma, 1930; *Cyphosaccus* Reinhard, 1958; *Dipterosaccus* Van Kampen & Boschma, 1925; *Galatheascus* Boschma, 1929; *Ommatogaster* Yoshida & Osawa in Yoshida et al., 2011; *Peltogaster* Rathke, 1842; *Peltogasterella* Krüger, 1912; *Pterogaster* Van Baal, 1937; *Septosaccus* Duboscq, 1912; *Temnascus* Boschma, 1951; *Tortugaster* Reinhard, 1948; *Trachelosaccus* Boschma, 1928

Family Sacculinidae Lilljeborg, 1860

Type genus: *Sacculina* Thompson, 1836
Diagnosis in Øksnebjerg (2000). Polyphyletic.
Genera: *Drepanorchis* Boschma, 1927; *Heterosaccus* Smith, 1906; *Loxothylacus* Boschma, 1928; *Polyascus* Glenner et al., 2003; *Ptychascus* Boschma, 1933; *Sacculina* Thompson, 1836; *Sesarmaxenos* Annandale, 1911

9.21 Concluding Remarks

Almost two centuries after Thompson (1836) placed Rhizocephala in the Cirripedia, molecular phylogenetic studies have finally provided a framework for tracing evolution within this remarkable taxon of metazoan parasites. Species-level taxonomy is severely impeded by the difficulty of comparing new material with existing descriptions. Therefore, whenever possible, DNA data should be sampled, when new rhizocephalan species are described or existing ones sampled again. Furthermore, histological sections of the externa are critical for correlation with existing descriptions. By these means we can hope for a revised taxonomy that also better reflects actual phylogenetic relationships within Rhizocephala (Kobayashi et al. 2018). The considerable amount of data concerning larval structure and development in rhizocephalans can now be plotted onto increasingly robust phylogenies and thus yield both biological insight and potential morphological apomorphies for the monophyletic clades. An even more interesting enterprise is to map details of the reproductive system onto the tree. While all rhizocephalans have separate sexes, there are variations in sex determination, the number and location of the dwarf males, reproductive output and longevity of the host-parasite system (Høeg 1991, 1995; Yamaguchi et al. 2014). Combining the new phylogenetic framework with ecological data will yield insight into how and why this variation evolved, just as has recently been done for thoracican barnacles (Yusa et al. 2012; Lin et al. 2015). Another important avenue is to understand host-parasite evolution within rhizocephalans. All species of Kentrogonida, and many Akentrogonida (all Clistosaccidae, most Thompsoniidae), infest decapods, and non-decapod hosts occur only in akentrogonid species nested deep within rhizocephalans. Therefore, decapods were clearly the original hosts for Rhizocephala. Consequently, it is an interesting problem why some extant rhizocephalan taxa are confined to a single host group, while other taxa, such as “Akentrogonida” in general and Thompsoniidae in particular, have “jumped” large taxonomic gaps (Table 9.2). Finally, we now have some solid basis for speculating how the ancestral rhizocephalan evolved from their nonparasitic barnacles ancestors (Glenner and Høeg 2002).

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Chapter 10
The Ecological Significance of Parasitic Crustaceans

Paul C. Sikkel and Rachel L. Welicky

Abstract Despite that aquatic parasite diversity and abundance likely surpasses that of terrestrial parasites, our understanding of aquatic parasites lags far behind our knowledge of terrestrial parasites. This is undoubtedly attributable to our being terrestrial primates and the associated logistical challenges of studying most aquatic environments. However, with improving technology that allows for more extended exploration of aquatic environments and the continued maturation of host-parasite ecology and functional biodiversity as fields of inquiry, our understanding of parasitic crustaceans is rapidly extending beyond identification and description of life cycles to describing the role of parasites in ecosystems. Both field and laboratory studies have demonstrated that parasitic organisms play critical roles at the individual, population and community levels. In this chapter, we explore these roles for parasitic isopods and copepods in particular and highlight recent studies that employ current methodologies in ecological research such as molecular and stable isotope analyses. This chapter should demonstrate to readers that there are still far more questions than answers about the role of parasitic Crustacea in aquatic systems, but based on what we know today, we can say they are likely one of the most critical players in aquatic ecosystem dynamics.

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10.1 Introduction

The major challenge facing aquatic ecologists is to understand the complex biological interactions that occur within and between associated aquatic habitats. Most research on the biocomplexity of aquatic ecosystems focuses on the macrofauna that is easily seen and surveyed by human observers. Smaller organisms are often neglected, and their species richness has until recently been underappreciated (Plaisance et al. 2009; Leray and Knowlton 2014). Indeed, most ecological research has proceeded with the implicit assumption that small organisms have few interactions with larger organisms, except as food items for some functional feeding guilds. This assumption persists despite the fact that parasitism is the most common animal lifestyle and thus the most common biological interaction (Hudson et al. 2006). Parasites make up about 40% of the Earth's biodiversity (Hatcher and Dunn 2011). For some phyla, the diversity of parasites is greater in aquatic than terrestrial environments (Poulin and Morand 2000), and parasites make up the majority of animals in some aquatic ecosystems. For example, within the Capricorn section of the Great Barrier Reef, it has been estimated that over 20,000 parasite species are associated with 1000 fish species (Rohde 1976).

By definition, parasites have negative effects on hosts. However, the extent to which this translates into population- and community-level effects depends on the nature of the individual effects, the abundance and biomass of parasites and other environmental factors that influence interactions between and consequences of host-parasite interactions. As with most areas of ecology, our understanding of community ecology, host-parasite interactions, and especially the interface between the two in aquatic and especially marine ecosystems lags far behind terrestrial systems (Hatcher and Dunn 2011). Because of their substantial biomass, they can influence aquatic community interactions in many ways (Kuris et al. 2008). Directly, they can produce a significant increase in trophic efficiency (Arias-González and Morand 2006), link density, and connectivity in food webs (Amundsen et al. 2009), and by consuming host tissue, they could collectively over time contribute significantly to host carbon transfer. Indirectly, parasites may influence community interactions by altering host movement and other behavioural patterns (Huebner and Chadwick 2012a, b; Sato et al. 2012). The historical omission of parasites from community ecology appears to stem from their small size ("out of sight, out of mind"), a basic assumption of ecological models that larger organisms eat smaller organisms, and the fact that most ecologists receive no training in and have limited understanding of relevant aspects of parasitology and host-parasite interactions (Hatcher and Dunn 2011). The realisation that a complete understanding of aquatic community ecology requires understanding the role of parasites in the system creates an opportunity for the small, but increasing, number of parasite ecologists to reshape the future direction of research in aquatic ecology (reviewed by Poulin et al. 2016).

Among known parasites, approximately 70,000 species live on the external surface of their host. These ectoparasites are distributed among five animal phyla and infest vertebrate and invertebrate hosts in terrestrial, freshwater and marine ecosystems (Poulin 2007). Ectoparasites offer a convenient and promising starting point for the integration of parasites into aquatic community descriptions. Unlike internal parasites, they can often be seen with the naked eye and, thus, can be collected and counted without sacrificing the host. Perhaps most importantly, in contrast to internal parasites, certain ectoparasites can impact community composition through their role both as “micropredators” and “microprey”. Although historically overlooked in ecology (Raffel et al. 2008), the importance of parasites as micropredators is increasingly being recognised and has been well-documented in some terrestrial systems (e.g. Raffel et al. 2008; Rohr et al. 2009). For example, North American moose [*Alces alces* (Linnaeus, 1758)] are subject to winter ticks [*Dermacentor albipictus* (Packard, 1869)], ectoparasites whose periodic population peaks often lead to adult and calf mortality—calves may lose up to twice their total blood volume to tick feeding in one season (Bergeron and Perkins 2014). Moose-host mortality is highest for sick and weakened individuals (Rines 2015). Ticks may also increase the benefit of partial migration for European cervids, as tick [*Ixodes ricinus* (Linnaeus, 1758)] density is lower in the migratory summer grazing areas (Qviller et al. 2013).

Such extensive work on ectoparasite-host interactions in terrestrial systems creates an opportunity for comparative studies in aquatic systems. Aquatic ectoparasitic invertebrates include the monogeneans and crustaceans. The latter, which constitute the focus of this book, are the most diverse and include representatives from the Copepoda, Isopoda, Amphipoda, Branchiura and Tantulocarida. This chapter aims both to review what is currently known about the ecology of parasitic crustaceans by synthesising relevant literature in parasitology and aquatic ecology and to chart the course of future study in this field. Crustacean parasitologists should come away inspired by the contributions their work can make to the science of aquatic ecology, and aquatic ecologists should come away with an appreciation for the important role crustacean parasites play in the ecological systems. Students should find ample fodder for thesis and dissertation projects. Given that the research focus of the authors is on host-parasite interactions in marine reef fishes, we emphasise the ecology of parasitic isopods and copepods in marine systems. We examine separately individual- and population-level phenomena for isopods (gnathiids and cymothoids) and for copepods and conclude with a combined section on community-level considerations and further suggestions for future research. An overview summary of what is known about the host-parasite ecology of each group covered in this chapter is provided in a series of tables (Tables 10.1, 10.2 and 10.3).

10.2 Isopoda

Arthropod ectoparasites include approximately 14,000 species from 400 genera that feed largely or exclusively on vertebrate blood and body fluids (Graça-Souza et al. 2006). The Isopoda are one of the largest and most diverse orders of crustaceans, with 89% of members inhabiting marine environments (Kensley 1998). Like most marine

Table 10.1 Gnathiid quick references

Effects of gnathiids[a,b]			
Host physiology	Host behaviour	Population dynamics	Community dynamics
Larger hosts are more susceptible to infestation (Grutter 1995; Sikkel et al. 2000)	Gnathiids cause hosts to interact with cleaners (Grutter 2001)	Micropredatory corrallanid isopods kill injured fish at night (Stepien and Brusca 1985)	Cleaner fishes and cleaner shrimps consume gnathiids (Grutter 2001, 2002; Grutter et al. 2003; Becker and Grutter 2004; Cheney and Cote 2005)
Reduced haematocrit (Jones and Grutter 2005) and increased corticosteroids (Triki et al. 2016) found in infected hosts	Interactions with cleaners vary with sex of host fish and habitat (Sikkel et al. 2000)	Gnathiids impact growth and survivorship of settlement-stage reef fish (Grutter et al. 2008, 2017; Jones and Grutter 2008; Penfold et al. 2008; Artim et al. 2015; Sellers et al. 2019)	Gnathiid infestation on host fishes increases on coral reefs without cleaner wrasses (Grutter et al. 2018)
Injured hosts are more susceptible to gnathiid infestation (Jenkins et al. 2018a)	Interactions with cleaners is correlated with diel changes in gnathiid activity (Côté and Molloy 2003; Sikkel et al. 2004)	Gnathiid "superinfections" kill adult fishes (Mugridge and Stallybrass 1983; Hayes et al. 2011)	Gnathiids are consumed by diurnal and nocturnal microcarnivorous fishes (Penfold et al. 2008; Grutter and Feeney 2016; Artim et al. 2017)
	Female yellowtail damselfish compensate for missed cleaning opportunities associated with dawn spawning (Sikkel et al. 2005)	Gnathiids rely heavily on olfactory cues to find hosts (Nagel et al. 2008; Sikkel et al. 2011)	Some host fishes are more commonly infested than others (Jones et al. 2007)
	Infestation by gnathiids reduces competitive performance in juvenile territorial damselfish (Sellers et al. 2019)		Host fish species exhibit high variation in susceptibility (Coile and Sikkel 2013)
	Nocturnal migration in French grunt reduces exposure to gnathiids (Sikkel et al. 2017)		Invasive red lionfish are not highly susceptible to gnathiids in either their native or introduced range (Sikkel et al. 2014)

(continued)

Table 10.1 (continued)

Effects of gnathiids[a,b]			
Host physiology	Host behaviour	Population dynamics	Community dynamics
	Gnathiid infestation impacts components of cognitive performance in damselfish (Binning et al. 2018)		Gnathiids transmit blood parasites (Davies et al. 1994, 2009; Curtis et al. 2013)
			Gnathiid activity and size distribution vary with time of day (Grutter 1999; Grutter et al. 2000; Sikkel et al. 2006, 2009; Welicky et al. 2013, 2018a)
			Gnathiids avoid and are consumed by live hard coral (Artim and Sikkel 2013)
			Effect of lunar periodicity on gnathiid activity at Lizard Island, GBR (Grutter et al. 2000) but not the Eastern Caribbean (Welicky et al. 2013)
			Stable isotopes help reveal the role of parasites and consumers of parasites in carbon transfer within coral reef ecosystems (Demopoulos and Sikkel 2015; Jenkins et al. 2018b)

[a] Includes one example from Corallanids
[b] Some examples may fit more than one category

invertebrates, they appear to be most diverse in coral reef systems, where it is estimated that over 5000 species have yet to be described (Kensley 1998). Among the described marine isopod species, 9% are parasites of fishes (Williams and Bunkley-Williams 1996). There are three families of temporary fish parasites (Gnathiidae, Corallanidae and Aegidae) and one family of obligate parasites (Cymothoidae), totalling over 500 species of known fish-parasitic isopods (Poore and Bruce 2012). In addition, approximately 795 (7.7%) of all isopod species, from the families Dajidae, Bopyridae and Cryptoniscidae, are parasitic on other crustaceans (Williams and Boyko 2012).

