

Chapter 4

Crustacean parasites

Of all the metazoan groups discussed in this book, the crustaceans are the most diverse and ubiquitous. Among them, the copepods are dominant. They, jointly with the monogeneans, are the most speciose group of metazoan ectoparasites of marine fishes; in addition, they infect a wide range of marine invertebrates. Thousands of species are already known, but many potential host groups have not been examined, and for this reason even approximate estimates of species numbers are impossible. Reflecting the diversity of hosts, copepods show an amazing variety of adaptations which secure infection of and survival on the hosts. Many copepods have great economic importance as agents of disease in wild and aquacultured fish populations. Isopods are primarily found in warm waters, they infect fish but also other crustaceans. Larval isopod parasites of the family Gnathiidae are abundant on the gills of tropical marine fish and represent a primary source of food for cleaner fish. Most branchiurans occur in fresh water, but a few species of the genus *Argulus* are ectoparasites on the skin of marine fish. The tiny tantulocarids are ectoparasites of other crustaceans. To date only 28 species have been described, and little is known about their biology. Thoracica and Rhizocephala are included in the Cirripedia. Few species of the Thoracica are parasitic (on dogfish and polychaetes), whereas the rhizocephalans parasitise other crustaceans. The latter are particularly fascinating because of their extreme sexual dimorphism, the extreme reduction of morphological complexity in the parasitic female, and their ability to change the behaviour of host crabs which benefits the parasite. The Ascothoracida infect various echinoderms and cnidarians. Amphipoda use many groups of marine animals as hosts, including medusae, siphonophores, ctenophores, and thaliaceans. Others (including the whale-lice) infect various marine mammals. When occurring in large numbers, whale-lice may even damage very large humpback whales.

Copepoda (copepods)

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Introduction

Copepods are typically small and inconspicuous aquatic crustaceans but they are extremely abundant. They outnumber even the insects since free-living copepods dominate the zooplankton community in the open pelagic water column, the largest biome on the planet. About 11 500 valid species are known, about half of which live in symbiotic associations. Most of these are probably parasitic but the precise nature of the relationship with the host has yet to be elucidated for the majority. Because of this uncertainty, such forms are typically referred to using the neutral term 'associates' in the copepod literature. Parasitic copepods utilise an extraordinary

range of hosts, occurring on virtually every available phylum in the marine environment from the sponges and cnidarians up to the echinoderms and chordates, including sea squirts, fishes and even mammals. They occupy a similarly wide range of microhabitats on their hosts, both as ectoparasites and as endoparasites. Most research has been conducted on the fish parasites and the biology of the parasites of marine invertebrate hosts is relatively less well known, with the exception of a few species found on commercially important invertebrates such as mussels or scallops. The classification of copepods is in a labile state. Numerous lineages have moved independently into parasitism as a mode of life and the old concept of Copepoda Parasitica as a taxon has no validity (Kabata 1979). Ten orders were recognised by Huys and Boxshall (1991) on the basis of morphological characters, but only nine were adopted by Boxshall and Halsey (2004), four of which are either wholly parasitic (order Monstrilloida), largely parasitic (orders Siphonostomatoida and Cyclopoida) or contain some parasitic forms (order Harpacticoida). Molecular methods based on DNA sequence data are of immense power in the analysis of phylogenetic relationships, but they have yet to fully impact copepod systematics; a period of profound change is to be expected.

Morphology

Basic structure

Copepods exhibit two body plans: the gymnoplean plan in which the body is divided into two tagmata, an anterior prosome and posterior urosome, at the articulation between fifth pedigerous (leg-bearing) and genital segments (referred to as somites by convention), and the podoplean plan in which the prosome and urosome articulate one somite nearer to the head, between the fourth and fifth pedigerous somites (Fig. 4.1). All the parasites conform to the latter type and, though many are profoundly modified, all can be derived from the basic cyclopiform body plan. Cyclopiform copepods are so-called because they resemble the free-living copepod *Cyclops* in possessing well-defined body segmentation, clear tagmosis and the entire set of limbs. The prosome comprises a cephalosome made up of the five cephalic somites typical of all crustaceans plus the incorporated maxilliped-bearing (first thoracic) somite, and the first to fourth pedigerous somites. The urosome typically comprises the fifth pedigerous, genital and four free abdominal somites. In adult males all these somites are separate but in most females the genital and first abdominal somites secondarily fuse at the final moult, to form a genital double-somite. Podoplean copepods typically carry their eggs in paired egg sacs, which are extruded from the paired genital apertures and carried by the female until ready to hatch. The presence of paired egg sacs is a useful clue to the identity of very transformed copepod parasites that lack any other morphological characteristics.

The basic set of appendages comprises five cephalic and seven thoracic limbs, plus the paired caudal rami located on the anal somite. In order from the front the limbs are: antennules, antennae, mandibles, maxillules, maxillae, maxillipeds and first to sixth swimming legs. The ancestral segmentation and setation patterns were hypothesised for all appendages by Huys and Boxshall (1991), who noted that the dominant evolutionary trend in copepods is oligomerisation (fusion of body somites and reduction and loss of appendage segments and setal elements). Oligomerisation typically results from progressive reduction and loss, culminating in the extreme simplification exhibited by the terminal branches of several parasitic lineages within the copepods.

