

Marine Parasitology

Klaus Rohde (Editor)

This book is available from **CSIRO PUBLISHING** through our secure online ordering facility at <http://www.publish.csiro.au> or from:

Customer Service
CSIRO PUBLISHING
PO Box 1139
Collingwood Victoria 3066
Australia

Telephone +61 3 9662 7666
Local call 1300 788 000 (Australia only)
Fax +61 3 9662 7555
Email publishing.sales@csiro.au

© CSIRO 2005

The sample pages following are provided solely for information purposes and may not be reproduced, stored or transmitted in any form or by any means without prior permission of the copyright owner. Contact **CSIRO PUBLISHING** for all permission requests.

Chapter 1

The nature of parasitism

This chapter consists of two sections. The first gives definitions of terms and a brief discussion of some adaptations to a parasitic way of life, such as body size, reproductive capacity, reduction and increase in complexity, and dispersal. The second discusses the distribution of parasites and in particular of marine parasites in the 'tree of life'. It is emphasised that life originated in an aqueous and probably marine environment, and that every marine organism is a potential host to parasites.

Definitions, and adaptations to a parasitic way of life

Klaus Rohde

Introduction

Biologists approach the study of parasites from different angles: some are interested in their physiology, others in their ecology, or medical and economic aspects, to mention only a few. Consequently, definitions of parasitism vary greatly, reflecting the research interests and biases of particular research workers. Baer (1952), Esch and Fernández (1993) and Rohde (1993, 2001) have discussed definitions and adaptations of parasites.

In most sections of this book, *parasitism* is understood to be a close association of two organisms, in which one – the parasite – depends on the other – the host – deriving some benefit from it. This benefit often is food. In some sections, however, the term *parasite* is used in a wider sense. For example, peritrich ciliates leading to severe problems in shrimp aquaculture are really fouling organisms that become pathogenic and fatal in heavy infections.

Many bacteria, viruses and fungi are parasitic. These organisms have traditionally been studied by microbiologists, and only protistan and metazoan parasites are considered to be objects of study by parasitologists *sensu strictu*, although the border between protistans and fungi is somewhat blurred. In this book, only protistan and metazoan parasites are discussed.

Related associations

Several types of associations are related to parasitism and cannot always be clearly distinguished from it. They include commensalism, phoresis (phoresy), mutualism, and symbiosis.

- *Commensalism* occurs where organisms use food supplied in the internal or external environment of a host without affecting the host in any way. Examples are certain barnacles on the skin of marine mammals.
- In *phoresis*, organisms use a host for transport or shelter. Examples again are certain barnacles on whales, or sea anemones on gastropod shells.

- A mutualistic association (*mutualism*) is one in which both organisms derive a benefit but the association is not obligatory. For example, cleaner fish and shrimp feed on parasites of hosts: the host is cleaned – an obvious benefit to it – and the cleaner derives food from the host; however, many cleaners can also feed on free-living animals and the association is therefore not obligatory.
- In a symbiotic relationship (*symbiosis*) the association is compulsory. The relationship of male and female echinurans or certain deep-sea fish, in which the dwarf male ‘parasitises’ the much larger female, can be considered symbiotic, because the male cannot live without the female and the female depends on the male for fertilising the eggs. The term symbiosis is also used to describe any association between organisms, such as parasitism, commensalism, mutualism, phoresis, and *symbiosis sensu strictu*.
- In *predation*, a predator kills and eats prey, in contrast to a parasite, which feeds on the host but often and usually does not kill it (although parasitic effects may sometimes be lethal in the long term).

A parasite, under certain conditions, may become a commensal, mutualist or predator. In many cases we know too little about a species to clearly state which kind of relationship it has with a host. Such species are included in many sections of this book.