Table 10.2 Cymothoid quick references

Effects of cymothoids			
Host physiology	Host behaviour	Population dynamics	Community dynamics
Smaller length and mass compared to uninfected fish (Adlard and Lester 1994; Östlund-Nilsson et al. 2005; Fogelman et al. 2009; Parker and Booth 2013; Roche et al. 2013a, b)	Males do not mouthbrood (Fogelman et al. 2009)	Inversely correlated with host population and aggregation size (Welicky and Sikkel 2014)	Blue and brown chromis typically do not live at the same locality (Williams et al. 1982)
Flesh-infesting parasites (Fogelman and Grutter 2008), but not gill chamber-infesting parasites are correlated with host size (Welicky et al. 2019). Male and female, but not juvenile, mouth-infesting parasites are correlated with host size (Welicky et al. 2019)	Reduced agonistic interactions with heterospecifics (Meadows and Meadows 2003)	Seasonal fluctuations in prevalence (Aneesh et al. 2013)	Pederson shrimp only successful organism to clean off mancae (Bunkley-Williams and Williams 1998b)
Reduced gonad and ova size (Fogelman et al. 2009)	Reduced territory size (Meadows and Meadows 2003)	Host survival reduced (Adlard and Lester 1994; Bunkley-Williams and Williams 1998a; Athanassopoulou et al. 2001; Fogelman and Grutter 2008)	Stable isotope signatures of parasites are similar to that of hosts (Pinnegar et al. 2001; Demopoulos and Sikkel 2015)
Failure to mouthbrood (Fogelman et al. 2009)	Reduced feeding (Meadows and Meadows 2003)		Stable isotope signatures of infected and uninfected fish diets similar (Parker and Booth 2013; Welicky et al. 2017b)
Increased number of pectoral beats (Östlund-Nilsson et al. 2005)	Predator escape response associated with infected host size (Binning et al. 2014)		
Increased metabolic demands (Östlund-Nilsson et al. 2005; Binning et al. 2013)	Altered diel migratory activity patterns associated with infection (Welicky and Sikkel 2015)		
Increased drag (Östlund-Nilsson et al. 2005; Binning et al. 2013)			

(continued)

Table 10.2 (continued)

Effects of cymothoids			
Host physiology	Host behaviour	Population dynamics	Community dynamics
Lateralisation/side bias (Roche et al. 2013a, b)			
Altered otoliths chemistry (Heagney et al. 2013)			
Gill damage and reduced gill growth (Stephenson 1976)			
Anaemia (Horton and Okamura 2003)			
Increased susceptibility to secondary infection (Rameshkumar et al. 2013)			
Reduced muscle condition (Welicky et al. 2018b)			

10.2.1 Gnathiids

Gnathiid isopods (Fig. 10.1) are common mobile benthic invertebrates found in all oceans, from tide pools to the deep ocean. Excellent reviews of their biology can be found in Smit and Davies (2004) and Tanaka (2007) (also see Chap. 5 of this volume). These small (1–3 mm), highly mobile "ticks of the sea" are only parasitic during each of their three larval phases (instars) and thus are considered "protelean" parasites. Because of their temporary association with hosts, they may also be considered "micropredators" (Lafferty et al. 2008). Larval gnathiids emerge from the substratum and find a host fish, and when engorged on blood and body fluids, return to the substratum and moult into the next larval stage (Smit and Davies 2004; Tanaka 2007). After the final blood meal, third-stage larvae metamorphose into adults that live in the benthos and do not feed. Females retain eggs in a brood pouch (marsupium) until the hatching of post-embryonic first-stage juveniles that live in the benthos and begin seeking a fish host (Manship et al. 2011). The gnathiid life cycle in a coral reef system is depicted in Fig. 10.2. Their strong association with the benthos and the potential for predation on both their feeding and free-living stages has important ecological implications. While terrestrial blood-feeding arthropods include multiple classes, orders and families, gnathiids, corallanids and aegiids (all of which are isopods) are, along with leeches, the only mobile blood-feeding specialists in the marine environment, although certain cirolanid isopods may include fish blood when attacking injured fishes (e.g. Stepien and Brusca 1985). In spite of their ecological similarities to terrestrial blood-feeding parasites, and the fact that the biomass of gnathiids likely rivals that of all terrestrial blood-feeding arthropods combined, during the past 5 years, 20 times more papers were published

Table 10.3 Copepod quick references

Effects of copepods			
Host physiology	Host behaviour	Population dynamics	Community dynamics
Reduced growth rate (Finley and Forrester 2003; Boxshall 2005; Johnson et al. 2004)	"Sluggish" activity (Heckmann 2003)	Seasonal fluctuations associated with host migratory patterns (Brooker et al. 2007)	Parasites escape predation by transferring from host to predator of host (Connors et al. 2008)
Respiratory problems (Finley and Forrester 2003; Heckmann 2003; Boxshall 2005)	Parasite abundance greater in reproducing than non-reproducing clams (Taskinen and Saarinen 1999)	Parasites undergo vertical migration for feeding, timed with diel activity times of other organisms (Heuch et al. 1995)	Parasite transmission between cultured and wild populations, varies with temperature and currents (Brooks 2005; Frazer 2009)
Anaemia (Boxshall 2005)	Secondary sex traits positively associated with parasite intensity (Brønseth and Folstad 1997)	Influence host susceptibility (Pino-Marambio et al. 2007)	Parasites are known to be infected with viruses and may be able to transmit them (Dunlap et al. 2013)
Discoloration (Heckmann 2003) or change in colour (Folstad et al. 1994)		Physical and chemical cues aid parasites in locating hosts (Mordue and Birkett 2009)	Infection increases host mortality when combined with other environmental variables (i.e. increased fish density and decreased number of refuges) (Forrester and Finley 2006)
Compromised immunity (Tully and Nolan 2002)		Parasites increase host-locating activities when hosts are nearby (Poulin et al. 1990)	Infection significantly reduces recruitment (Krkošek et al. 2013)
Production of smaller larvae (Palacios-Fuentes et al. 2012)		Infestation levels related to light level and water depth (Hevrøy et al. 2003)	Parasite developmental rate is temperature dependent (Costello 2006)
Location of infection varies by host size (Kabata and Cousens 1977)			Parasites sensitive to acidic seepage waters and hydrogen sulphide (Heckmann 2003)
Stressed clam hosts more susceptible to parasitism (Saarinen and Taskinen 2005)			Cleaner fish can be used as a form of biological control to remove parasites (Heckmann 2003)

(continued)

Table 10.3 (continued)

Effects of copepods			
Host physiology	Host behaviour	Population dynamics	Community dynamics
Reduced/altered cardiorespiratory function (Behrens et al. 2014)			Some cleaner fishes remove larger parasites, but an increasing number of smaller parasites keeps density of parasites constant (Gorlick et al. 1987)
Uneven/aggregated infestation across fins, may influence swimming performance (Loot et al. 2004)			N^{15} signature of parasite and host are similar in some species and may vary by parasite developmental stage, parasites depleted in ^{13}C (Deudero et al. 2002)

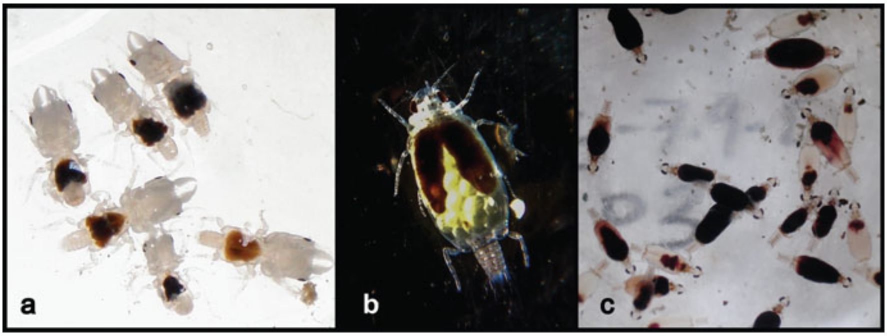

Fig. 10.1 (**a**) Male, (**b**) female and (**c**) fed larval-stage gnathiid isopods (*Gnathia marleyi* Farquharson, Smit & Sikkel, 2012), respectively. Images (**a**) and (**c**) © A.M. Coile; image (**b**) © M.D. Nicholson

on ixodid ticks and 60 times more on culicid mosquitoes alone than on gnathiid isopods. Indeed, there are entire journals devoted to the biology of ticks and mosquitoes. This is likely driven by their impacts on human and livestock hosts.

10.2.1.1 Potential Effects on Individual Hosts

Up until the mid-1990s, research on gnathiids was largely limited to species descriptions and descriptions of life cycles from specimens collected in tidal pools or obtained from ship-based benthic samples, mostly in temperate and polar seas (Smit and Davies 2004; Tanaka and Nishi 2008). The few studies with ecological implications focused on effects on individual hosts. By using piercing mouthparts to

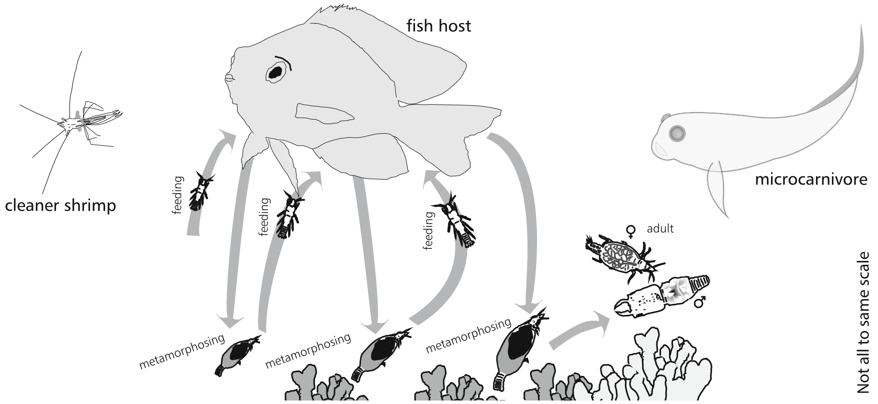

Fig. 10.2 The gnathiid life cycle includes three larval stages, each of which has a feeding phase and a resting phase. Each stage is subject to predation. Gnathiid predators may favour one or more gnathiid life cycle stages over others. The resting phase juveniles and reproductive adults reside on substrate. Image © J.M. Artim and P.C. Sikkel

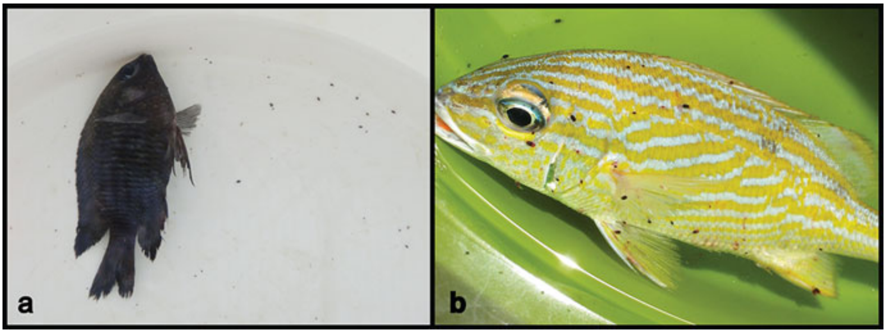

Fig. 10.3 (**a**) Longfin damselfish, *Stegastes diencaeus* (Jordan & Rutter, 1897) and (**b**) French grunt *Haemulon flavolineatum* (Desmarest, 1823), with super infestation of gnathiid isopods. Image (**a**) © P.C. Sikkel; image (**b**) © E.R. Brill

feed on host body fluids, gnathiids can affect individual hosts in multiple ways (Table 10.1). In the most extreme cases, blood loss can result in the death of the host (Paperna and Por 1977). While this is extremely difficult to document under natural field conditions, it has been documented for caged adult-size fishes in the ocean (Mugridge and Stallybrass 1983; Sikkel unpublished data; see Fig. 10.3) and under captive conditions for both adult (Hayes et al. 2011) and early juvenile-stage hosts (e.g. Grutter et al. 2008; Artim et al. 2015; Sellers et al. 2019; see Fig. 10.4). Even when blood loss is not sufficient to cause death, sublethal blood loss can result in reduced haematocrit (Jones and Grutter 2005). While high infestations by gnathiids could be considered a source of stress, Grutter and Pankhurst (2000) found no relationship between levels of gnathiid infestation and corticosteroid stress hormones or glucose in captive thicklip wrasse, *Hemigymnus melapterus* (Bloch,

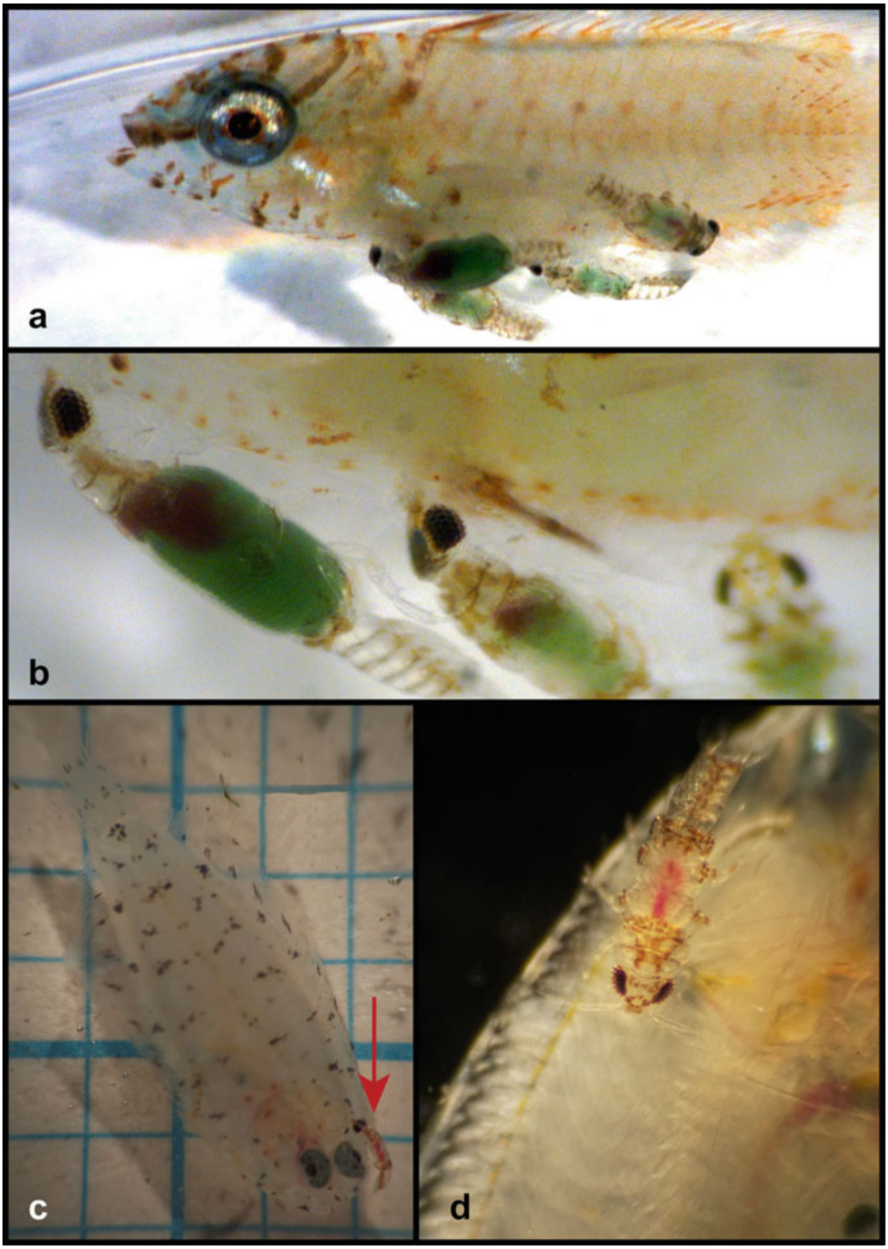

Fig. 10.4 Microphotographs of the larval fish and gnathiids attached to them. (**a**) *Starksia* sp. fish larvae showing four of the five attached feeding gnathiid larvae with the fifth gnathiid attached on the opposite side of the fish, (**b**) close-up of gnathiids attached to the ventral surface of the *Starksia* sp. larvae, (**c**) *Bothus* sp. fish larvae with the attached gnathiid (arrow), (**d**) close-up of the gnathiid attachment on this *Bothus* sp. fish. (Artim et al. 2015). Images © J.M. Artim

1791). As with any lesion, wounds caused by gnathiid piercing structures can facilitate infections (Honma and Chiba 1991; Bunkley-Williams and Williams 1998a; Heupel and Bennett 1999). Finally, gnathiids may transmit potentially harmful microorganisms to their hosts. Blood-borne parasites known or believed to be transmitted by gnathiids include haemogregarine-like apicomplexan protozoans, reported in gnathiids from the United Kingdom, South Africa, Australia and the Caribbean (Davies 1982, 1995; Davies et al. 1994; Smit and Davies 1999; Davies and Smit 2001; Smit et al. 2006; Curtis et al. 2013; Cook et al. 2015; also see Chap. 7 of this volume). In addition to apicomplexans, various developmental stages of possible filarial nematodes, flagellates, fungal structures and viral-like conditions of fishes have also been reported from gnathiid larvae (see Smit and Davies 2004; Davies et al. 2009). While further research is required to determine the extent to which gnathiids serve as vectors of microparasites and the effects of such parasites on their hosts, the likelihood and extent of such vector-mediated effects on hosts will depend on factors that influence gnathiid distribution and abundance.