The reader is referred to Kabata (1979), Huys and Boxshall (1991) and Boxshall and Halsey (2004) for detailed illustrated accounts of copepod morphology.

Parasites of fishes

Copepods have been parasitic on fishes at least since the Lower Cretaceous, about 110 to 120 million years ago. Nearly 30 families of copepods contain parasites that utilise fishes as hosts

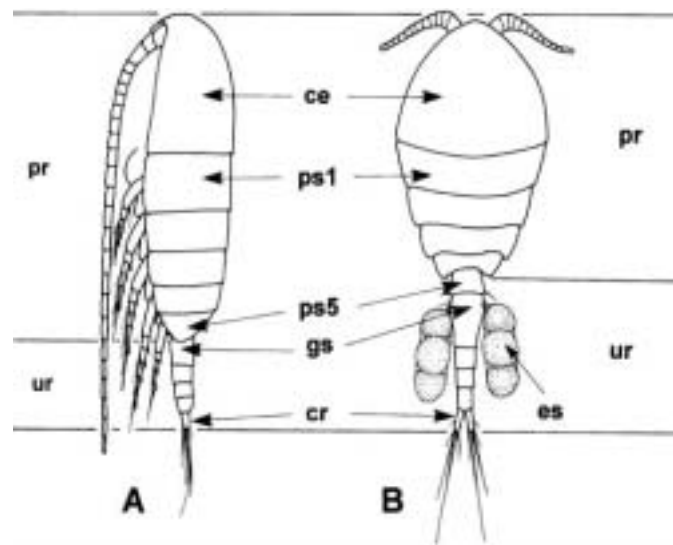


Figure 4.1 Body plans in the Copepoda. **A.** Gymnoplean plan, showing division between prosome and urosome located posterior to the fifth leg-bearing somite. **B.** Podoplean plan, showing division between prosome and urosome located anterior to the fifth leg-bearing somite. Abbreviations: ce, cephalosome; cr, caudal rami; es, egg sac; gs, genital double-somite; pr, prosome; ps1–5, pedigerous somites 1 to 5; ur, urosome.

(Table 4.1) and most are found exclusively on fishes. The body form of fish parasites varies from cyclopiform through to highly metamorphic (rather amorphous bodies that lack expressed segmentation and either have reduced limbs or may lack limbs altogether). Accompanying this trend towards a more transformed morphology is a tendency towards larger body size. Parasites with cyclopiform bodies, such as the Bomolochidae (Fig. 4.2A) and Taeniacanthidae, are typically small (about 1.0–2.0 mm in body length) whereas members of strongly metamorphic families often attain larger body sizes, in the range of 5 mm to 20 mm or greater. There are a few closely related (i.e. bomolochid-like) families, such as the Tegobomolochidae, Telsidae and Tuccidae, that have more transformed, swollen bodies and larger body size. Similar trends can be noted within particular families. The Ergasilidae, for example, contains many estuarine and coastal forms (as well as freshwater species) and exhibits a range from cyclopiform to vermiform, metamorphic bodies. Cyclopiform ergasilids rarely exceed 1.0 mm in body length whereas metamorphic forms commonly attain larger body sizes.

Table 4.1 Copepod families parasitic on marine fishes

Common	Intermediate abundance	Rare
Caligidae	Cecropidae	Lernaeosoleidae
Bomolochidae	Dichelesthiidae	Hyponeoidae
Chondracanthidae	Dissonidae	Tanypleuridae
Ergasilidae	Eudactylinidae	Anthessiidae ^A
Hatschekiidae	Pseudocycnidae	Macrochironidae ^A
Pandaridae	Shiinoidae	Tisbidae ^A
Pennellidae	Sphyriidae	
Lernaeopodidae	Tegobomolochidae	
Lernanthropidae	Telsidae	
Philichthyidae	Tuccidae	
Taeniacanthidae		

^A Large families with only one species on fish host.