Types of parasites, parasitic life cycles and hosts

Parasites can be divided into several different types:

- *Ectoparasites* are parasites that live on the surface of a host, while *endoparasites* live in the host’s interior. For example, most trematodes are endoparasitic in the internal tissues and digestive tract, whereas almost all monogeneans live on the gills or skin of fish (see pp. 55–72).
- Most species of parasites are *obligate parasites*, which need a host for survival at least during certain stages of their life cycle. A few (e.g. some ciliates) are *facultative parasites* and are able to survive in the free environment during their whole life but can parasitise a host as well (see pp. 37–41).
- *Temporary parasites*, such as leeches, infect their hosts only for short periods, whereas *permanent parasites*, such as roundworms or trematodes in the digestive tract of many marine animals, infect hosts for a long time (see pp. 72–87 and 104–115).
- *Larval parasites* are parasitic only during their larval stage (e.g. pranzia larvae of isopods) (see p. 144 and Fig. 6.5).
- *Periodic parasites*, such as leeches, visit their hosts in intervals (see pp. 196–202).
- *Hyperparasites* are parasites of parasites. In the marine environment, not many hyperparasites are known, but new ones are being described frequently. An example is the monogenean *Udonella* that infects copepod ectoparasites of fishes (see pp. 293–298).
- *Microparasites* (which include the protistans and some helminths) are small and have short generation times, reproduce in or on a host at high rates, the duration of infection is often shorter than the life span of hosts, and they induce immune responses in their vertebrate hosts. In contrast, *macroparasites* (arthropods and most helminths) are larger, do not multiply in or on the host, and have longer generation times than microparasites. They induce no or only weak immune responses depending on infection intensity, and infections are usually long lasting, leading to morbidity rather than mortality.

Parasite life cycles also can be divided into different types. Parasites with *direct life cycles* have only a single host. For example, most adult monogeneans are found on fish, whereas their larvae are free-living (see pp. 52–72). Parasites with *indirect life cycles* have several hosts. Adult digeneans

ans, for instance, are found in various vertebrates and their larvae infect at least one and often several hosts (see pp. 76–87).

Similarly, hosts of parasites can be divided into different types. *Definitive* or *final hosts* harbour the sexually mature stage of a parasite; *intermediate hosts* harbour immature, developing stages; and *paratentic hosts* (also called *transport hosts*) harbour larval forms that do not develop within the host.

Adaptations

All animal species, whether free-living or parasitic, must be adapted to their habitats in order to survive. The conditions necessary for survival may be very restricted or they may be wide. Thus, the degree of specificity for certain environmental conditions varies greatly between species. The question arises whether all or perhaps a great range of parasites share similar adaptations to a parasitic way of life. And indeed, all parasites have certain characteristics in common.

Parasites are always smaller than their host, in spite of the existence of some very large parasites. Didymozoid trematodes, common parasites in many marine fish, may be very large. A species infecting the sunfish *Mola mola* reaches a length of 12 m; however, its diameter is very small and the host may be as heavy as one ton. Thus, based on a comparison of volume, the parasite still is minute relative to its host. Interestingly, free-living species are often considerably smaller than related parasitic species. Free-living turbellarians, for instance, are usually one to a few millimetres long, whereas parasitic flatworms are much larger, trematodes up to several centimetres, and cestodes up to several metres in length. Reasons for this may be twofold. First, parasites have an almost unlimited and secure food supply provided by the host. Second, selection may favour larger worms with larger reproductive organs because production of many offspring is even more important for parasitic than for free-living species since only a minute proportion of offspring ever manages to infect a host. However, selection may favour the smaller body size of parasites, because too large a size might damage the host on whose survival the parasite depends. In an evolutionary context there will therefore be a trade-off between selection favouring larger and selection favouring smaller body size.

As pointed out above, parasites depend for survival on the production of many offspring, and data show that reproductive capacity is often greater in parasitic species than in related free-living forms. This is well shown in the Platyhelminthes. In spite of the great variability in the number of offspring (as measured by the number of eggs/larvae produced plus multiplication at the larval stage), there are clear trends: free-living turbellarians produce about 10 or so eggs throughout their life on average, and there is no multiplication of larval stages; ectoparasitic Monogenea produce about 1000 eggs, without multiplication of larvae; endoparasitic trematodes may produce millions of eggs and larvae do multiply. Endoparasitic cestodes also may produce millions of eggs and may have multiplication of larvae. Larval multiplication is particularly well developed in the trematodes. A single egg produces one miracidium that infects a mollusc. In the mollusc intermediate host, the miracidium develops into a sporocyst which gives rise to numerous rediae. Rediae, in turn, produce numerous cercariae which leave the snail and infect the final host. Thus, a single egg can produce tens of thousands of offspring.