Gnathiids can also influence the behaviour of their hosts (Table 10.1). In both temperate and tropical reef systems, many species of fish visit cleaner fishes and shrimps that consume ectoparasites from the body of the host fishes (termed “clients” when visiting cleaners). These interactions are among the best studied symbiotic interactions in the ocean, and the literature on them is vast and will not be reviewed here (see, e.g. Limbaugh 1961; Hobson 1971; Losey 1972; Gorlick et al. 1978; Côté 2000; Côté and Soares 2011; Vaughan et al. 2017 for reviews). Cleaning only appears to occur during the day (see Bonaldo et al. (2015) for reports of apparent nocturnal cleaning), and in tropical systems, gnathiid isopods are the primary food item consumed by cleaner fishes from the bodies of clients (Losey 1974; Grutter 1996, 2002; Arnal and Côté 2000; and see below). On shallow Caribbean reefs, variation in host fish (client) interaction time with cleaners corresponds with variation in daytime gnathiid loads on hosts (Chambers and Sikkel 2002; Sikkel et al. 2004), both being highest at dawn. For territorial tropical damselfish, females must leave their territory to lay eggs in nests located in territories of egg-guarding males. Spawning in male nests occurs at dawn (Thresher 1984; Petersen 1995; Sikkel and Kramer 2006) when both daytime gnathiid loads and cleaning activity are highest. Thus, spawning conflicts with and reduces opportunities for females to visit cleaning stations. Female yellowtail damselfish, *Microspathodon chrysurus* (Cuvier, 1830), appear to compensate for this by interrupting spawning and visiting cleaners near the male’s nest and further by increasing interactions with cleaners in their own territory upon returning following the completion of spawning (Sikkel et al. 2005). Finally, in captivity, fishes that are exposed to gnathiids exhibit increased interactions with cleaners compared to unexposed control fish, indicating a direct effect of gnathiids on host behaviour (Grutter 2001).

One of the most peculiar behaviours among reef-dwelling fishes is the mucus cocoons produced by some parrotfishes at night while resting. The benefits of such cocoons have been the subject of debate. Gnathiids tend to be most active between dusk and dawn (Grutter 1999; Chambers and Sikkel 2002; Côté and Molloy 2003; Sikkel et al. 2006, 2009; Santos and Sikkel 2017), a time when diurnally active hosts are sedentary and thus easy target for gnathiids. In a recent experimental study, parrotfishes with intact cocoons and with cocoons "popped" were exposed to high densities of gnathiids. Fish with intact cocoons received significantly fewer gnathiid bites, suggesting that cocoons were an effective barrier to gnathiid infestation (Grutter et al. 2011). In the Caribbean, fishes that undergo nocturnal migrations off the reef into seagrass beds are also the most susceptible to gnathiid infestation (Coile and Sikkel 2013). Migration begins just as gnathiid activity is increasing, and fishes return the next morning as gnathiid activity is subsiding. Fishes in the night-time feeding habitat experience significantly lower gnathiid densities than if they were to remain on the reef at night (Sikkel et al. 2017), thereby decreasing their overall exposure to gnathiids. However, the hypothesis that gnathiid infestation plays a causal role in this migratory behaviour needs to be more thoroughly investigated.

Gnathiids have recently been shown to influence measures of behavioural performance in small reef fishes. For example, Binning et al. (2018) found that Ambon damselfish, *Pomacentrus amboinensis* Bleeker, 1868, collected from patch reefs from which cleaner wrasses had been removed (and thus where per capita gnathiid burden on fish was lower—Grutter et al. 2018), performed worse in a visual discrimination test than conspecifics from patch reefs with cleaners. Visual discrimination performance was also impaired in damselfish experimentally infected with gnathiids. More recently, Sellers et al. (2019) showed that juveniles of the Caribbean damselfish *Stegastes leucostictus* (Castlenau, 1855) experimentally infested with only 2–3 gnathiids were significantly more likely to lose to uninfested fish in competition over shelter sites.

10.2.1.2 Population Level Effects on Hosts

While no studies have directly examined the effects of gnathiids at the host population level, any of the individual-level effects described above has the potential to cause host morbidity and mortality which could influence host population structure and dynamics. The extent of such effects are likely to be a function of gnathiid abundance or, more specifically, the ratio of gnathiid to host biomass and the susceptibility of individual hosts and host species to gnathiid infestation. Although regarded as host generalists, differences in the preference of the parasite, resistance by the host and/or differences in parasite and host behaviour affecting encounter rates influence patterns of host infestation. Gnathiids on coral reefs not only appear more active between dusk and dawn but also exhibit size-specific variation in activity peaks (Grutter 1999; Sikkel et al. 2006, 2009). In the Eastern Caribbean, this reflects an ontogenetic niche shift in time within a single species (Sikkel et al. 2009). Thus, different size classes of gnathiids differ in their encounter rates with different potential hosts (which also vary in diel activity patterns). For example, first-stage *Gnathia marleyi* Farquharson, Smit and Sikkel, 2012 are most active at dawn with low levels of activity during the remainder of the day (see Farquharson et al. 2012). They are therefore more likely to encounter site-attached diurnal species, as well as nocturnal species that "rest" on the reef during the day. In contrast, larger *G. marleyi* with activity peaks near midnight are more likely to encounter diurnal species that rest on the reef at night. Although *G. marleyi* infests at least 20 different host species, field experiments suggest that species of grunts and snappers, which are nocturnally-active and site-attached in aggregations during the day, were most susceptible (Coile and Sikkel 2013).

On the Great Barrier Reef, Ferreira et al. (2009) documented a similarly broad range of hosts for *Gnathia aureamaculosa* Ferreira and Smit, 2009 in Ferreira et al. (2009). Sequencing of blood meals from two gnathiid species collected from light traps further revealed that while gnathiids fed on a wide range of hosts, certain hosts were more frequently infested (Jones et al. 2007). However, these data were not compared with the availability (relative abundance) of different potential hosts near collection sites. Thus, in both the Caribbean and Indo-Pacific, there is evidence that certain hosts may be more subject to infestation than others and that different hosts may impart different fitness consequences on gnathiids (Coile and Sikkel 2013; Sikkel et al. 2014). Additional studies that examine patterns of host infestation relative to host availability are needed. Furthermore, it remains unclear what combination of host resistance and parasite preference influences host susceptibility and whether the most susceptible species are also the most heavily exploited by gnathiids.

Some of the observed among-host variation in infestation may be attributable to injury. Minor injuries associated with conspecific aggression, or escape from predation, are common among fishes. Jenkins et al. (2018a) found that for all three host species tested, the probability of infestation by gnathiids was significantly greater for those individuals that were subject to experimental injury similar to those observed in the wild. However, among infested fish, injury did not influence the intensity of the infestation. A possible explanation for this is that injured fishes release more chemical cues attractive to gnathiids and that gnathiids themselves create wounds, such that an injured fish and an infested one are both more attractive to other gnathiids. This study did not examine effects of feeding on injured versus non-injured hosts on gnathiids.

Of the individual host effects cited above (summarised in Table 10.1), effects on early life history stages would appear to have the greatest potential to impact host population sizes. Super infestations by terrestrial blood-feeding arthropods are known to contribute to morbidity and mortality of hosts (e.g. Bergeron and Perkins 2014). One of the most recent developments in research on the ecology of gnathiids is their potential effect on early life history stages of fishes. In tetrapod hosts, newborn stages are still much larger than the parasites, requiring high levels of infestation to significantly harm them. In contrast, reef fishes are "born" at much smaller sizes and are therefore much more susceptible to injury or mortality from even a single ectoparasite. Larvae evade reef-based parasites through their pelagic larval stages, and escape from "micropredator" ectoparasites has been hypothesised as a major selective force behind pelagic larval stages in reef fishes (Strathmann et al. 2002; Sun et al. 2012; Grutter et al. 2017). However, the transition between habitats still occurs at a small size and is associated with significant changes in morphology and exposure to reef-based predators. Predation on early post-settlement stages can have significant effects on recruitment to reefs, and, consequently, the density and dynamics of reef fish populations (e.g. Carr and Hixon 1995; reviewed by Hixon 2015). The source of this predation on fish larvae at time of settlement is believed to be small piscivorous fishes. Could micropredatory ectoparasites such as gnathiids also impose significant predation pressure on settling reef fishes? Nocturnal settlement of larval reef fishes is thought to reduce risk of predation by diurnally active piscivorous fishes (Carr and Hixon 1995). However, night-time settlement exposes transitional fishes to high gnathiid activity on coral reefs (Grutter 1999; Sikkel et al. 2006, 2009). Recent studies on Lizard Island, Great Barrier Reef, Australia (Grutter et al. 2008, 2017; Jones and Grutter 2008; Penfold et al. 2008) and in the eastern Caribbean (Artim et al. 2015; Sellers et al. 2019) have shown that as few as one gnathiid can kill a settlement-size reef fish (Fig. 10.4). Sellers et al. (2019) found that for some species, mortality risk remained high even after a doubling in size, but for others mortality risk dropped rapidly as the fish grew post-settlement, suggesting that impacts may vary among species. The extent of micropredation by gnathiid isopods on settlement-stage and juvenile fishes among various species and localities in the wild, the conditions under which it occurs, and its consequences at the population and community level clearly deserve further attention.

10.2.1.3 Environmental Factors Influencing Gnathiid Population Size and Distribution

Multiple studies have demonstrated variation in gnathiid abundance across multiple spatial scales. Variation in abundance over large spatial scales (among reefs) has been shown in both Australia (Grutter and Poulin 1998; Jones and Grutter 2007) and the Caribbean (Cheney and Côté 2005; Welicky et al. 2013). Differences in ectoparasite abundance, including gnathiids, have also been found between zones within a reef. Sikkel et al. (2000) reported higher ectoparasite loads on yellowtail damselfish (*Microspathodon chrysurus*) occupying shoreward sections of spur and groove reefs compared with seaward sections. Perhaps most intriguing is the high degree of variation that occurs over smaller spatial scales. A consistent finding in studies on gnathiid abundance, regardless of the type of trap used, is high variation within sampling sites (Grutter 1999; Chambers and Sikkel 2002; Sikkel et al. 2006, 2009, 2011). Even among traps set within a few metres of each other at sites with overall high densities of gnathiids, many traps have no gnathiids, while others capture hundreds. In cases where such “jackpots” are associated with fish-baited traps (rather than unbaited emergence or light traps), the fish usually dies within 24 h (see Fig. 10.3). The suite of factors responsible for variation in gnathiid abundance on any spatial scale is relatively unknown. In South Africa, the abundance of *Gnathia africana* Barnard, 1914 does not seem correlated with tidal dynamics and tide zonation (Welicky et al. 2018a). However, with improvements in trapping techniques and improved understanding of the performance of those techniques in estimating gnathiid population sizes (Artim and Sikkel 2016), our capacity to identify these factors has greatly improved. Below we review what little has been discovered on the topic.

Host Quality and Availability

Given that gnathiids both depend on and influence their hosts, an understanding of the impact gnathiids have on host populations and reef communities requires a comprehensive understanding of the suite of factors that influence gnathiid population parameters, including the hosts that are infested by different gnathiid life history stages, and the consequences of that infestation on the survivorship, growth, reproductive output and immigration/emigration of the gnathiids. Although studies of terrestrial and freshwater ectoparasites have shown a positive relationship between host and parasite abundance, no such studies have been conducted for gnathiids.

While many studies have examined aspects of host susceptibility to parasitic infestation and the effects parasites have on components of their hosts' fitness (Fitze et al. 2004; Marzal et al. 2005), fewer studies have examined the effects that different potential hosts have on components of their parasites' fitness (Giorgi et al. 2004; Nagel and Grutter 2007; Khokhlova et al. 2010). For gnathiids, two studies have examined the fitness consequences of feeding on different host species. Nagel and Grutter (2007) found that *Gnathia aureamaculosa* from the Great Barrier Reef that fed on more preferred hosts (Labridae) had higher survival rates than those that fed on less-preferred hosts (Apogonidae). Subsequently, Coile et al. (2014) found that female *Gnathia marleyi* in the Caribbean that fed on more susceptible hosts (Haemulidae and Lutjanidae) produced larger but not more offspring than those that fed on less susceptible hosts (Holocentridae and Acanthuridae), suggesting a link between host choice and at least one measure of female reproductive success. This correlation suggests that host choice during the first and or second feeding may have influenced the number of offspring produced. Studies that examine a broader range of species, hosts and measures of reproductive success are clearly needed.

Benthic Habitat

Given that the majority of the gnathiid life cycle is spent in association with the substratum, it seems obvious that attributes of benthic habitat have a strong influence on the distribution and abundance of gnathiids. Gnathiids have been collected from a wide range of substrata, including mud, rock, algae, seagrass, sponge, coral rubble, shells, polychaete worm tubes and even wood, at depths from the intertidal to more than 3500 m (e.g. Monod 1926; Holidich and Harrison 1980; Cohen and Poore 1994; Smit et al. 2003; Tanaka and Nishi 2008; Cacabelos et al. 2010; Svavarsson and Bruce 2012; Quattrini and Demopoulos 2016; Welicky et al. 2018a). Different life history stages may have different habitat requirements. First- and second-stage gnathiids simply need to feed while avoiding being fed upon. In contrast, third-stage larvae that have recently fed on a host need to find other third-stage larvae or already metamorphosed adults and places suitable for reproduction. For some of the better-studied species, it is clear that adults or preadults occupy a very narrow range of habitats, for example, a single species of sponge or polychaete worm tube (e.g. Smit et al. 2003). If such breeding microhabitats are patchy and brood release is somewhat synchronous, this would result in locally high and highly variable abundance. Indeed, extremely high loads on caged fish retrieved at dawn in Caribbean studies are associated with disproportionately high numbers of first-stage juveniles (Sikkel et al. 2006, 2009; Coile and Sikkel 2013).