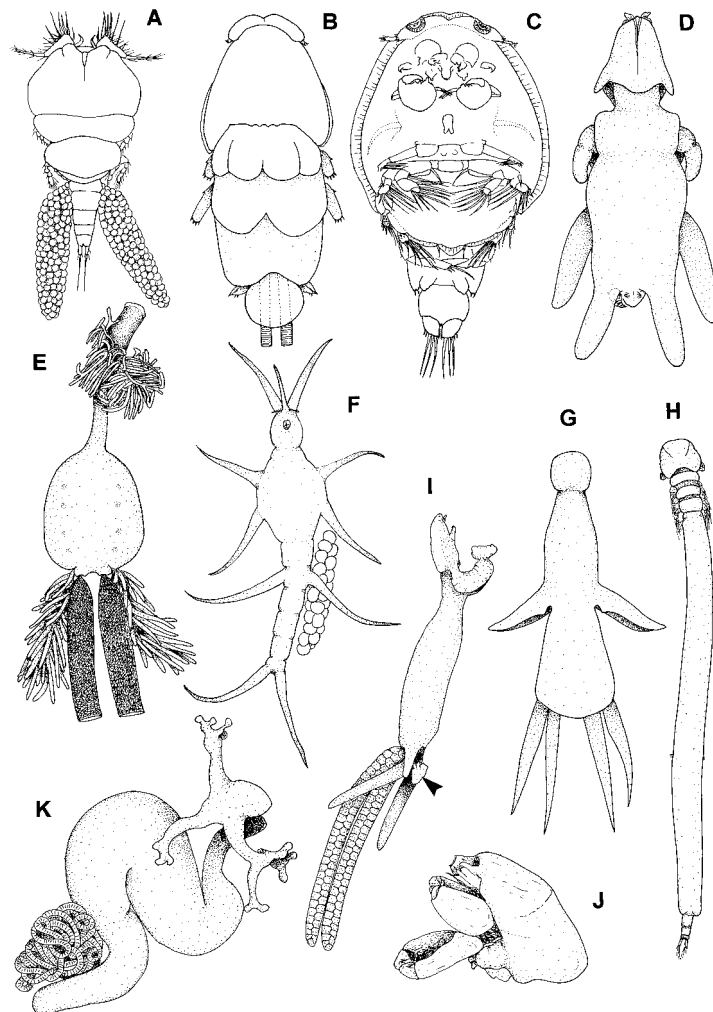


Figure 4.2 Range of gross morphology of copepod families parasitic on fishes. **A.** Bomolochidae, **B.** Pandaridae. **C.** Caligidae. **D.** Chondracanthidae female with male attached. **E.** Sphyriidae. **F.** Philichthyidae. **G.** Lernanthropidae. **H.** Kroyeriidae. **I.** Lernaeopodidae female, showing maxillary arms holding bulla (b) at tip, and with male attached (arrowhead); **J.** Male. **K.** Pennellidae.

Cyclopiform families frequently inhabit relatively sheltered microhabitats on their hosts including the gill chambers and nostrils, although some species may occur on the outer body surface, on the fins or around the eyes. They usually attach using clawed antennae, but some also display modifications of the ventral body surface and limbs that allow them to generate suction onto the surface of the host. In the Bomolochidae the antennules and first swimming legs are flattened and armed with swollen setae, and they function as part of the sucker rim that forms the seal against the mucous-covered skin of the host. Primary attachment is by claws: the suckers provide a secondary attachment mechanism, as does the embedding of the body in the more metamorphic ergasilids such as *Mugilicola*.

The caligiform families within the order Siphonostomatoida are characterised by dorso-ventrally flattened bodies divided into an anterior cephalothorax and a post-cephalothoracic genital trunk. These families can be viewed in sequence of increasing modification of body form,

particularly in the number of leg-bearing somites incorporated into the cephalothorax and fused beneath the dorsal cephalothoracic shield. In the Dissonidae and Pandaridae (Fig. 4.2B) only the first pedigerous somite is incorporated under the dorsal shield, in the Trebiidae the first and second are incorporated, while in the Caligidae the first to third are all incorporated. The Caligidae (Fig. 4.2C) is the most speciose family of fish parasitic copepods, comprising over 465 species, and includes the sea lice, which can cause severe economic losses to fin-fish aquaculture, particularly of salmonids (Boxshall and Defaye 1993, Pike and Wadsworth 1999). Caligids and related caligiform families typically attach to the host using a combination of claws and suction: the entire cephalothorax is rimmed with marginal membrane and modified limbs, and forms an effective seal against the host surface. On the ventral surface, within the cephalothoracic sucker, are the clawed antennae and maxillipeds, which serve primarily for attachment by hooking into the skin of the fish. In some caligids attachment is further enhanced by additional paired suckers, the lunules, located ventrally on the frontal plates, as well as by the various spines and processes which enhance friction between parasite and host. Despite these modifications most caligid adults are freely motile over the surface of their hosts and adults of several species are routinely taken in plankton samples. In addition to using clawed appendages to attach to the skin of their elasmobranch hosts most pandarids (Fig. 4.2B) also have adhesion pads located on the limbs or ventral cephalothoracic surface.