It is commonly believed that parasites have lost much of the complexity of free-living animals because they depend on the host for food and shelter and so supposedly do not need the same range of sensory receptors, a complex nervous system, sophisticated feeding organs and so on. This is indeed sometimes the case and an example of this is the rhizocephalan *Sacculina*, which parasitises marine crabs. The juvenile, free-living larva has all the characteristics of larval barnacles (to which the rhizocephalans are related) but the adult consists of a sac-like structure (the so-called externa) attached to the ventral surface of the crab's abdomen, and an extensive system of cytoplasmic processes that reach into the various host tissues, without any

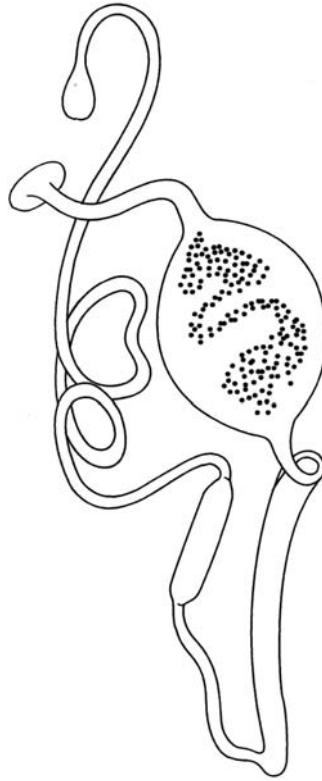


Figure 1.1 A parasitic snail from the body cavity of a sea cucumber. All external similarities with a snail (i.e. head with tentacles, eyes, foot and shell) have completely disappeared due to the endoparasitic way of life, leading to a worm-like appearance of the snail. Redrawn after Koehler and Vaney from Baer (1952).

morphological crustacean characteristics. Simplification of parasites is sometimes called ‘sacculinisation’, based on this example. Another example is illustrated in Figure 1.1, which shows a snail parasitic in a sea cucumber that has lost all characteristics of snails. Similarly, Figure 1.2 shows the gradual transformation of the copepod *Lernaeocera branchialis* from a free-living nauplius larva, with all the characteristics of other crustacean larvae, to the adult parasitic stage which has mouthparts inserted into a blood vessel of its fish host and a body completely transformed to a sac-like structure. Very often, however, sacculinisation is not evident and parasitic species may even be more complex than their free-living relatives. For example, detailed electron-microscopic studies of the aspidogastreaean *Lobatostoma manteri* have shown that the juvenile/adult stage (3–5 mm long) has about 20 000–40 000 sensory receptors of about 12 different types, many more than are found in most free-living flatworms, the turbellarians. Its nervous system also has a much greater complexity than that of turbellarians (for details see Rohde 1999). Importantly, *Lobatostoma manteri* does not have a single free-living stage; therefore, the function of receptors and nerves must be related to the endoparasitic way of life of the parasite. No experimental evidence is available but it is possible that the receptors are important in finding mating partners and microhabitats within the final host, and in preventing damage to the delicate host tissue in the intermediate snail host. Comparison of monogeneans parasitic on the gills and body surface of fish to free-living turbellarians shows that the former have a variety of complex attachment and copulatory structures while the latter do not.