Fig. 10.5 Praniza 3 gnathiid isopod being consumed by a coral polyp in the lab (Artim and Sikkel 2013). Images © J.M. Artim

Coral-reef gnathiids appear to be more generalist in their habitat associations than temperate species (Jones and Grutter 2005), although this may simply be due to the fact that more attention has been paid to individual species in temperate areas. The myriad substrates in which gnathiids have been reported from in earlier studies do not include live stony coral, although dead coral, including coral rubble, has (Svavarsson and Bruce 2012). In an experimental study examining substrate preferences by a coral-reef gnathiid in the Caribbean, Artim and Sikkel (2013) found that *Gnathia marleyi* preferentially associated with sponge, dead coral and algae, but avoided bare substrate (no cover) and live coral, which can consume gnathiids (Fig. 10.5; also see "Predation" below). In a more recent study, Santos and Sikkel (2017) found that fish-baited traps set on live coral collected fewer gnathiids than those set on dead standing coral or coral rubble. These findings suggest that live coral may not be suitable habitat for gnathiids (or any other parasitic crustaceans) and could influence the distribution and abundance of gnathiids on coral reefs. Even if substrate other than live coral is abundant, sufficiently high coral cover could constitute a major source of mortality for gnathiids.

As for many other benthic and demersal marine organisms, conspecifics are an important resource and may therefore be an important source of attraction. To our knowledge, only one experimental study has examined the role of conspecifics as attractants for gnathiids. Upton (1987a) demonstrated that larval stages of the temperate gnathiid, *Paragnathia formica* (Hesse, 1864), were attracted to the odour of mud containing conspecific males. Clearly more studies of this nature across a broader spectrum of species are needed.

Gnathiids do not have a pelagic larval phase, and unlike cymothoids which remain on hosts for life, gnathiids typically require a period of minutes to hours to complete feeding (Smit and Davies 2004). Thus, it seems surprising that some gnathiid species appear to occur over a broad geographic range (e.g. Monod 1926; Wägele 1987; Farquharson et al. 2012). Strong currents, especially those generated by storms such as hurricanes, would appear to be one means of dispersal over such distances. However, highly mobile host fishes may also be a source of dispersal: a gnathiid attaching to a host for even 30 min could be taken hundreds of metres from the site of infestation. After metamorphosis, it could then be transferred again via another such host. For example, Caribbean grunts and snappers undergo nocturnal migrations of hundreds of metres between reef and sand/seagrass habitat and are highly susceptible to gnathiids. Such migrations could therefore result in significant nocturnal “trafficking” of gnathiids between habitats (Sikkel et al. 2017). The longer host-association times and broad geographic distribution of species such as *Gnathia trimaculata* (Coetzee, Smit, Grutter & Davies, 2009) that infest highly mobile sharks (Coetzee et al. 2009; Ota et al. 2012) provide further evidence for the role of hosts in distribution of gnathiids over large spatial scales. Determining the extent of host attachment times, along with molecular identification of host blood meals (Jones et al. 2007), will help us understand the roll of host movement in determining the distribution and local abundance of gnathiids. Recent studies suggest that parasites with broader host ranges also have broader geographic ranges and reach greater local abundance (e.g. Krasnov et al. 2004; Blasco-Costa et al. 2015). Gnathiids would be ideal for testing predictions of this hypothesis.

10.2.1.4 Predation

Cleaner wrasses in the Indo-Pacific and cleaner gobies in the tropical Atlantic feed heavily on gnathiids and thus have the potential to influence gnathiid population size. While these have been shown to reduce gnathiid loads on caged fishes (Grutter 1999), the broader-scale effects on gnathiid population size and the resulting effects of gnathiid removal on hosts per se have not been determined. Moreover, in temperate intertidal systems, gnathiid abundance does not seem particularly high despite that females appear more fecund than their coral reef counterparts, and predation by cleaners does not occur. This prompts the question of what predators might regulate gnathiid population sizes in systems other than coral reefs (Welicky et al. 2018a). Thus, a better understanding of the totality of factors that influence gnathiid population sizes and direct manipulation of gnathiid population sizes under controlled field conditions (i.e. standardisation of recruitment and emigration) are needed to assess effects on host population parameters in the field.

Because gnathiids lack a pelagic phase, predation occurs when they are in the benthos, slightly above the benthos while seeking a host or while attached to the host. Most of what is known about predation on gnathiids occurs during host attachment. Losey’s comparative studies in Hawaii and Puerto Rico (Losey 1974) were the first to report the presence of gnathiids as food items for cleaner fishes and consequently sparked interest in the ecology of gnathiids on coral reefs. This work inspired further studies of diets in the Indo-Pacific cleaner wrasses by Grutter (e.g. Grutter 1995, 1996), Caribbean cleaner gobies by Côté (e.g. Arnal and Côté 2000; Whiteman and Côté 2002), as well as Mediterranean cleaner wrasses (Arnal and Morand 2001). These studies demonstrated that gnathiids are a primary food item of cleaner fishes and thus cleaner fishes have the potential to regulate gnathiid population sizes (Côté 2000). Much less is known about other sources of predation on gnathiids, particularly in colder latitudes. Some cleaner shrimps eat gnathiids (Becker and Grutter 2004; Demopoulos and Sikkel 2015), and gnathiids have been found in the guts of some microcarnivorous fish species (reviewed by Grutter 2002). However, gnathiids are likely to be missed or recorded as "miscellaneous/ unidentified" in routine gut content analyses due to a lack of familiarity and identification by most fish ecologists. Thus, how commonly non-cleaning specialists eat gnathiids and how this consumption compares with that of cleaners remains poorly understood. However, recent work in the tropical Pacific suggests that facultative cleaners may consume as many gnathiids as specialist cleaners (Grutter and Feeney 2016).

Microcarnivorous fishes (other than those that engage in heterospecific cleaning) will likely target free-living stages of gnathiids, while herbivorous or detritivorous fishes will likely ingest them incidentally. It is known that some physically-flexible, microcarnivorous hosts of gnathiids will consume them off their own bodies (Smit and Davies 2004). Shoaling species that engage in intraspecific cleaning (e.g. Sikkel 1986; Sikkel and Smit 2018) may also consume them off each other, providing both a means of protection against gnathiids as well as a source of food.

A recent study by Artim et al. (2017) is the only study to compare rates of consumption of gnathiids by non-cleaning microcarnivores with that of known cleaners. Given that gnathiids on shallow reefs in the Eastern Caribbean are most active at night, Artim et al. (2017) compared consumption of free-living gnathiids by nocturnal microcarnivores with early morning consumption by Caribbean cleaning gobies [*Elacatinus evelynae* (Böhlke & Robins, 1968)]. Only 4–5% of the gut content of cardinal fishes (Apogonidae) and grunts (Haemulidae), respectively, had gnathiids, but in both squirrelfish and soldierfish (Holocentridae) 26% had gnathiids in their gut contents (typically 1–2 per fish). Nearly all (93%) of cleaning gobies sampled had consumed gnathiids. While nocturnal microcarnivores ate far fewer gnathiids per individual, they were much more abundant than cleaning gobies and thus collectively could have an equal or greater impact on gnathiid populations (Fig. 10.6).

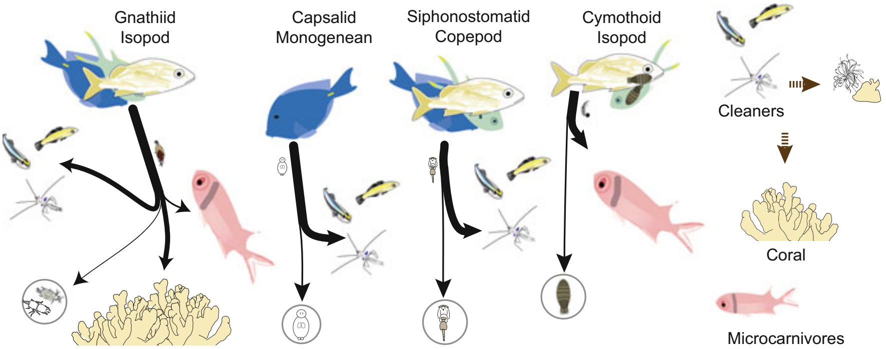

Fig. 10.6 Potential fates of four ectoparasite groups expressed as flow of carbon (solid arrows) from three host fish species to cleaners, predators and to the next generation of parasites (shown in the solid circles). Nutrient flow from detrital faecal matter is shown as dashed arrows. Image © J.M. Artim, A.M. McCammon, R.L. Welicky, and P.C. Sikkel

To our knowledge, only one study has examined predation of gnathiids by invertebrates other than cleaner shrimps. Artim and Sikkel (2013) demonstrated that coral polyps will consume gnathiids (Fig. 10.5). Thus, the myriad filter-feeding (e.g. polychaetes) and mobile carnivorous (e.g. amphipods) invertebrates associated with the benthos have strong potential to influence gnathiid population sizes and deserve further study. However, because of the means of consuming prey, quantifying or even documenting predation by these organisms will be more complicated than doing so for fishes.

10.2.1.5 Temporal Variation in Gnathiid Activity

The suite of factors that influence gnathiid spatial distribution and abundance can also affect temporal dynamics over both ecological and evolutionary time scales. Published studies on activity patterns over the course of a day (diel) and during a lunar cycle are limited mostly to coral reef systems, while studies on seasonal variation are limited to temperate gnathiids (e.g. Amanieu 1963). Diel activity patterns of gnathiid-host interactions have been studied at sites in the Caribbean and Indo-Pacific. As noted above, gnathiid activity on shallow tropical reefs in the Eastern Caribbean and Indo-Pacific (Great Barrier Reef and central Philippines) is greatest during crepuscular and nocturnal periods. Gnathiids that emerge at night are also significantly larger than those that emerge during daylight hours (e.g. Grutter 1997a, 1999; Côté and Molloy 2003; Sikkel et al. 2009, 2011; Santos and Sikkel 2017). On the Great Barrier Reef and in the Philippines where species diversity is higher, it is unclear whether differences in the size of gnathiids collected during different times of day can be attributed to among- or within-species differences in activity. However, in the Eastern Caribbean, where species diversity is low, diel ontogenetic niche shifts were documented within a single species (Sikkel et al. 2009). Perhaps the most surprising result from this study was that sex ratios from third-stage larvae collected at night versus dawn were distinctly opposite. In particular, females were virtually absent from dawn samples, while males appeared in both night and dawn samples. These data suggest that males remain on hosts longer and/or are more likely to be active near dawn than females and thus are also at increased risk of predation by cleaners. Since male gnathiids of some species are known to guard harems of females, sexual selection may be stronger on males to obtain larger blood meals that would enable them to compete more effectively for females. This result is not unexpected if we assume that males and females experience different trade-offs between resource acquisition, risk of predation and future mating opportunities and therefore have different patterns of activity (e.g. Jormalainen et al. 2001; Welbergen 2006; reviewed by Clutton-Brock and Parker 1992; Clutton-Brock 2007). The physiological mechanisms that regulate such within-species transitions deserve further study. Further study is also needed for gnathiids of temperate marine ecosystems. In the only study of diel activity in temperate species, the temperate intertidal species, *Gnathia africana*, appears most active during morning and afternoon, and tidal cycles do not appear to influence diel activity (Welicky et al. 2018a). These findings further demonstrate the complexity and variability in the activity patterns between species and environments and provide encouragement for additional comparative studies.

Why gnathiid activity in the tropics seems to vary among sizes or size classes remains unclear; however, the trade-off between the need to obtain a blood meal while avoiding predation likely plays a role (Grutter 2002). Cleaner fishes are active only during the day. Like other microplanktivores that have been examined, cleaner wrasses in the Indo-Pacific preferentially feed on larger gnathiids (Grutter 1997b). This may also hold true for Caribbean cleaner fishes. Larger gnathiids also require longer to feed. Thus, in order to obtain an adequate blood meal before daylight, larger gnathiids should become active as soon as cleaner fishes become inactive and should become inactive before dawn. However, this would not explain why the smallest gnathiids are inactive at night and are most active at dawn. One possible explanation is that dawn represents the optimal solution to the trade-off between finding a host (that may be facilitated by light) and minimising predation risk. Unlike larger gnathiids, smaller gnathiids can obtain a complete blood meal within the dawn period. An alternative explanation is that smaller gnathiids are more susceptible to predation by larger, nocturnal zooplankters that are more abundant at night (e.g. Yahel et al. 2005) or that there is competition among gnathiids for hosts.

The fact that so much gnathiid activity occurs at night suggests that gnathiids on tropical reefs must typically locate hosts during times of low ambient light, when many hosts are immobile and or under shelter. However, virtually nothing is known of the sensory mechanisms involved in locating hosts. Gnathiids have large, compound eyes that may enable them to see well at night. However, immobile hosts may still be difficult to locate when hidden. Gnathiids also have long antennae that may enable them to locate hosts using chemical cues (Nagel et al. 2008). In a laboratory study conducted to examine the role of visual and olfactory cues by gnathiids, Nagel et al. (2008) recorded behavioural responses in aquaria of third-stage gnathiids collected during the day and night from sites on the Great Barrier Reef, Australia. Gnathiids were presented with fish mucus versus a control substance and separately with a moving versus still model of a fish. Although there was a tendency for nocturnal gnathiids to respond first to the mucus versus the control when tested at night, the difference was not significant, although sample size was small. Gnathiids collected during the day showed no such trend, regardless of the light level during testing, nor did nocturnally captured gnathiids tested during daylight. In contrast, only daytime-captured gnathiids tested during daylight showed a strong response to moving versus stationary fish models. Their laboratory findings suggest that important sensory cues may vary among gnathiid species, depending on when they are typically active.

In their Caribbean field study, Sikkel et al. (2011) found that experimental traps providing both visual and olfactory cues from live fish attracted significantly more gnathiids than traps providing only visual cues or control traps (empty or with a rock), which were not significantly different from each other. In another experiment, traps providing both cues and only olfactory cues attracted significantly more gnathiids than empty control traps and were not significantly different from each other. These findings suggest that during nocturnal and crepuscular periods, visual cues provided by resting or slow-moving fish are not sufficient to attract gnathiids, while olfactory cues alone are. In contrast to Nagel et al. (2008), this field experimental study included all feeding stages of a single species. Most recently, Santos and Sikkel (2017) working in the Philippines found that fish-baited traps that provided only olfactory cues attracted significantly more gnathiids than control traps. However, these traps attracted multiple species that have yet to be identified. Given that olfactory cues appear to be important, studies isolating the molecules gnathiids use to locate hosts are needed.