The remaining families of siphonostomatoids that use fish as hosts can be divided into two categories: those exhibiting an intermediate level of transformation in body morphology (often elongate bodies typically retaining indications of external segmentation and attaching by clawed appendages) and those that have highly derived body forms (typically lacking expressed segmentation in adults, lacking functional swimming legs and often attaching by embedding of specialised anchor-like structures). The former group comprises families such as the Eudactylinidae, Kroyeriidae (Fig. 4.2H), Dichelethiidae, Hatschekiidae, Pseudocycnidae and Lernanthropidae (Fig. 4.2G), and can be found on a wide range of elasmobranch and actinopterygian fishes. Most species within these families inhabit the branchial chambers of their hosts, usually the gills, where they attach using clawed antennae, maxillipeds (if present) and/or maxillae. Adults are never found away from their hosts. The group of profoundly modified families includes the Lernaeopodidae, Pennellidae (Fig. 4.2K) and Sphyrriidae (Fig. 4.2E). Lernaeopodids typically have a large, fleshy body and attach to the host by means of the bulla (b, Fig. 4.2I), a small chitinous plug which is inserted into the host epidermis and held by the maxillary arms. Adult females are permanently anchored to the host by the bulla whereas males (Fig. 4.2J) are relatively tiny and hold on to the females using their strong antennae. The lernaeopodid *Naobranchia* has no bulla, attaching using ribbon-like maxillary arms to encircle the gill filaments of the host. Pennellids and sphyrriids are large parasites, with the former family including the largest of all copepods, *Pennella balaenopterae*, a parasite of baleen whales that can attain a body length in excess of 16 cm. These parasites are anchored to the host by a cephalic holdfast, formed by the entire head, which develops more or less complex processes and is deeply embedded in the host tissues. This form of attachment is secure for these large-bodied copepods.

There are several important fish parasitic families belonging to the order Cyclopoida, which now incorporates the Poecilostomatoida, formerly treated as a distinct order by Kabata (1979) and by Huys and Boxshall (1991). These have a flat, plate-like upper lip (labrum) and short, blade-like or toothed mandibles, and are readily distinguished from the siphonostomatoids which are characterised by possession of an oral tube, formed by the labrum and the fused paragnaths (Boxshall 1990a), containing the stylet-like mandibles. The more highly modified cyclopoids, such as the Chondracanthidae (Fig. 4.2D), Shiinoidae and Philichthyidae (Fig. 4.2F), typically have bodies lacking in expressed segmentation and lacking at least some of the swimming legs. The first two of these families are most frequently found in the branchial chamber of

the host where they attach by means of robust antennal claws. Security of attachment is often enhanced by the hyperplastic tissue response of the host, in which the epidermis overgrows the head of the parasite, effectively creating an anchor process. Most members of the Philichthyidae inhabit the subcutaneous spaces associated with the sensory canals of the lateral line and skull bones of their hosts. In both the Chondracanthidae and Philichthyidae the body is typically fleshy and may be provided with elaborate processes, the function of which is uncertain.

Parasites of marine invertebrates

The body form of copepods parasitic on marine invertebrates is astonishingly varied: many retain the basic cyclopiform body but some of the most extreme examples of secondary reduction in body segmentation combined with the loss of paired limbs are found in copepods from invertebrate hosts. Sponges, for example, act as host to a wide variety of copepods (particularly from the Siphonostomatoida) many of which, such as the Asterocheridae (Fig. 4.3A) and Dinopontiidae, are basically cyclopiform even though they inhabit the internal canals of the sponge. The Entomolepididae are more modified, having dorsoventrally flattened and rather scale-like bodies, but they are recognisably derived from a cyclopiform plan. Families such as the endoparasitic Spongiocnizontidae and Sponginticolidae have a highly derived morphology, with unsegmented, vermiform bodies and almost complete loss of limbs in the latter.

Copepods can be found as parasites across the entire range of cnidarian groups from the hard corals and sea anemones to the medusae and siphonophores (Humes 1985). Many common families, such as the Anchimolgidae, Asterocheridae and Rhynchomolgidae, are ectoparasitic, typically retaining cyclopiform morphology and attaching to their hosts by clawed antennae. Other families are more derived. Members of the Xarifiidae and Corallovexiidae (Fig. 4.3G) for example, which inhabit the gastrovascular cavities of scleractinian corals, have vermiform, unsegmented bodies and reduced limbs. More extreme are the Lamippidae which are endoparasitic in octocorals, particularly the alcyonacean soft corals. Some lamippids have unsegmented bodies equipped with enormous processes that give them a stellate appearance.

Relatively few species of copepods make use of host groups such as the Nemertea, Platyhelminthes, Bryozoa, Phoronida, Echiura, Brachiopoda, Enteropneusta, Hemichordata, Vestimentifera and Sipuncula (Boxshall and Halsey 2004). Those that parasitise these taxa mostly retain cyclopiform bodies and attach by clawed cephalic limbs. The exceptions are the Echiuophilidae, which can have elongate body processes, some Catiniidae which attach to their sipunculan hosts using antennal suckers, and the *Akessonia*- and *Ive*-groups that are endoparasitic in sipunculans and acorn worms, respectively, and have highly transformed vermiform or lobate bodies, lacking several limbs.