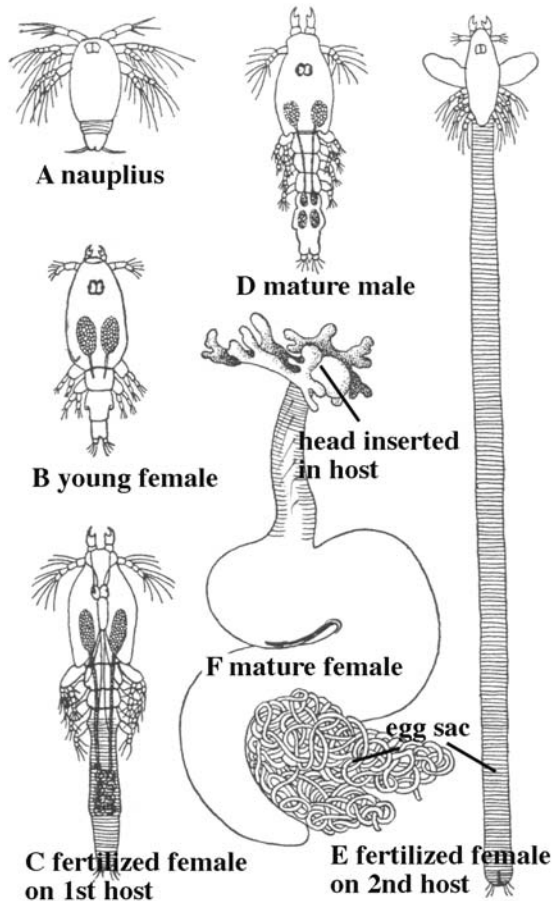


Figure 1.2 Transformation of *Lernaecocera branchialis*. A. Free-living larva. C–F. Adult stage. After Scott from Baer (1952).

All animal species disperse at some stage of their life cycle. This is essential for the survival of a species because populations restricted to a small area will become extinct if conditions deteriorate, and also because inbreeding in a small, restricted population may lead to loss of evolutionary versatility and to extinction. For parasites, dispersal must be particularly effective because hosts are difficult to find. Dispersal of parasites may result from host dispersal, as occurs when eggs of various helminths are spread by migrations of fish and mammal hosts. Alternatively, the parasites themselves may have dispersal mechanisms. Thus, eggs of various helminths are dispersed by migrations of fish or mammal hosts, whereas trematode larvae (cercariae), for instance, have various morphological adaptations such as finfolds or hair-like extensions of the tail that serve as flotation mechanisms, leading to dispersal by water currents.

Unique to parasites are mechanisms of infections, of which there is a great variety. A few examples are given here: trypanosomes are injected into the blood of fish by blood-sucking leeches; many trematodes are acquired by ingesting cysts (metacercariae); *Anisakis* is acquired by eating transport hosts, and *Diphyllobothrium* by eating infected intermediate hosts; and schistosomes penetrate the skin of marine birds. (For a fuller discussion see sections on the various parasite groups and pp. 280–286). Not infrequently, parasites induce behaviour changes in their host which increase the likelihood of infecting the next host in the life cycle (see pp. 259–264).

Many parasites either have asexual/parthenogenetic reproduction or are hermaphroditic, that is, even a single parasite individual can build up a population. This has definite advantages for them given that the likelihood of reaching a host is very small.

All species, whether parasitic or not, have restricted habitat requirements. In parasites this is expressed as host and site specificity. There is no universal parasite that infects all hosts and sites within a host equally, although the degree of specificity varies. Some trematodes, for example, infect a wide range of marine fish species whereas some monogeneans are restricted to a single host species and are always found on a small segment of the gills (see p. 292).

Besides the characteristics shared by many taxa and resulting from adaptations to a parasitic way of life, all parasites have special adaptations, including physiological ones, that are very specific, determined by the phylogenetic position of the parasite and by its host. Such specific adaptations are discussed in the various sections on parasite groups.

Important references

The following authors give detailed discussions of important aspects of parasitism, including definitions and adaptations: Baer (1952), Esch and Fernández (1993) and Rohde (1993, 2001).

Marine parasites and the tree of life

DTJ Littlewood

Introduction

It seems unlikely any species escapes being parasitised, except perhaps the very smallest organism that, simply because of its size, cannot house or provide sustenance to another. As such, much of biodiversity (species richness) may be viewed as a diversity of hosts for parasites. Nearly all organisms expend at least some energy in avoiding parasites or ameliorating their effects. Individuals may spend their life parasite-free, but few species have evolved without parasitism having at least some part in the natural selective processes that have shaped their present form and biology.