To our knowledge, only three studies have investigated the role of lunar periodicity on gnathiid isopod activity. Two of these were carried out on the Great Barrier Reef. On Heron Reef, Jacoby and Greenwood (1988) found that zuphea (unfed) gnathiids were most abundant in emergence traps during new and full moon. Off Lizard Island, Grutter et al. (2000) observed a similar pattern and further noted that the number of unfed gnathiids captured during the day was also greater than at night. Welicky et al. (2013) examined data collected over multiple years using two different sampling techniques at multiple sites in the Caribbean. While they found strong differences associated with sampling sites, there was no consistent effect of lunar phase on the number of gnathiids captured. Given that both the strength of currents and ambient light vary with both lunar phase and sampling locality, future studies should examine these variables independently.

Annual population fluctuations have been reported for two temperate intertidal species, *Paragnathia formica* which burrows in mud (Amanieu 1963; Upton 1987b) and sponge-dwelling *Elaphognathia cornigera* (Nunomura, 1992), which occupies sponges (Tanaka and Aoki 2000; Tanaka 2003). This is associated with periods of limited female emergence but continuous occurrence of males during some months and a larval developmental halt during winter. In a study examining the different size classes of *Gnathia africana* collected over time, the greatest number of first-stage gnathiids were observed in autumn and winter compared to summer, but spring data were not available for comparison. Nevertheless, the results of this study may reflect the fact that female gnathiids release their larvae more often during particular times of year (Welicky et al. 2018a). This is not surprising given the large temperature fluctuations typical of temperate intertidal habitat.

10.2.2 Cymothoids

Cymothoid isopods are obligate fish parasites, occurring in nearly all aquatic environments, with the vast majority inhabiting shallow tropical or subtropical areas. The family Cymothoidae is among the larger of the isopod families comprising some 43 genera, with more than 369 species found in the marine and freshwater environment (Smit et al. 2014). Because of their relatively large body size and conspicuousness (Fig. 10.7), cymothoids are one of the best-known groups of isopods among the general public. They are familiar to fishers and anglers, and are of interest to fish

Fig. 10.7 Red hind, *Epinephelus guttatus* (Linnaeus, 1758), with *Anilocra brillae* Welicky, Hadfield, Sikkel and Smit, 2017. Image © E.R. Brill

biologists and to the aquaculture industry as potential pests or disease vectors. Despite this, the life history for most individual cymothoid species, along with their effects on individual hosts, and host populations is poorly known. As a consequence, even less is known about the factors that influence their own populations and their community-level effects.

Cymothoids are known to parasitise representatives of almost every family of marine teleost as well as a number of chondrichthyan fishes. A particular challenge, indeed an impediment to progress on the taxonomy of this family, is the high level of variability shown by many species (Smit et al. 2014). In the historic period of cymothoid taxonomy, it is clear that intraspecific variation became confounded with interspecific differences. The present high level of names in synonymy attests to this difficulty. Although there are varying degrees of host specificity, there exists a general trend for host specificity to increase with decreasing latitude (Smit et al. 2014). However, taxonomic uncertainties obscure our understanding of host specificity. Earlier studies provided the foundation for determining generic differences (e.g. Bruce 1987a, b), and it is only recently that researchers have been able to begin to reclassify cymothoids to the correct species level, thereby resolving misidentifications of various specimens (e.g. Hadfield et al. 2013, 2014, 2015, 2016; Welicky et al. 2017a). Although a paucity of information exists on the life strategy of most cymothoids, it is generally accepted that they have a juvenile stage (manca) that is well equipped for swimming. If mancae attach to a host and the host is not suitable, then they can drop off and moult into a second free-swimming stage (aegathoid) for several days such that they can swim and locate an appropriate final host (Jones et al. 2008).

The majority of ecological cymothoid research has been conducted on the genus *Anilocra* Leach, 1818 with the other commonly encountered genera such as *Ceratothoa* Dana, 1852 and *Cymothoa* Fabricius, 1793 remaining vastly understudied. Many existing studies describe the effects of parasitism at the individual level. Yet these findings suggest that there should be indirect and/or secondary, "knock-on" effects at the population and ecosystem level. Here we review the effects of cymothoid infection on individuals, populations and communities, with particular emphasis on those belonging to *Anilocra*.

10.2.2.1 Potential Effects on Individual Hosts

Considering that cymothoid parasites rely on their hosts for habitat and food, infection is rarely associated with mortality as killing their host would be detrimental to their own survival. Only in the most extreme cases will a single host be infested by many mancae and subsequently lose the majority of their blood and plasma, thereby increasing the probability of host mortality (Bowman 1960). Thus their effects on hosts are more likely to compromise host health and behaviour, but not survivorship. Perhaps the most obvious effect of parasitism on hosts is reduced crypsis, as cymothoid parasites such as *Anilocra* spp. are large and conspicuous. The visually obvious lesions that the parasites create from attachment may further reduce crypsis, and these lesions may also promote secondary infection (Bunkley-Williams and Williams 1998a).

In addition to reducing crypsis, infection by cymothoids can compromise host growth. Some *Anilocra* spp. weigh a significant proportion of their hosts' body weight, and this may cause an energetic drain on hosts (Adlard and Lester 1994; Fogelman et al. 2009). *Anilocra apogonae* Bruce, 1987 is known to weigh approximately 4% the mass of its host, *Cheilodipterus quinquelineatus* Cuvier, 1828, and infected male *C. quinquelineatus* on average weigh about 1.04 g less than uninfected males (Fogelman and Grutter 2008). Even more striking observations on reduced growth rate were noted by Roche et al. (2013a, b) who reported that *Anilocra nemipteri* Bruce, 1987-infected *Scolopsis bilineatus* (Bloch, 1793) were 25% smaller than uninfected conspecifics. Other proxies of growth rate, such as muscle condition and composition, have also been used to identify the effects of *Anilocra* spp. infection on hosts. For example, studies on French grunt infected with *A. haemuli* Williams and Williams, 1981 determined that infected fishes have reduced muscle condition but similar caloric values and gut content volumes compared to uninfected conspecifics (Welicky et al. 2018b). Interestingly, this same study determined that *Anilocra chromis* Williams and Williams, 1981-infected brown chromis, *Chromis multilineata* Guichenot, 1853, had similar muscle condition and caloric values as compared to uninfected conspecifics, demonstrating that the effects of *Anilocra* spp. infection may vary by host species. These differential effects of congeneric parasites on various species of fish demonstrate that some fishes may be better adapted for, or more resilient to parasitism, and the fishes' capacity to endure parasitism may also be regulated by a suite of abiotic and biotic factors.

Some of the most important effects of cymothoid infection on their host fish are related to reduced fecundity and reproductive output (Fogelman et al. 2009; Adlard and Lester 1994). *Anilocra* spp. infection has been associated with reduced host gonad size (Fogelman et al. 2009), compromised mouthbrooding (i.e. males rearing/guarding the females' eggs in their mouth) (Fogelman et al. 2009) and decreased egg production (Adlard and Lester 1994). Infection by *A. apogonae* was associated with female *C. quinquelineatus* having smaller gonads and producing 42.6% fewer ova than uninfected females. Moreover, of the ova produced, infected females had about one third the amount of mature ova compared with uninfected females (Fogelman et al. 2009). Similar patterns have been reported for *Anilocra pomacentri* Bruce, 1987 and its host, *Chromis nitida* (Whitley, 1928): infected individuals produce only 12% of the number of eggs produced by uninfected females (Adlard and Lester 1994). Male fishes have also been reported to have reduced reproductive efforts in association with *Anilocra* spp. parasitism. Only 1 in 78 infected male *C. quinquelineatus* were observed mouthbrooding, and this male's brood was less than half the average brood size of an uninfected male (Fogelman et al. 2009). In contrast, Robinson (2005) noted that although *Stegastes partitus* (Poey, 1868) infected with *Anilocra partiti* Williams and Williams, 1981 have a decreased probability of courting and mating, they were equally successful at brooding eggs.

Across several host species, altered host swimming performance has been associated with *Anilocra* spp. infection. Some of the most notable effects of parasitism on host swimming are increased host drag (Östlund-Nilsson et al. 2005) and respiratory demands (e.g. Binning et al. 2013) and reduced swimming abilities (Table 10.2; Östlund-Nilsson et al. 2005; Binning et al. 2013). One of the simplest types of data to collect, and a well-documented proxy of energetic demand, is the rate at which the pectoral fin beats and the number of fin beats a fish takes. Fish with higher energetic demands should have a greater number of pectoral fin beats, and such patterns have been observed in *A. apogonae*-infected *C. quinquelineatus* when compared to uninfected conspecifics. Interestingly, when *A. apogonae* were removed, the pectoral fin beat frequency of previously parasitised hosts returned to similar levels as uninfected conspecifics (Östlund-Nilsson et al. 2005). Parasite removal studies have also been used to better understand how *Anilocra* spp. infection influences host drag and respiration. For example, infection by *A. nemipteri* on *Scolopsis bilineatus* has been reported to increase host side bias significantly, but when parasite removal occurs, side bias decreases (Roche et al. 2013a, b). In other parasite removal studies that examined infected fish respiration, *A. apogonae*-infected *C. quinquelineatus* (see Östlund-Nilsson et al. 2005), *A. nemipteri*-infected *S. bilineatus* (see Binning et al. 2013) and *Anilocra haemuli*-infected *Haemulon flavolineatum* (Desmarest, 1823) (Welicky et al. unpublished data) all had increased oxygen demands compared to uninfected conspecifics. In two of these three studies, infected fish respiration and swimming performance decreased to levels similar to that of uninfected fish (Östlund-Nilsson et al. 2005; Binning et al. 2013), and in the third study, infected fish respiration remained high after parasite removal (Welicky unpublished data).

Östlund-Nilsson et al. (2005) and Binning et al. (2013) suggested that the drag effect created by the parasite was associated with increased respiratory demands, such that when the drag effect/parasite was removed, respiration levels returned to those of uninfected conspecifics. Thus, *Anilocra* parasitism may have long-term or permanent effects for some host fishes, while other fishes may only be affected during parasitism (Östlund-Nilsson et al. 2005; Binning et al. 2013).

Given the severity of physiological effects of infection, it is not surprising that infection is also associated with changes in behaviour of host fishes. For example, in territorial fish such as *Chaetodon capistratus* Linnaeus, 1758 (four-eye butterflyfish), infection by a cymothoid isopod was associated with reductions in host-feeding rates by 24.3% and territory size by 3%, as well as increased number of agonistic interactions among conspecifics (Meadows and Meadows 2003). In fact, compared to uninfected conspecifics, infected *C. capistratus* chased fish three times as often and were chased by other fishes four times as often (Meadows and Meadows 2003). In other studies of *Anilocra*-infected fish, infection was associated with increased risk-taking behaviour. For example, initiation of a predator escape response of *Anilocra nemipteri*-infected *Scolopsis bilineatus* was delayed compared to uninfected conspecifics, and this varied with respect to infected host size, such that larger parasitised fish tended to flee at a greater distance from a threat than smaller parasitised fish (Binning et al. 2014). In addition to delayed escape responses, infection by other *Anilocra* spp. is associated with changes in host movement patterns. The diel migratory reef fish, *H. flavolineatum*, typically migrates from reef to seagrass habitat at dusk. However, infected individuals were less likely to migrate than their uninfected conspecifics (Welicky and Sikkel 2015). The mechanisms driving this altered behaviour are unknown but may be related to agonistic interactions with schoolmates.

Because they remain permanently attached to their hosts, cymothoids would appear incapable of serving as vectors for viruses and other microorganisms. However, infective manca stages can switch hosts during the process of finding an appropriate permanent host and in the process serve as a vector. Currently no information is available on the feeding of these manca stages and thus whether they have the ability to act as vectors of blood infections during host switching.

10.2.2.2 Population-Level Effects on Hosts

The population dynamics of *Anilocra*-infected fish have only been described in relation to prevalence, social affiliation, seasonal change and host survival. In a study investigating *A. haemuli* prevalence on *H. flavolineatum*, prevalence of infection was greater on solitary than aggregating fish. Addtionally, prevalence of infection varied greatly by site (0–66%) but was positively autocorrelated within bay among years (Welicky and Sikkel 2014). Off the coast of Malabar, India, prevalence of *Nerocila* Leach, 1818 infection was associated with seasonal changes, and seasonal changes were moderated by monsoons (Aneesh et al. 2013). Prior to the monsoon season, the time period when salinity is highest, prevalence of infection was highest. Correspondingly, prevalence was lowest after monsoon season, when salinity is low because of freshwater input from the monsoonal rains. While this may suggest that parasites have reduced tolerance for low salinity water, ovigerous parasites were observed throughout the entire study period, suggesting that parasites can still reproduce under suboptimal conditions (Aneesh et al. 2013).

Considering that high levels of mancae infestation have been associated with reduced survival of hosts (i.e. Bunkley-Williams and Williams 1998a) and that cymothoids infect numerous fish species (Williams and Bunkley-Williams 1996), understanding population-level effects of infection are imperative to better understanding both fish and parasite population dynamics. Both host and parasite populations can have extensive geographic distributions and a diversity of activity patterns; general patterns about population-level effects of parasites have not been gleaned. Another factor that may complicate our understanding of the population-level effects of infection is that parasites may infect different hosts depending on whether they are found in wild or captive environments (Horton and Okamura 2003). Moreover, there is inherent natural and anthropogenic-caused variation between localities even of the same habitat type, exacerbating the difficulty of detecting generalised population-level effects.

10.2.2.3 Environmental Factors Influencing Cymothoid Population Size and Distribution

Cymothoid isopods have a global distribution, and the environmental factors that affect their distribution and population size are poorly understood. While there are correlative data that suggest that salinity plays a role in the prevalence of cymothoid infection (Aneesh et al. 2013, see above), salinity is directly and indirectly associated with numerous environmental factors which may regulate parasite population dynamics. Hence correlative data must be interpreted with caution. Nonetheless, parasite population size and the effects of parasites on their hosts are likely correlated with habitat differences. For example, Sala-Bonzano et al. (2012) reported notable differences in the effects of *Ceratothoa italica* Schioedte and Meinert, 1883 on *Lithognathus mormyrus* (Linnaeus, 1758) in marine protected areas versus anthropogenic impacted areas. In marine protected areas, infected fish showed negligible differences in measures of host condition (growth and hepatosomatic index scores) compared to uninfected conspecifics. In contrast, in anthropogenically impacted areas, infected fish growth and hepatosomatic index scores were greatly reduced compared to uninfected conspecifics. The authors of this work suggested that host condition may be associated with habitat quality and that deteriorating habitat quality may alter host condition and indirectly influence parasite virulence (Sala-Bonzano et al. 2012).