Eleven families of copepods are recorded exclusively from polychaete worms, but most are rarely encountered. Few retain cyclopiform morphology, such as members of the Eunicicolidae and Clausiidae. Even some clausiids are modified by reduction of expressed body segmentation and increase in body size, as are members of the Anomoclausiidae, Entobiidae, Spiophanicolidae and Serpulidicolidae. All of these families attach by means of clawed cephalic appendages. The Herpyllobiidae, found on polynoid worms, contains some of the most extremely modified parasitic copepods known. Adult females are sac-like (Fig. 4.3J), lacking any segmentation and all limbs, and can only be identified as copepods by reference to their paired egg sacs and their early larval stages. They are mesoparasites – living with the anterior portion, the endosoma, embedded in the host and with the posterior portion, the ectosoma, sticking out from the host's surface and carrying the egg sacs. Dwarf males are found attached to the genital region of the female. Four other families, also mesoparasites of polychaetes, exhibit similar extreme oligomerisation, these are the Bradophilidae, Phyllocolidae, Saccopsidae and Xenocoelomatidae.

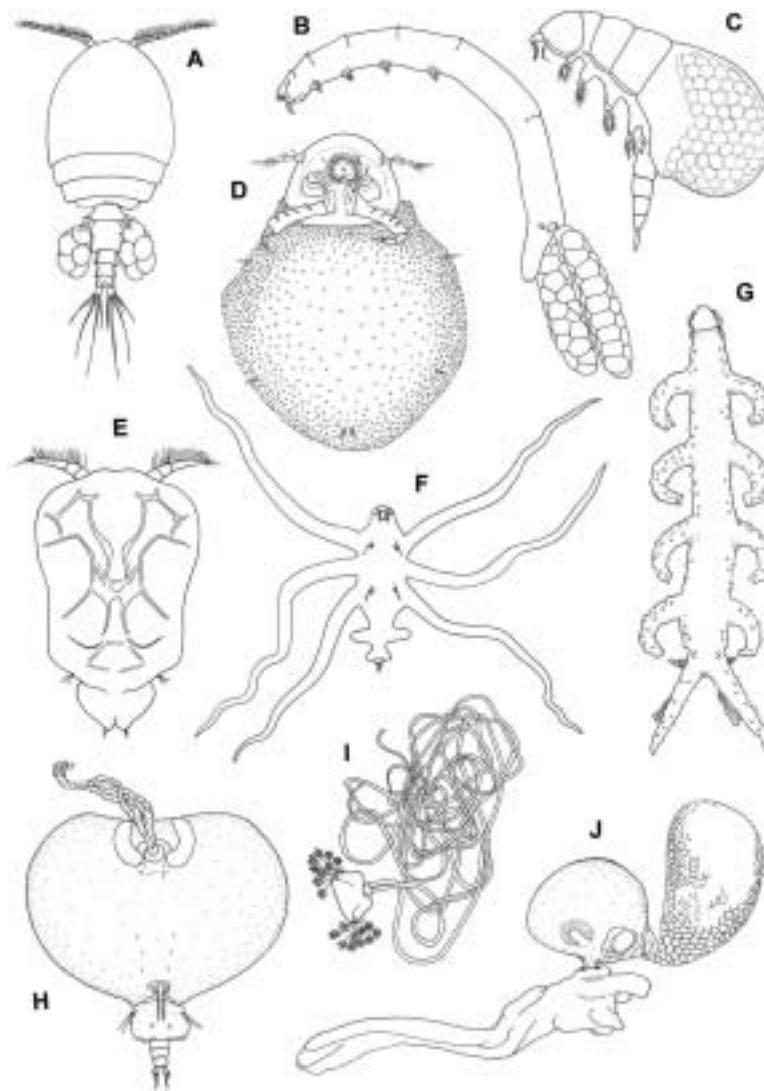


Figure 4.3 Range of gross morphology of copepod families parasitic on invertebrate hosts. A. Asterocheridae. B. Mytilicolidae. C. Notodelphyidae. D. Nicothoidae. E. Stellicomitidae. F. Splanchnotrophidae. G. Corallovexiidae. H. Nicothoidae (*Nicorhiza*, showing rootlet system derived from oral tube). I. Chitonophilidae, with rootlets. J. Herpyllobiidae, showing body divided into endosoma and ectosoma, bearing egg sac (other sac removed).

Copepods parasitise most molluscan groups, from aplacophorans and polyplacophorans to the cephalopods. Most have bodies that are cyclopiform or only slightly modified and this applies particularly to ectoparasitic forms found on the gills of bivalves or in the mantle cavity of gastropods. Important families include the Anthessiidae and Lichomolgidae, species of which attach using clawed antennae. More modified forms with elongate bodies, often with reduced segmentation and appendages, include the Mytilicolidae (Fig. 4.3B) and Mycolidae, many of which inhabit the intestinal tracts of their hosts. Some of these are major pests in commercial bivalve culture. The Splanchnotrophidae (Fig. 4.3F), which live in the tissue sinuses and hepatic diverticulae of their nudibranch and sacoglossan hosts, have highly transformed bodies

equipped with elongate processes. Most highly metamorphic of all are the mesoparasitic Chitonophilidae (Fig. 4.3I), which are reduced to a sac-like or vermiform body plus a rootlet-system that penetrates the tissues of their chiton and gastropod hosts.