Parasitism is a highly successful, but often underrated and certainly underscored, life history strategy. A cryptic life stage or a fleeting association with a host may make it a difficult phenomenon to detect. Additionally, even when parasites are large, persistent and low prevalence levels may compromise their detection. Parasitism is a biological trait that is defined predominantly in ecological terms (see e.g. Combes 2001). It unites a plethora of species that may or may not be closely related phylogenetically. However, when viewed in the light of phylogeny, parasitism has evolved many times over. Even among predominantly free-living groups usually at least one lineage engaging in this life style can be detected. Frequently, whole clades of species (phyla, classes, orders and families) have evolved obligate parasitism. These groups are dealt with separately in this volume. Curiously, it seems that once parasitic, a lineage never gives rise to a free-living form; in evolutionary terms, parasitism is irreversible. Lineages that have successfully adopted parasitism are often species rich and are at least as diverse as the hosts they interact with. Parasitism itself is a driving force in genetic diversity (e.g. Frank 1993).

The evolutionary history of either the parasite or host cannot be viewed in isolation if we are to understand the nature and evolutionary ecology of parasitism (Poulin 1998). Complex life cycles, where more than one host species is involved, renders the subject of parasite evolutionary ecology even more problematical. In any case, the tree of life, or at least a phylogeny of parasites and their hosts, is an eminently suitable starting point; coevolutionary studies tracking both host and parasite phylogenies are proving to be even more powerful (Page 2003) (see also pp. 327–339).

The tree of life

An understanding of the interrelationships between organisms, through the construction of a phylogeny, provides us with a means to track the origins and radiation of novelties and adaptations through evolutionary time. With morphology alone, phylogeneticists find it difficult to determine relationships between, and sometimes within, plant and animal phyla. The advent of molecular and biochemical systematic tools, and the growth of phylogenetics as a discipline from the latter half of the 20th century onwards, has allowed many of these barriers to be overcome (Balter 1997), although in some cases these developments have fanned the flames of old controversies and generated some new ones. Modern molecular systematic methods are the foundation for understanding microbial and other relatively simple organisms, but have contributed also to our understanding of morphologically complex taxa. Studies of parasitic taxa that have converged on similar morphologies or that have poorly distinguishable life stages have benefited also from these new tools in resolving species boundaries and inter-relatedness. Indeed, whole clades owe their names to molecular evidence [e.g. the Ecdysozoa and the Syndermata (rotifers and acanthocephalans)]. Armed with molecular sequencing, bioinformatics, and increasingly faster computers that allow large quantities of data to be handled (including nucleotides, amino acids, proteins, genomes and, of course, morphology), researchers have begun to estimate the entire tree of life (e.g. Cracraft and Donoghue 2004). There is only one tree of life, recapitulating each and every branching point in the evolutionary history of life, but achieving its resolution, with every tip in its rightful place, is no simple task. One preliminary approximation, based on a multitude of published empirical studies and a consensus opinion of a subsample of researchers is shown in Figure 1.3 (after Pennisi 2003; with an online and interactive version also available).

Most major groups appear to be well resolved in the overall scheme but insufficient data, or even conflict between independent sets of data, have yielded unresolved branching points. Such *polytomies* are not uncommon, regardless of the taxonomic level under investigation, even among closely related species based on multiple data sets, and yet in spite of incongruence or poor nodal support, the tree of life is taking shape. The paucity of systematists, and the large collective effort required, limits the progress of the Tree of Life project, but for many purposes there is already sufficient useful resolution. Further websites from which interrelationships between organisms can be viewed include the Tree of Life Web Project and TreeBase.

Marine life

It is generally agreed that life itself probably arose in the marine, or at least a watery, environment (e.g. Whitfield 2004). Thus, it is not surprising to see how many organisms have representatives, or are indeed restricted to, living in seas and oceans. If we consider extinct as well as extant organisms, it is also clear that the marine environment has been abandoned and recolonised many times through evolutionary history. Mammals, turtles, snakes and crocodiles include obvious examples of terrestrial-born lineages that have colonised saltwater habitats since their appearance, sometimes bringing their parasites with them, although more usually being parasitised by many new species as they adapted to their different environment. Even groups and lineages we generally consider to be strictly terrestrial, or to have very little to do with the marine environment, include examples with some connection to the sea; for example, parasitic lice of marine birds renders the Paraneoptera as having both marine and marine parasitic representatives (Fig. 1.3). Even spiders, collembolans and beetles have marine representatives when we consider those intertidal examples that hide, trapped in air pockets in rock pools, at high tide. Organisms that we might not consider to be marine *per se* may at least interact with the marine environment and certainly, from a parasitological perspective, may be hosts in marine parasite life cycles (e.g. birds visiting and feeding in the intertidal zone).