Host Quality and Availability

Cymothoids are permanent parasites, typically relying on one host for their entire life, although in some species juveniles might utilise a variety of hosts until settling on a final specific host (see Chap. 5 of this volume). Given that cymothoids are mainly host obligates, one may assume that parasite population size should be proportional to the number of available hosts. Surprisingly, this has not been observed in the majority of host-parasite surveys. For example, the abundance of infected and uninfected *S. bilineatus* was observed across 12 sites on the Great Barrier Reef, and the abundances of infected, previously infected, and uninfected fish varied greatly within and among sites, showing no patterns in prevalence of infection (Roche et al. 2013a, b). In a 3-year study by Welicky and Sikkel (2014), the prevalence of *A. haemuli* infection appeared to decrease quickly with increasing French grunt population and aggregation size and then remained consistently low, with about 0–2 parasites per aggregation. This relationship was statistically significant in 1 year of study and nearly significant in one other year of the study. Nevertheless, the relationship between the average French grunt aggregation size and average number of infected fish per aggregation was inconsistent and only significant in 1 of the 3 years of their study (Welicky and Sikkel 2014).

Although host availability does not seem to be a predictor of parasite abundance, it is possible that host quality plays a role in cymothoid infection. A suite of interacting factors may determine host quality, and how these factors influence cymothoid abundance has not been investigated. Further research in this area is necessary.

Benthic Habitat
The role that benthic habitat plays on adult cymothoid parasites is likely minor as they remain attached to their hosts throughout the majority of their lives. For infective mancae stages, the benthic habitat may play a more integral role in survivorship. However, this potential environmental influence is not well understood. Mancae are morphologically adapted for swimming and can continue searching for available hosts several days after brood release (Adlard and Lester 1994; Jones et al. 2008). The amount of time spent and activities they conduct in the water column and in the benthos are not well understood. The lack of data on this subject is in part related to the difficulty of tracking free-swimming mancae as they are small and difficult to see. Moreover, there is no published information on spatial and temporal patterns of brood release, making studies of mancae dispersal and host finding difficult. Consequently, studies of mancae have thus far been opportunistic, and we have a very limited understanding of the ecology and life history strategies of cymothoids at this life stage.

10.2.2.4 Predation

Predation of cymothoids has rarely been reported or studied. From the few studies that exist, we cautiously suggest that the frequency of predation events on cymothoids is low. Losey (1974) conducted gut content analysis on both *Gobiosoma* Girard, 1858 spp. and *Thalassoma bifasciatum* (Bloch, 1791) and found that zero of seven *Gobiosoma* spp. and two of eight *T. bifasciatum* consumed cymothoids.

Moreover, the number of cymothoids observed per gut was negligible compared to the number of gnathiids observed per gut. Given that there was approximately 1 cymothoid for every 52 gnathiids in a gut sample, it is likely that gnathiid availability is greater in general and that most cleaners do not typically prey on cymothoids. The later prediction is supported by a study that examined the ability of eight cleaner organisms (four shrimp species, four fish species) to clean and prey upon juvenile *A. haemuli* attached to their French grunt hosts. Only one cleaner, *Ancylomenes pedersoni* (Chace, 1958), was observed to successfully clean and consume the juvenile cymothoid isopods (Bunkley-Williams and Williams 1998b). In addition to these studies, there is limited anecdotal evidence of cymothoid predation events. However, some of these predation events may not necessarily result in complete prey consumption. Brusca (1978) reported that adult *Nerocila* spp. have been observed with damaged pleotelsons and uropods, suggesting that non-lethal injuries are possibly a result of predation by cleaner fishes (Brusca 1978). In the only documented case of predation on adult cymothoids, Narvaez et al. (2015) reported cymothoids in the guts of approximately 5% of lizardfish (Synodontidae) sampled in the Azores. More interestingly, some of the lizardfish sampled had nothing but cymothoids in their guts (no hosts). What is also noteworthy is that this is the only example of predation on this fish parasitic isopod family by a non-cleaner.

10.2.2.5 Temporal Variation in Cymothoid Activity

Temporal variation in cymothoid activity has not been investigated. As noted above, we have no information about the timing and mechanisms behind cymothoid brood release and the timing of infestation. To the best of our knowledge, the only *Anilocra* spp. life cycle that has been fully described is that of *Anilocra pomacentri* (see Adlard and Lester 1994). From that study we know that *A. pomacentri* ovigerous females brood for approximately 62 days, and brood releases occur naturally within a period of 1–3 h. The lifespan of this parasite is approximately 12–14 months (Adlard and Lester 1994), but cymothoid experts speculate that these parasites can live for many years.

10.3 Copepoda

10.3.1 Copepods

Copepods include a highly diverse group of parasitic crustaceans. Parasitic members that inhabit a variety of marine and freshwater habitats, exhibit extreme cases of sexual dimorphism, are associated with endo-, meso-, ecto- and free-living parasitic lifestyles and that infect both invertebrates and vertebrates. Of the 10,000 described species, about 20% are parasites of fishes, and these parasites are organised into some 12 different families (Williams and Bunkley-Williams 1996). One family of particular importance and on which the majority of parasitic copepod research has been conducted is the family Caligidae. Caligids infect several commercially important fishes such as salmonids, and loss of these fishes due to parasite infection can be devastating to fishery-based industries (Johnson et al. 2004). Their life histories are diverse and complex, and it is only recently that the life stages of *Caligus* Müller, 1785 and *Lepeophtheirus* von Nordmann, 1832 were determined to have some differences. *Caligus* has eight life stages (two naupliar, one copepodid and four chalimus stages prior to becoming an adult), whereas *Lepeophtheirus* has two naupliar, one copepodid, two chalimus and two pre-adult stages prior to becoming an adult (Maran et al. 2013). As such the majority of information available on copepods is related to how they influence host health and survival, as well as their modes of transmission. Here we review how copepod infection influences host health and behaviour and synthesise findings from transmission studies to examine the role of copepods at the population level.

10.3.1.1 Potential Effects on Individual Hosts

Unlike most other types of parasitic Crustacea, we do have a basic working knowledge of what factors influence copepod infestation of both fish and non-fish hosts. From several studies, we know that copepod abundance and intensity of infection are correlated with aspects of host physiology and size. For example, the abundance of copepods *Paraergasilus rylovi* Markevich, 1937, infesting the freshwater bivalve host, *Anodonta piscinalis* Nilsson, 1823, changes with respect to the reproductive period of the host. Abundance of *P. rylovi* is greatest during non-reproductive periods, and this may be a result of the clam's filtration behaviour during non-reproductive periods as it may promote parasite attachment (Taskinen and Saarinen 1999). Additionally, the energy the clam allocates towards future reproductive efforts during non-reproductive periods may reduce the energy it allocates to immune response, thereby potentially increasing the hosts' risk of parasitism (Saarinen and Taskinen 2005). In some fish hosts, copepod abundance has been associated with host size, such that as host size increases, the risk of higher parasite burden to hosts increases, too. For example, the abundance of *Schistocephalus* Creplin, 1829 spp., *Diplostomum* Nordmann, 1832 spp. and *Diphyllobothrium* Cobbold, 1858 spp. found on male three-spined sticklebacks (*Gasterosteus aculeatus*, Linnaeus, 1758) was directly correlated with host fin size when adjusted for host condition, and this is likely an artefact of larger finned hosts having more area for parasites to infest (Brønseth and Folstad 1997). Interestingly, although high parasite intensity would seemingly result in some negative consequences for hosts, increased fin size and ability to withstand heavier levels of parasitism may demonstrate a high level of fitness. Thus parasitism may increase the likelihood of hosts mating (Brønseth and Folstad 1997) and consequently provide a potential benefit to hosts. Other studies demonstrate more expected patterns, such that cestode infection on sticklebacks is associated with reduced fecundity and reproductive success (Schultz et al. 2006).

Although high parasite intensity in some cases may be a positive fitness cue, parasitism by copepods has been associated with reduced host condition (Boxshall 2005) and compromised immunity (Tully and Nolan 2002). Studies on *Lepeophtheirus salmonis* (Krøyer, 1837), a parasite of salmonids distributed across the Pacific and Atlantic oceans, suggest that infestation is associated with eliciting a stress response in hosts, which in turn compromises host immunity and the host's ability to resist secondary parasitic infections (Tully and Nolan 2002). Increased susceptibility to infection from stress has also been observed in non-fish hosts such as clams, which are infected by *P. rylovi* (see Saarinen and Taskinen 2005).

In addition to increased susceptibility to parasites, infection by copepods on hosts is associated with a suite of other consequences including reduced growth (Finley and Forrester 2003; Palacios-Fuentes et al. 2012), anaemia, lethargy, discolouration (Heckmann 2003) and/or change in colour (Folstad et al. 1994). In larval fish, copepod infection may have near-immediate effects on host growth. Larval *Helcogrammoides chilensis* (Cancino, 1960) when grouped by age showed a significant difference in growth as compared to uninfected same-aged conspecifics, and this difference was apparent within a 5-day period. Such effects may indirectly influence the duration of larval development and the likelihood of successful settlement (Palacios-Fuentes et al. 2012). Reduced growth is also common in settled fishes (Finley and Forrester 2003), and for those fishes that are of reproductive age, parasitism may play a unique role in breeding. For example, for some three-spined sticklebacks, breeding success is associated with deeper red colouration, and this colouration may be obtained from consuming copepods that are rich in carotenoids (Folstad et al. 1994). As the number of parasitic copepods increases, the colour of the host intensifies, potentially increasing the likelihood that the host will be selected for mating and also signalling to potential mates their ability to resist/endure the effects of infection. The cost-benefit relationship of sustaining parasitism to aid in breeding must be "weighed" carefully as parasitic copepods may not only be detrimental to host immunity and condition, but the copepods themselves may carry parasites or diseases (Folstad et al. 1994), which thereby reduce overall host fitness.

Perhaps some of the most detrimental effects of parasitism on hosts at the individual level are associated with reduced respiratory and cardiac function. *Salmincola* Wilson, 1915 spp. are known to infect the gills, opercula, mouth and tongue of fishes. Consequently, Brook trout [*Salvelinus fontinalis* (Mitchill, 1814)] infected by *Salmincola edwardsii* (Olsson, 1869) have increased branchial mucous production compared to uninfected conspecifics, and this may negatively influence the ability of infected hosts to respire (Heckmann 2003). Perhaps increased mucous production increases the difficulty for more parasites to attach and infect an already compromised host. Some parasites such as *Lernaeocera branchialis* (Linnaeus, 1767) are associated with impaired cardiac and respiratory function of fish hosts. Atlantic cod, *Gadus morhua* Linnaeus, 1758, infected by *L. branchialis* were reported to have irregular heart rhythms and decreased cardio output and oxygen consumption as compared to uninfected conspecifics (Behrens et al. 2014). Warm water reef fishes infected with copepods have also been observed with altered respiration rate. *Pharodes tortugensis* Wilson, 1935 infests the gill cavity of bridled goby, *Coryphopterus glaucofraenum* Gill, 1863, and infested fish had significantly more gill ventilations per observation period than uninfected conspecifics (Finley and Forrester 2003).

As noted above, our knowledge of the effects of copepod infection on hosts has been driven greatly by its negatives effects on commercial fishes. Accordingly, future research should be directed towards understanding effects on species not only of commercial importance but of ecological significance as well. Future studies should also validate potential environmental, behavioural and physiological correlates of infestation by using experimental approaches. Moreover, given that copepod morphology and behaviour vary greatly by life stage, analysing the transmission of copepods, their efficacy and their role on host populations should be examined with respect to the developmental stage of both the copepod and its host.

10.3.1.2 Population-Level Effects on Hosts

The majority of research examining the effects of parasitic copepods on host population dynamics is focused on host survival, as many hosts are considered to be commercially important species. Few field studies have been conducted on infected host populations, and the main focus of these studies has been to determine if parasite infection influences host mortality, as mortality is associated with significant economic loss. In a field study conducted by Krkošek et al. (2013), the authors determined that Atlantic salmon that were not treated with parasiticide had a mortality rate of 39%. Considering that this mortality rate is high for wild untreated fish, the population dynamics of wild fishes may be significantly influenced by parasite prevalence and intensity (Krkošek et al. 2013). Furthermore, larger, reproductively active fish may be at greatest risk, as studies of prevalence of sea lice-infected Pacific salmon spp. have determined that prevalence of infection, mean intensity and abundance tend to increase as host size/age increases (Nagasawa et al. 1993). Thus, the viability of host salmon populations may be at risk if infection remains greatest on reproductively mature fishes. The risk of copepod infection on host fishes may also vary with season as prevalence of infection and abundance of some copepods have been documented to be greatest during summer (Boxshall 1974; Nie and Yao 2000).

10.3.1.3 Environmental Factors Influencing Copepod Population Size and Distribution

Parasitic copepod species are both morphologically diverse and widely distributed across almost the entire global gradient (e.g. Boxshall 1974; Oldewage 1992). Despite their abundance and vast distribution, our knowledge on environmental factors that influence parasitic copepods specifically is limited. The majority of research describing the distribution of copepods comes from plankton sampling and does not describe if the copepods collected are parasitic in any of their life stages. Studies that have used copepod sampling as a way to identify their distribution suggest that environmental factors such as water temperature, salinity, chlorophyll-a levels (Gaard et al. 2008), currents (Beaugrand et al. 2000; Hsieh et al. 2004), upwelling (Escribano and Hidalgo 2000) and turbulent mixing (e.g. Mackas et al. 1993; Incze et al. 2001) can all influence the distribution and size of copepod populations. To the extent to which this applies to parasitic copepods has not been determined, and further investigation is needed.

Host Quality and Availability

Given the diverse natural biology and ecology of parasitic copepods and their hosts, generalised patterns of infection with respect to host abundance may be difficult to describe. Moreover, identifying generalised patterns takes years of data collection, and few long-term studies are available as they are costly and difficult to manage with consistency. Consequently, the long-term studies available are typically on commercially important fishes, such as salmon, and are not always in agreement. In a 7-year study, the abundance of salmonids and the number of *Lepeophtheirus salmonis* infecting them were quantified. The annual abundance of pink salmon [*Oncorhynchus gorbuscha* (Walbaum, 1792)] was highly variable, and copepod prevalence coincided with pink salmon abundance, such that years of high fish abundance were associated with high prevalence of infection and vice versa. For other species such as chum salmon [*Oncorhynchus keta* (Walbaum, 1792)], fish abundance was relatively constant and high over the study period, yet copepod prevalence of infection on this host species was generally and consistently low (Nagasawa 2001). In a shorter, 2-year study on the same host-parasite assemblage, abundance of sea lice infection was similar on pink and chum salmon, with 0–2 sea lice infections per fish (Jones and Hargreaves 2007). Hence generalised patterns in prevalence across localities and hosts are difficult to make.

The role of host quality in copepod population dynamics is not well understood. While there are numerous papers that examine the effects of copepods on hosts, few studies have been conducted investigating the effects of hosts on copepods. We do know that some salmonid hosts may reduce copepod populations by altering their behaviour and condition by producing proteases as an immune response to copepod infection. These proteases are associated with reduced copepod feeding activity, growth, development and fecundity and increased likelihood of copepod detachment and mortality (Wagner et al. 2008). Nevertheless copepods may be able to neutralise or limit these effects as copepods can release trypsin, which is thought to aid in feeding and reducing hosts' immune response. Moreover, hosts may vary in their immune response and ability to release "parasite-fighting" proteases, such that host quality for copepods will vary, too (Wagner et al. 2008).