One family, the Nicothoidae, parasitises other crustaceans. Many of these inhabit the brood chamber or marsupium of their hosts and have a globular body form (Fig. 4.3D) that mimics the eggs of the host in size as well as shape. They apparently feed on the host's eggs. The most highly derived forms within the family, however, are mesoparasitic with the adult females reduced to an external sac-like body anchored by a rootlet system (Fig. 4.3H), which penetrates extensively through the host tissues.

Thirteen families of copepods are known to occur exclusively on echinoderm hosts, each of which is specific to a particular host class (Boxshall and Halsey 2004). Other families, such as the Asterocheridae, Taeniacanthidae, Rhynchomolgidae and Pseudanthessiidae, parasitise echinoderms, but not exclusively. These generalist families are typically cyclopidiform and attach to the outer surface of their hosts by clawed antennae and maxillipeds. They can be extremely abundant: Humes (1973) reported a total of 27 209 specimens of the asterocherid *Collocherides astroboa* and the rhynchomolgid *Doridicola micropus* from just three individual basket stars of the genus *Astroboa*. Most specialist echinoderm parasites are characterised by small body size and, although there is some reduction and loss of external segmentation, the bodies are relatively weakly transformed. These tiny parasites (Fig. 4.3E) can also reach enormous population densities: Humes (1971) reported 1420 individuals of a stellicomitid, *Stellicomes supplicans*, on two individual seastars. Members of the Calverocheridae and Pionodesmotidae form cysts in their sea urchin hosts and have swollen, rather globular bodies. The most highly transformed morphology is found in the Cucumaricolidae, the species of which have lobate bodies and inhabit the coelom of sea cucumbers, and the Chordeumiidae which live in cysts or within the genital bursae of their brittle star hosts.

Copepods are very commonly associated with both solitary and colonial tunicates, and can be found in all parts of the zooids and in the matrix of colonial forms. Among these, the Notodelphyidae and Botryllophilidae are widely distributed and are most frequently reported, perhaps because their large body size renders them readily visible through the body tunic of their hosts. Within a single family, such as the Notodelphyidae (Fig. 4.3C), morphology can vary from cyclopidiform to vermiform, lobate or stellate body shapes.

Sexual dimorphism

Most parasitic copepods are sexually dimorphic in body form and in appendage structure. Females are typically larger than males, have more transformed bodies and may have more robust attachment mechanisms, whereas males typically have at least one pair of limbs (either the antennules or maxillipeds) adapted for grasping the female during copulation. Sensory systems associated with mate detection and mate recognition behaviour are also dimorphic, typically being better developed in males. In families such as the Lernaeopodidae (Figs 4.2I, J) and Chondracanthidae (Fig. 4.2D), the size differential is very pronounced and males are often referred to as dwarves, although comparison with free-living relatives suggests that in such cases it is equally appropriate to interpret the females as giants. In the Chondracanthidae the tiny males attach to special glandular organs on the females, the nuptial organs, which may directly provide them with nutrients. The most extreme form of sexual dimorphism within the copepods is cryptogonochorism. In the Xenocoelomatidae and in the unrelated genus *Gonophysema* males are tiny. They penetrate the female and move into a special receptacle, the receptaculum masculinum, where they undergo a metamorphic reduction to become what is effectively a functional 'testis', resulting in a pseudohermaphrodite condition (Bresciani and Lützen 1961).

In certain Notodelphyidae and Myicolidae, parasites of invertebrate hosts, there are two forms of adult males: a sedentary or typical form and a swimming or atypical form. Isolated

atypical males are capable of moving to alternative host individuals containing females. In the notodelphyid *Pachypygus*, atypical males have a unique sensory organ, the cephalic pleural organ, which may act as a chemosensor involved in the detection of pheromones produced by the female, or of metabolites produced by the female/host complex (Hippeau-Jacquotte 1987).

Life cycles

Basic life cycle pattern

The basic life cycle of copepods comprises two phases, naupliar and copepodid. The egg typically hatches into a nauplius larva defined by its small, unsegmented body and the possession of only three pairs of functional appendages, antennules, antennae and mandibles. There is a maximum of six naupliar stages (designated NI–NVI) and all six are retained in most free-living copepods and in some parasites. Nauplii may be planktotrophic, feeding on other planktonic organisms, or lecithotrophic, relying on yolk stores for nutrients. Parasitic copepods typically have lecithotrophic nauplii characterised by reduced setation on the three limb pairs and by the absence of the so-called naupliar feeding process on the coxa of the antenna. The final nauplius stage, primitively NVI, undergoes a metamorphic moult to the first copepodid, which has a segmented body, a full adult set of cephalic appendages and the first and second swimming legs. In free-living copepods there is a maximum of five copepodid stages (designated CoI–CoV) and one body somite is added at each moult through this phase. In both sexes the fifth copepodid stage moults into the adult. This is a definitive or final moult and the female becomes sexually receptive on moulting.