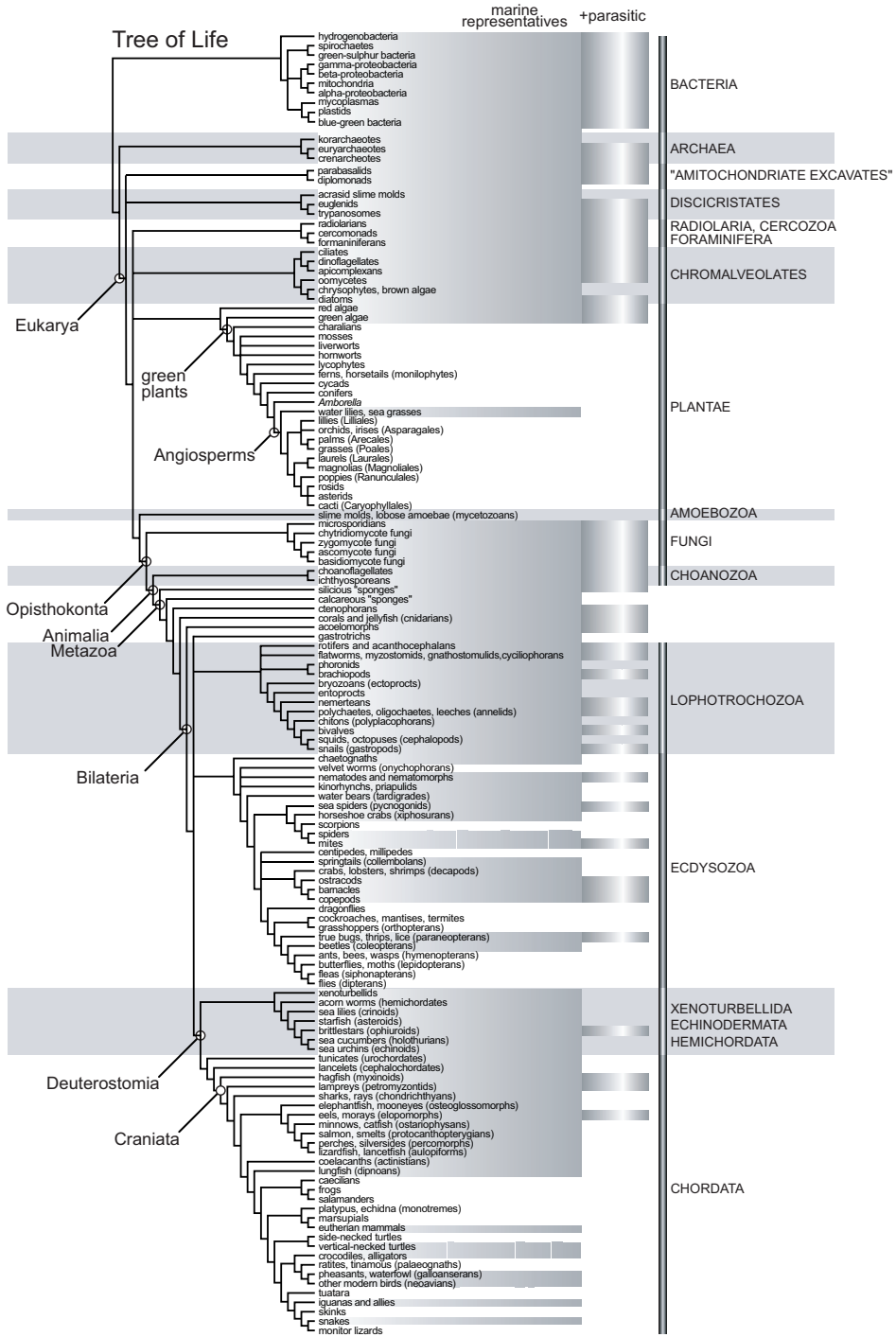


Figure 1.3 The tree of life based on a consensus of studies and opinions, originally published in Pennisi (2003) but modified and further annotated here, with an indication of which clades have marine representatives and which of these include parasitic forms. A web-based copy of the tree, with links to sites covering individual groups, is available at: *The American Association for the Advancement of Science* (2004) reproduced with permission.