Benthic Habitat

Benthic habitat structures provide shelter for susceptible fish, and in doing so, habitats may provide refuge from free-swimming parasites and predators. In a correlative study examining the factors that influence the survival rate of bridled gobies, the best-fit model determined that survival success was predicted by an interaction between refuge/habitat availability, goby density and copepod infection. The combination of higher host density and fewer refuges was associated with reduced bridled goby survival in infected and uninfected fish, and survival was lower for copepod-infected individuals (Forrester and Finley 2006).

10.3.1.4 Predation

Similar to cymothoid isopods, adult parasitic copepods depend on hosts for survival. However, like gnathiid isopods, they are often small and highly mobile. Such mobility may aid them in predator avoidance, both when predation attempts are directed towards the host (e.g. by piscivores) and the parasite. For example, in an experimental test of predator, prey and copepod interactions, sea lice escaped predation when their host fish was being preyed upon, by switching to the predator fish. This occurred in approximately 70% of the experimental trials (Connors et al. 2008). In another sea lice host-switching study, the escape response of sea lice was also influenced by resource and mate availability (Connors et al. 2011).

Predation directly on copepods by cleaner fish can help regulate the intensity of host infection and accordingly influence coral reef fish host population dynamics. In an early study by Gorlick et al. (1987), cleaner fish, *Labroides dimidiatus* (Valenciennes, 1839), were experimentally removed from some coral reefs and maintained on others, and observations on copepod abundance and size and host density were recorded. The size of hosts and the number of copepods per host were not different for control and manipulated reefs. Interestingly, there was a significant difference in copepod size on control and manipulated reefs, such that reefs that had the cleaner fish removed had hosts that were infected with significantly larger copepods. Hence the findings of this study suggest that the removal of parasites by cleaner fish may only influence parasite size and composition, and not parasite density and host size (Gorlick et al. 1987). However, in this study, the effects on copepod infection on host size were only examined over a period of 6 months, and the authors note this may not be a long enough time period to observe significant effects on copepod infection on host growth. In a similar study, which was conducted over a long-term 6-year period, cleaner fish removal did influence copepod abundance and host size (Clauge et al. 2011). On reefs where cleaner fish, *Labroides dimidiatus*, was removed, the damselfish *Pomacentrus moluccensis* Bleeker, 1853 were smaller, and there was a higher abundance of copepods, particularly on larger fish (Clague et al. 2011). On reefs where *L. dimidiatus* were not manipulated, the overall size of fish was greater than those on cleaner fish removed reefs, suggesting that the presence of cleaner fish indirectly influenced the growth and development of *P. moluccensis* (see Clague et al. 2011). Accordingly, if cleaner fish are removed from reefs, host population dynamics may be negatively impacted as parasitism is known to reduce growth, and therefore it may influence hosts' reproductive capacity and output (Clague et al. 2011). Parasitic copepods may also be consumed by conspecifics of infected hosts (e.g. Sikkel 1986) and by birds that prey on large parasitic copepods infesting fish, such as the *Mola mola* (Linnaeus, 1758) (see Abe et al. 2012).

10.3.1.5 Temporal Variation in Copepod Activity

Many copepod activity patterns related to foraging and infesting hosts occur on a diel cycle (Heuch et al. 1995). Diel cycles are associated with shifts in light availability, and different ambient light levels may aid copepods in locating prey and hosts as well as avoiding predators (Heuch et al. 1995; Hevrøy et al. 2003). Given that light penetrates different water depths over the course of a day, and copepods and their host movement patterns are influenced by light, diel vertical migration patterns are common (Hevrøy et al. 2003; Brooker et al. 2007). Generalised patterns in wild copepod movement through the water column are difficult to make as studies on different species have demonstrated a variety of vertical migration activity patterns, and the vast majority of these studies have not been conducted in situ. For example, in a laboratory study conducted by Heuch et al. (1995), salmon louse, *Lepeophtheirus salmonis*, were found in greater density at the surface when subjected to light treatments mimicking daylight and more widely dispersed across different depths at light levels mimicking night light. Other studies investigating copepod diel vertical migration have noted that the vertical migration behaviours of copepods may change with respect for the copepods' developmental stage (Johannesen 1978; Heuch et al. 1995; Flamarique et al. 2000) and their ability to detect the visual and chemical cues of their preys and hosts.

Copepod activity patterns also occur seasonally, and seasonality is associated with host and light availability. For example, high prevalence of infection by *Lernaeocera branchialis* on *Merlangius merlangus* (Linnaeus, 1758) occurs typically during winter months when both intermediate and definitive hosts inhabit the same inshore shallow waters (Brooker et al. 2007). In an experimental study on *L. salmonis* infection rate of Atlantic salmon, infection was greatest at shallow depths and varied at the different artificial light levels, which served as a proxy for seasonally changing light levels (Hevrøy et al. 2003).

Although diel and seasonal activity patterns are typically correlated with lunar periodicity, the effects of lunar periodicity on the activity patterns of parasitic copepods are poorly documented. One reason for the limited data are that copepod diversity studies collect all types of copepods, and parasitic copepod abundance is sometimes proportionally very small compared to non-parasitic isopods. The small sample size of parasitic copepods collected makes it particularly difficult to examine the associations between lunar periodicity and parasitic copepod activity using statistical analyses (e.g. Chew et al. 2015), as there is not enough statistical power to complete basic analyses. Thus future studies that investigate lunar periodicity should focus on the activity patterns of parasitic copepods and conduct their studies at localities and during specific times of year where collecting a large number of parasitic copepods is likely.

10.4 Community-Level Effects

10.4.1 Aquatic Food Webs and Habitat Connectivity

Ecological communities are characterised and integrated by the transfer of energy among their constituents, and food webs are a tool to trace this transfer of energy by representing the structure of trophic relationships (Pimm 2002). Thus, food webs constitute an important unifying theme in ecology. While parasites have historically been ignored in both theoretical and empirical analyses of ecological food webs (Morand and Arias González 1997; Arias-González and Morand 2006; Dunne et al. 2013), some ecologically minded parasitologists have recently called attention to this gap (Marcogliese and Cone 1997; Wood et al. 2007; Byers 2009; Johnson et al. 2010), drawing comparisons between parasites and "micropredators" (Raffel et al. 2008) and exposing them as the "ultimate missing link" in our understanding of trophic ecology (Lafferty et al. 2008). In spite of this, few aquatic food web studies within the past two decades have incorporated parasites (but see Morand and Arias González 1997; Arias-González and Morand 2006; Lafferty et al. 2008; Johnson et al. 2010; Hatcher and Dunn 2011; Sato et al. 2012; Dunne et al. 2013). A major challenge is the difficulty of retrofitting parasites into existing food web models (Petchey et al. 2008; Sukhdeo 2010). Thus, parasite ecologists must "begin at square one" by quantifying the direct and indirect effects of parasites in terms of energy flow (or biomass).

External or "ecto" parasites offer a convenient and promising starting point for the integration of parasites into food webs. Unlike internal parasites, they can often be seen with the naked eye and thus be collected and counted without sacrificing the host. Perhaps most importantly, in contrast to internal parasites, ectoparasites can impact food webs through direct consumption by other organisms (Johnson et al. 2010). The best known example of this in aquatic environments is cleaning symbioses, in which a cleaner eats parasites from a heterospecific host body surface. While intraspecific cleaning ("grooming") is common among social terrestrial animals, it is rare in the ocean (but see Sikkel 1986). In contrast, cleaning of heterospecifics is rare in terrestrial environments but very common in the ocean, especially in coral reef systems (Côté 2000). While marine cleaning interactions have become a model system for the study of symbiotic mutualisms, most research on marine cleaning symbioses has examined their evolution, benefits to host-client fishes and how cleaners impact parasite populations and has focused primarily on Indo-Pacific cleaner wrasses (e.g. Grutter et al. 2003). Little consideration has been given to how these interactions, or other effects of ectoparasites on host behaviour, contribute to the overall flow of energy through associated habitats.

By consuming host tissue and being eaten by cleaning organisms or other microcarnivores, ectoparasites directly impact food webs and contribute to trophic (carbon transfer) linkages between habitats and energy budgets (Johnson et al. 2010). For example, reef fishes that feed nocturnally over sand or seagrass beds on benthic invertebrates (e.g. many grunts and snappers) return to the reef at dawn when activity of parasitic gnathiid isopods and cleaning activity are greatest. Fish not only visit cleaner fishes found in the reef but also visit cleaner shrimps that live in obligate association with anemones at the sand-reef interface (Huebner and Chadwick 2012a, b). While some parasites are eaten by cleaners, others dislodge from the fish and continue living in the benthos where they can be consumed by other predators; both are effective mechanisms for transferring energy between habitats. Parasites may even link systems separated by hundreds of metres or kilometres as when nocturnal species depart the reef each night and feed over sand or seagrass beds (Sikkel et al. 2017), or when large species such as groupers and snappers migrate periodically from shallow to deeper reefs to spawn, and may link pelagic to reef environments when diurnal planktivorous reef fishes return to the reef at night where they are subsequently infested with substrate-associated parasitic isopods. However, marine food web studies have largely overlooked parasites in their contribution to reef biomass and carbon transfer. Thus, studies that address this gap are sorely needed. Potential pathways through which crustacean and other parasites contribute to food web linkages include direct predation on parasites by cleaners and other microcarnivores, predation by planktivorous invertebrates such as cnidarians and the effects of parasites on movement patterns of hosts (Fig. 10.6; Shaw and Binning 2016).

Overall individual and population-level effects of parasites on hosts are likely to have indirect consequences on community and ecosystem function. These indirect effects on ecosystem function may be the cause or consequence of changes in the direction and intensity of trophic level interactions (Raffel et al. 2008; Terborgh and Estes 2010; Hatcher and Dunn 2011). In terrestrial systems, parasites can dampen or heighten oscillations in population dynamics of predators and prey (Chap. 3 in Hatcher and Dunn 2011), yet information on how parasites may influence the population cycling of aquatic organisms is unknown. Theoretical studies have suggested that parasites may indirectly influence host fish population dynamics. If host density is low, then parasite infection on hosts may be concentrated and/or severe. In turn this can alter the survival and fitness of available hosts and thus indirectly influence population dynamics (Wood et al. 2007). Such effects caused by parasites are indeed likely as parasites have been shown to influence connectedness, number and length of food chain links and species richness (Lafferty et al. 2006).

10.4.2 Stable Isotope Analysis and Community Ecology of Parasitic Crustacea

Stable isotope analysis is a promising tool that can provide an indirect measure of parasite trophic ecology (Gomez-Diaz and Gonzalez-Solis 2010). Stable carbon isotopes (δ13C) are used to aid in the identification of the type and location of food sources consumed by organisms as they indicate the relative contributions of primary sources of carbon to local food webs, with a typical trophic shift (percent change from one trophic level to another) of 0–1‰ (DeNiro and Epstein 1981; McCutchan et al. 2003). In contrast, stable nitrogen isotope (δ15N) values increase with trophic level, typically 2–3‰ (Minagawa and Wada 1984; Post 2002; McCutchan et al. 2003), and are more useful when estimating trophic level (Post 2002; McCutchan et al. 2003). Smaller trophic shifts in δ15N are associated with animals raised on invertebrate diets (1.4 ± 0.2‰, McCutchan et al. 2003). Thus, stable isotope analysis could assist with understanding the complexity of the cryptic trophic relationships involving parasitic Crustacea and other symbionts in biologically complex systems.

If parasites function as predators, we would predict a stepwise enrichment in 15N of parasites relative to hosts, on the order of 2–3‰ (DeNiro and Epstein 1981; Post 2002). However, applications of stable isotope analysis and published trophic fractionation values to examine parasite-host isotopic relationships have yielded variable results (Lafferty et al. 2008; Doi et al. 2010; Gomez-Diaz and Gonzalez-Solis 2010). Isotope patterns are influenced by the feeding strategy or life history stage of the parasite (Iken et al. 2001; Pinnegar et al. 2001; O'Grady and Dearing 2006; Jenkins et al. 2018b), and the level of enrichment can vary in a parasite species found among multiple hosts (Deudero et al. 2002; Jenkins et al. 2018b) or among different parasite taxa within hosts (Boag et al. 1998; Neilson et al. 2005; Gomez-Diaz and Gonzalez-Solis 2010). In addition, interpretation and comparison of results from different parasite isotope studies are often limited by the selection of tissue analysed for isotopic comparison with parasites (Power and Klein 2004; Stapp and Salkeld 2009). For haematophagous parasites (e.g. gnathiids and cymothoids), estimates of trophic shift should be based on isotopic differences between fluids (blood) and consumers (ectoparasites) rather than differences between muscle or bulk tissue and consumers (e.g. McCutchan et al. 2003; Doi et al. 2010), because blood may differ isotopically from muscle tissue or whole organisms (Pinnegar et al. 2001). Future studies should examine multiple parasites and hosts simultaneously (Gomez-Diaz and Gonzalez-Solis 2010) and incorporate feeding studies in which hosts are fed a diet of known quantity and isotopic composition.

In a recent study, Demopoulos and Sikkel (2015) performed stable isotope analysis on three common Caribbean reef fish hosts and two parasitic isopods: the gnathiid *Gnathia marleyi* and the cymothoids *Anilocra haemuli* and *A. holocentri* Williams and Williams, 1981. To further track the transfer of fish-derived carbon (energy) from parasites to parasite consumers, gnathiids from host fish were also fed to captive Pederson shrimp (*Ancylomenes pedersoni*) for at least 1 month. Parasitic isopods had δ13C and δ15N values similar to their host, comparable with results from the small number of other host-parasite studies that have employed stable isotopes. Adult gnathiids were enriched in 15N and depleted in 13C relative to juvenile gnathiids, thereby suggesting that adult stages of gnathiids are tropically higher than those of juveniles and that juveniles are consuming and processing host blood. Such study provides insight into the potential isotopic fractionation associated with blood-meal assimilation and subsequent metamorphosis. Gnathiid-fed Pedersen shrimp also had δ13C values consistent with their food source and enriched in 15N as predicted due to trophic fractionation.

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In a subsequent study, Jenkins et al. (2018b) compared gnathiids that had fed on nine different Caribbean reef fishes. As expected, blood-engorged juvenile gnathiids were in most cases indistinguishable from their hosts' blood, but significant isotope discrimination was again apparent in adults. Adult males were, in general, lower in $\delta^{13}C$ and $\delta^{15}N$ than host blood, whereas host-specific isotopic discrimination for females varied among the different species of host fish. Model predictions indicated that there was a significant effect of host blood isotope ratios on the rate of stable carbon and nitrogen isotopic discrimination between gnathiids and host blood. Thus, general differences in the feeding ecology and trophic positions of the different host species were reflected in their associated gnathiids, indicating that stable isotope analysis of wild-caught gnathiids can indeed provide significant details concerning previous hosts. These results provide a foundation for future studies involving a greater variety of hosts, parasites and consumers of different life stages of parasitic crustaceans.