Mating takes place soon after the female becomes sexually receptive and adult males may engage in pre-copulatory mate guarding, holding pre-adult females until the final moult (Boxshall 1990b). The sequence of mating behaviours consists of mate detection, mate recognition and mate capture, culminating in copulation during which sperm-containing spermatophore(s) are transferred to the female. There is strong evidence that mate detection and recognition behaviours are chemically mediated, with males using an array of chemosensory aesthetascs on their antennules to detect pheromones produced by females. Spermatophores typically discharge via copulatory pores, into seminal receptacle(s) located internally within the genital region of the female and sperm are stored until required for fertilisation. Fertilisation occurs as egg batches are laid and a single female may produce several batches of eggs during the course of her reproductive life. Most parasitic copepods extrude their eggs into paired egg sacs or uniseriate egg strings, although some, for example some Notodelphyidae (Fig. 4.3C) and the genus *Pectenophilus*, store eggs internally.

The full life cycle comprising six naupliar stages and five copepodid stages preceding the adult is retained in many families of parasitic copepods, especially those utilising invertebrates as hosts (Fig. 4.4). Examples include the Asterocheridae and Cancerillidae among the Siphonostomatoida, and the Myicolidae and Notodelphyidae among the Cyclopoida. Rarely is the full number of stages retained in fish parasites, the only example being the Ergasilidae, which is unusual in that the naupliar stages are planktotrophic (Fig. 4.5A), feeding on unicellular algae. In parasitic copepods the infective larva is, with rare exceptions, the first copepodid and life cycles are direct, involving only a single host. One of the exceptions is the Notodelphyidae, in which it is the second copepodid that serves as the infective larva. The infective copepodid larva provides the transition between the preceding dispersal phase and the parasitic phase.

Modification of the nauplius phase

In many parasites the naupliar phase of the life cycle is more or less abbreviated, occasionally it is lost altogether. In fish parasites, particularly in siphonostomatoids, the nauplius phase is reduced to two stages (NI and NII) and these are lecithotrophic (Fig. 4.5B). Most siphonostomatoids on

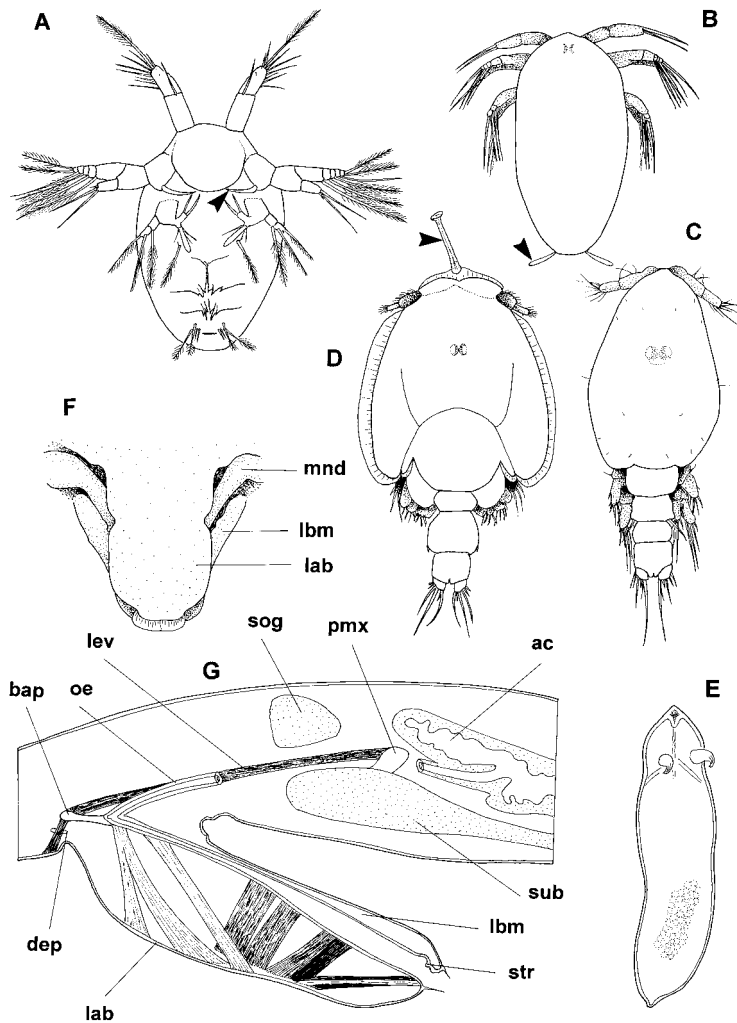


Figure 4.5 Larval stages. **A.** Planktotrophic nauplius (NVI) of Ergasilidae, showing feeding process (arrowed) on coxa of antenna. **B.** Lecithotrophic nauplius of *Lepeophtheirus* (Caligidae), showing paired balancers (arrowed). **C.** First copepodid larva of *Lepeophtheirus*. **D.** Chalimus larva of *Lepeophtheirus*, showing frontal filament (arrowed). **E.** Onychopodid larva of *Gonophysema*. Oral tube of Caligidae. **F.** Ventral view of oral tube, showing mandible entering tube via lateral slit between labrum and labium. **G.** Median longitudinal section through oral tube showing musculature. Abbreviations: ac, anterior midgut caecum; bap, buccal apodeme; dep, oral tube depressor muscle; lab, labrum; lbm, labium; lev, oral tube levator muscle; mnd, mandible; pmx, postmaxillary apodeme; oe, oesophagus; sog, supraoesophageal ganglion; str, strigil; sub, suboesophageal ganglion.