Marine organisms as hosts

The enormous variety of marine environments and prevailing marine conditions that exist globally is equally matched by the diversity of organisms that make these habitats their home. Every marine organism is potentially a host to a parasite, but depending on locality, season, local ecology and parasite species in question, any candidate host may or may not be parasitised. Clearly, not every organism is a suitable host for every parasite, but to understand fully the taxonomic range of host-parasite interactions, we need to consider obligate and facultative interactions, and even the paratenic hosts that help to bridge trophic gaps. Beyond individual studies of hosts and their parasites, there exist few resources for quantifying the extent to which parasitic taxa occur within and between different host species. One such resource, covering five phyla (flatworms, nematodes, acanthocephalans, nematomorphs and mesozoans) is the Host-Parasite Database (Natural History Museum 2004).

Size of the host limits the upper, but usually not the lower, size of the parasites that manage to infect it. This contributes to the many factors determining which parasites we may expect to find in any given species at any time during its development. Larval stages are readily parasitised but not necessarily by the same taxa that infect adult stages. Host size, host ecology and parasite life history strategy constrain the taxonomic range of possible host-parasite combinations, not to mention host-specificity or host defence mechanisms. Small multicellular (metazoan) animals tend to be parasitised by unicellular organisms. Correspondingly, bigger animals become suitable hosts for bigger (unicellular and/or metazoan) parasites, and may even increase levels of prevalence within a species. The largest living animals, the cetaceans, are host to the longest nematodes and tapeworms and the sheer abundance of these parasites, measured as numbers or biomass, shows how host size may have a profound effect on the biology of the parasites that infect them. Nevertheless, in isolation, the tree of life of hosts indicates few patterns or trends that shed light on the evolution of marine parasitism.

Marine parasites and the origins of marine parasitism

Many of the lineages in the tree of life are exclusively marine, but considerably fewer are exclusively parasitic. The tree of life showing marine parasites (Fig. 1.3) indicates, perhaps obviously, that marine parasitism is generally restricted to marine hosts. However, the origins of marine parasites are not necessarily marine. Among the parasite lineages that have remained exclusively marine, or at least aquatic, since their divergence (e.g. copepods) we might safely deduce that parasitism originated in the marine environment. This appears to be true in most cases. Exceptions include mites of marine mammals that presumably had terrestrial origins and are themselves not truly marine, although they infect air pockets within marine hosts (e.g. nasal mites of seals and sea otters). To determine the origins of parasitism requires knowledge of sister group relationships within and between parasite lineages, the determination of free-living sister groups and the inference of ancestral life history strategies. Such an approach has been used to investigate the origins and radiation of parasitism in some groups (e.g. the Digenea, Cribb *et al.* 2003; the Nematoda, Blaxter 2003), but to a great extent most tips of the tree of life still lack sufficient resolution.

Although many lineages on the tree of life include marine parasitic representatives, there are a few groups of significant interest, including the various protistan, helminth and crustacean parasites. Among each of these groups are obligate parasite lineages that have radiated very successfully, in terms of biomass, species number, host diversity and geographic distribution. Estimating parasite numbers is as difficult as estimating the number of species on Earth. However, to illustrate their success, few species of aquatic vertebrate escape parasitism by at least one (and usually many more) species of digenean, cestode, monogenean, nematode and acanthocephalan (the helminths) and one or more crustacean species. The protistan parasites appear to be even

more widespread and we know less about the invertebrates as hosts. Further study will reveal the true diversity of marine parasites, but given the small fraction of marine biodiversity studied so far, at least from a parasitological viewpoint, we can expect the number of parasites to represent a substantial and significant proportion.

Important references

Molecular data are increasingly used to clarify phylogenetic relationships, but morphology has to be considered as well. Important references in this field are by Balter (1997), Blaxter (2003) for nematodes, chapters in Page (2003), Pennisi (2003), Cracraft and Donoghue (2004) and Cribb *et al.* (2003) for the Digenea.