10.4.3 Indirect Effects on Community Structure via Host Movement

"Cleaner fishes" are effective at reducing the numbers of parasitic crustaceans on hosts and thus really do clean (Grutter 1999), and parasitic crustaceans, particularly gnathiids, influence the interaction between cleaners and hosts (Grutter 2001; Sikkel et al. 2004, 2005; Cheney and Côté 2005). It is therefore clear that an understanding of the cleaning interactions that are so common on tropical and temperate reefs requires an in-depth understanding of the ectoparasites, mostly crustaceans, which are the major "brokers" of the interactions between cleaner and client. It is now evident that the distribution of cleaners can influence the local distribution and abundance of reef fishes and therefore shape local community structure (Grutter et al. 2003; Floeter et al. 2007; Guimarães et al. 2007). This has been demonstrated most convincingly by manipulation of cleaner fishes off Lizard Island, GBR, that resulted in the redistribution of large, mobile, fish species, increasing fish abundance on patch reefs with versus without cleaners (Grutter et al. 2003). The altered distribution of fishes could result in localised nutrient enrichment (around cleaning stations) via the release of waste products while fish are "queuing" at cleaning stations. Local enrichment from fish waste has been shown to increase growth of cnidarians (Cantrell et al. 2015). However, determining whether gnathiids or other parasitic Crustacea are ultimately driving the redistribution of fishes requires characterisation and manipulation of local ectoparasite abundance.

From the available research, we know that *Anilocra* spp. infection alters host movement (e.g. Binning et al. 2013; Roche et al. 2013a, b). However, its relationship to community structure and in particular trophic dynamics is just starting to be investigated. Reduced swimming performance has been suggested to likely influence host habitat use, dispersal and foraging activity patterns (e.g. Binning et al. 2013). Welicky and Sikkel (2015) determined that the diel migratory patterns of the trophically important French grunt are influenced by *A. haemuli* infection. Nearly half of the infected fish observed did not complete their diel migration between the reef and seagrass habitats, whereas all of the uninfected fishes were observed migrating off the reef. Accordingly, the authors suggested that the exchange of biomass between these two systems may be altered, and this in turn may change nutrient flow and trophic connectivity between these two habitats. Additionally, given that haemulid biomass has been associated with improving coral growth (Meyer and Schultz 1985; Shantz et al. 2015), if French grunt biomass is diminished or altered, then coral growth may also be affected.

Stable isotope analyses have also been used to elucidate host movement and feeding patterns of *A. chromis* and *A. haemuli*-infected and uninfected fish. Studies of brown chromis, *Chromis multilineata*, have determined that *A. chromis*-infected and uninfected brown chromis tissues were within the range of zooplankton (Cocheret de la Morinière et al. 2003; Demopoulos et al. unpublished data), demonstrating that they feed on similar organisms and at the same trophic level (Welicky et al. 2017b). The interpretation of stable isotope analysis results is not always as straightforward, as fractionation patterns can be influenced by host and site conditions. As noted above, *A. haemuli*-infected French grunt leave the reef significantly less often than uninfected conspecifics and thus likely forage in seagrass significantly less often (Welicky and Sikkel 2015). Accordingly, infected French grunt tissues would be expected to yield significantly different stable carbon isotope values, but this was not the case: *A. haemuli*-infected and uninfected French grunt tissues all fell within the range of $\delta^{13}C$ values associated with seagrass environments (Cocheret de la Morinière et al. 2003; Demopoulos et al. unpublished data). While these data suggest that infected French grunt may still forage in seagrass environments (Welicky et al. 2017b), this information must be interpreted with caution. *Anilocra haemuli*-infected French grunt have reduced physiological condition, and poor condition can influence stable isotope fractionation patterns (Doucett et al. 1999; Papastamatiou et al. 2010). Thus reduced host condition may yield similar stable isotope values to seagrass environments, even if infected fishes are not foraging in seagrass environments. This study is a prime example of the challenges of interpreting the meaning of stable isotope analysis and emphasises the need for multiple approaches in assessing community-level contributions of parasitic Crustacea. The emergence of compound-specific stable isotope analysis, which is rapidly increasing in popularity for studies of marine food webs in general (e.g. Popp et al. 2007; Budge et al. 2008; De Troch et al. 2012), will likely become useful for studies involving parasitic Crustacea.

10.5 Concluding Remarks

Throughout this chapter we have endeavoured to both summarise the current state of knowledge of the ecology of parasitic Crustacea and highlight areas in need of further study. As has been emphasised earlier in this chapter and in previous reviews,

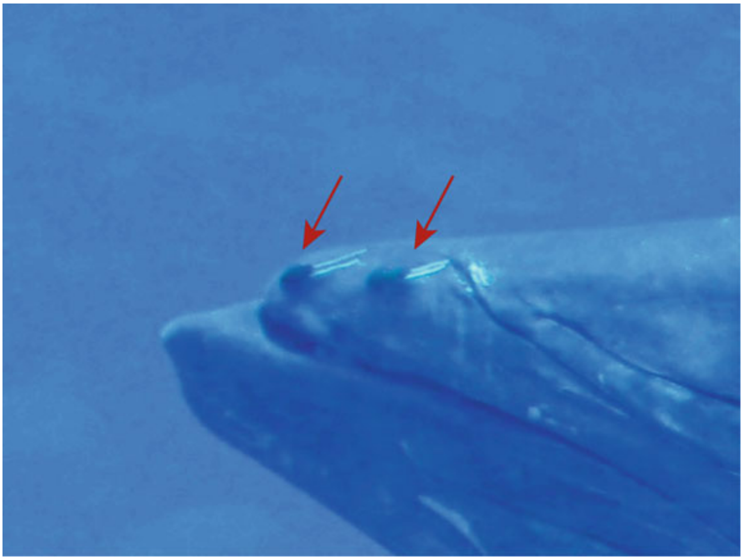

Fig. 10.8 Caribbean Great Barracuda, *Sphyraena barracuda* (Edwards, 1771), with parasitic copepods on snout (arrows). Image © E.R. Brill

a major limiting factor in our understanding of the ecology of parasitic organisms is the lack of cross-training in relevant aspects of parasitology among ecologists and vice versa. Progress in marine systems has been further limited by the fact that humans are terrestrial primates and the innate characteristics that have made humans adapted for living on land do not provide them the same benefits in water, further increasing the challenges to working in aquatic systems (Poulin et al. 2016). Although study of the terrestrial equivalents of parasitic Crustacea (terrestrial arthropods like ticks, fleas and mites) offers many logistic advantages, there are some unique aspects of the biology of parasitic Crustacea in the ocean that are unparalleled on land or fresh water. For example, coral reef environments and the site fidelity of some coral reef fishes are an ideal combination for studies on behavioural effects of parasites on hosts and population genetic structuring of parasite populations. Moreover, some parasitic Crustacea such as cymothoid isopods in the genus *Anilocra* and some parasitic copepods (Figs. 10.7 and 10.8) can easily be observed at a distance on hosts. Many other cymothoids such as tongue-replacing isopods are easily visible close-up, and anglers regularly observe them. The mechanisms and reasons for the large size and location of attachment of these parasites is a shared curiosity among citizens and scientists. Accordingly, this common inquiry draws non-specialists into participating in ecological studies of parasitic Crustacea, making "citizen science" research more likely to succeed. The investment of citizens is much needed as advances in trapping methodologies for parasitic Crustacea with mobile life history stages (Artim and Sikkel 2016) have opened the door for the inclusion of parasitic Crustacea by long-term ecological monitoring programs, and such programs rely on numerous people for data collection. The joint efforts of citizens and scientists to implement the most modern sampling and monitoring protocols will allow for important longitudinal studies on host-parasite and environmental interactions to be conducted.

The effects of anthropogenic activities on host-parasite interactions in aquatic environments have received considerable attention (e.g. Lafferty and Kuris 1999). Historically, the main focus has been on the effects of pollution on parasite communities and the role of parasites as indicators of pollution levels and habitat quality (e.g. Mackenzie 1999; Sures et al. 1999; Williams and Mackenzie 2003; Sasal et al. 2007). However, parasites may be impacted by or exacerbate other anthropogenic activities. For example, it is now well established that parasites in general can influence invasions by introduced aquatic organisms via multiple pathways (Torchin et al. 2001; Blakeslee et al. 2013). Introduced species may (1) lose parasites during the invasion (enemy release, specifically parasite loss); (2) gain parasites in the new range, which may then dilute or amplify the threat of infection in native hosts (Thieltges et al. 2008; Paterson et al. 2011); and/or (3) serve as vectors/transport hosts that introduce new parasites, which spillover to native hosts (Hatcher and Dunn 2011; Strauss et al. 2012). However, little is known about the role of parasitic Crustacea per se. Indo-Pacific lionfish (*Pterois volitans*) that have spread throughout the Caribbean region have been shown to be relatively resistant to gnathiid isopods in both their native and introduced ranges (Sikkel et al. 2014). However, in their native range, they have heavy loads of parasitic copepods, which are lacking in their introduced range (Tuttle et al. 2017). Thus, parasitic copepods (or lack thereof) could play a role in their successful invasion in the Caribbean (Tuttle et al. 2017). Given the large numbers of these copepods on native hosts, it is possible that they could be introduced to the Caribbean. At least two species of parasitic copepods have invaded the Mediterranean (Galil 2000).

The increasing interest in and use of marine protected areas to mitigate the impacts of increasing global fishing pressure has created the opportunity to study the effects of fishing pressure on parasite populations and host-parasite interactions (e.g. Sonnenholzner et al. 2011). Because of the myriad life history strategies and host associations of parasites and varied types and levels of exploitation in fished areas, it is difficult to make general predictions about the impacts of fishing on parasites. Studies by Wood et al. (2010, 2014), and Wood and Lafferty (2015), provide a conceptual framework to guide further investigation by accounting for differences in life history strategies and distinguishing between effects on parasite abundance and diversity and effects on parasite burden on hosts (parasites per host or unit biomass). In general, because most parasitic crustaceans infest hosts via free-living stages (some of which are planktonic) rather than through trophic transfer, effects of fishing on their abundance and host burden will likely differ and may indeed be opposite, from effects on most other parasites. There are at least two considerations for directly testing effects of fishing on parasitic crustaceans: (1) the need for adequate site replication—for example, in many localities, there is only a single protected area, and (2) the need for different sampling techniques given the differences in life history and host-exploitation strategies—for example, given that gnathiids are highly mobile and often nocturnal, simply collecting fish hosts, especially during the day, is not sufficient to estimate their abundance or burden on hosts.

As with fishing pressure, the phylogenetic diversity and myriad life history strategies among parasites, including parasitic Crustacea, make it difficult to predict general effects of climate change on their populations, impacts on hosts and community-level effects (Brooks and Hoberg 2007; Marcogliese 2001, 2008, Adlard et al. 2015). This is especially true given the joint impacts of climate change on both parasites and hosts. In aquatic environments, increasing water temperatures (and in some freshwater bodies, increasing drought and/or flood conditions) along with increased acidity can impact multiple aspects of both parasites and host metabolism, behaviour, growth and reproduction. These can similarly impact host-finding and exploitation by the parasite, as well as susceptibility to the parasite by the host. Understanding these impacts and how they are likely to impact host-parasite interactions and co-evolution will require experimental studies. Many marine laboratories now have facilities that enable macrocosm experiments in which both temperature and acidity can be manipulated (Albright and Langdon 2011; Hall et al. 2012).

Trait-based approaches are gaining increasing popularity in studies of aquatic communities (e.g. Green and Côté 2014). Rather than being viewed solely in terms of assemblages of species per se, "functional" or "trait-based" approaches view communities as assemblages of functional traits and view an understanding of these traits as essential to understanding community dynamics (e.g. Messier et al. 2010). These traits include morphological, behavioural and even genetic characteristics. Trait-based approaches have recently been used to predict which parasites are most susceptible to climate change (Cizauskas et al. 2017). A necessary first step in all trait-based studies is characterising the myriad ecologically relevant, functional traits within communities. Given the abundance and diversity of parasitic Crustacea in aquatic systems and the paucity of aquatic ecologists with relevant training in parasitology, there is almost unlimited potential for students with the appropriate backgrounds to make substantial contributions to this rapidly growing field.

Perhaps the greatest ecological frontier on the planet is the deep ocean. Most ecological studies in the deep ocean have ignored parasites of any kind (Poulin et al. 2016), and the few studies that have incorporated parasite sampling into their methodology may be sampling in a manner that overlooks entire parasite groups. These studies have relied on the dissection of organisms that were retrieved from the ocean depths, and accordingly only internal parasites may be identified as most ectoparasitic Crustacea would have dislodged during retrieval. These challenges can be overcome as new technology and techniques become available. For example, a study on deep-sea benthic fish assemblages used high-resolution cameras mounted on submersibles, and the video footage revealed a rich assemblage of parasitic Crustacea easily seen on hosts (Fig. 10.9; Quattrini and Demopoulos 2016). This study as well as similar ones set the stage for at least community-level correlative studies on deep ocean parasitic Crustacea. As more correlative data on these organisms are collected, then more complex questions and experimental studies can be conducted.

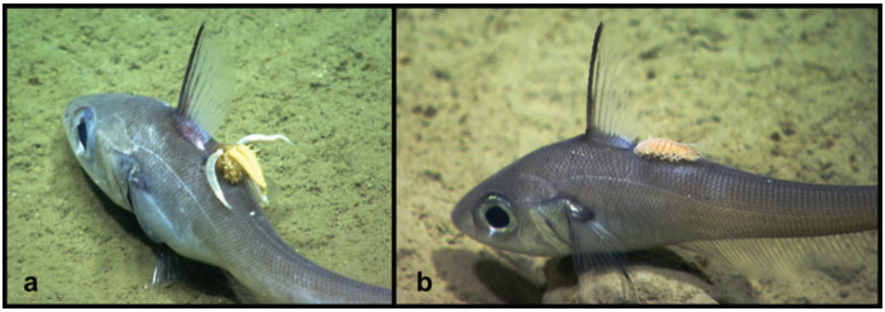

Fig. 10.9 Two deep-sea parasites on the Marlin-spike grenadier, *Nezumia bairdii* (Goode & Bean, 1877), a species of rattail fishes. (**a**) A sphyriid copepod parasitised by eight leeches can be seen on *N. bairdii* at a depth of 1035 m, (**b**) an aegid isopod has also been reported on *N. bairdii* at 780 m. See Quattrini and Demopoulos (2016) for more details. Images © NOAA Okeanos Explorer Program, Andrea M. Quattrini and Amanda W.J. Demopoulos

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