fishes have uniseriate egg strings in which disc-shaped eggs are closely packed into a single row extending the length of the string. Nauplii hatching from such egg strings have a single pair of modified caudal setae known as balancers, although their function is unknown. Related families that have multiseriate egg strings, namely Lernaeopodidae, Sphyrriidae and two genera of Hatschekiidae, have nauplii that lack balancers. The NI moults quickly, usually within six hours to 24 hours, and the NII moult into the first copepodid is equally rapid, so from hatching to the infective stage usually takes one to two days depending on temperature. In some

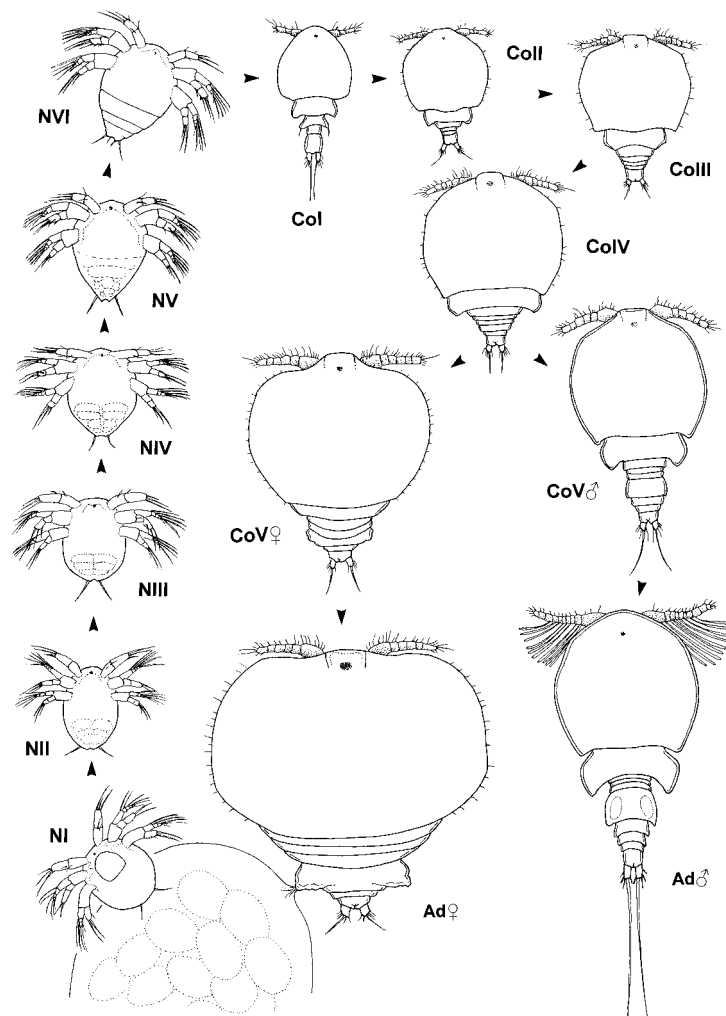


Figure 4.4 Life cycle of *Cancerilla tubulata* comprising six nauplius stages and five copepodid stages plus the adults of both sexes. Abbreviations: NI – NVI, nauplius stages 1 to 6; Col – CoV, copepodid stage 1 to 5; Ad, adult.

Lernaeopodidae the nauplius phase is reduced to a single stage, as in *Allela*, *Clavella* and *Nectobranchia*. In other Lernaeopodidae and some Pennellidae, such as *Salmincola*, *Cardiodectes* and *Peroderma*, it is lost completely and developing eggs hatch directly into the infective first copepodid.

Abbreviation of the life cycle is not just a feature of fish parasites, some parasites of invertebrates also have abbreviated cycles but the information available is so fragmentary that no definitive pattern can be identified. The Herpyllobiidae and the mytilicolid *Trochicola* have only two naupliar stages and only a single nauplius is reported for *Gonophysema* and for some genera of Nicothoidae. In other genera of Nicothoidae, as well as in some Chordeumiidae and the Cucumaricolidae, the entire nauplius phase is lost.

The most spectacular modification in biology of the nauplius phase is the order Monstrilloida (Fig. 4.6). All monstrilloids have endoparasitic naupliar stages and free-swimming, non-feeding adults. Females carry their eggs on long ovigerous spines. These eggs hatch into infective

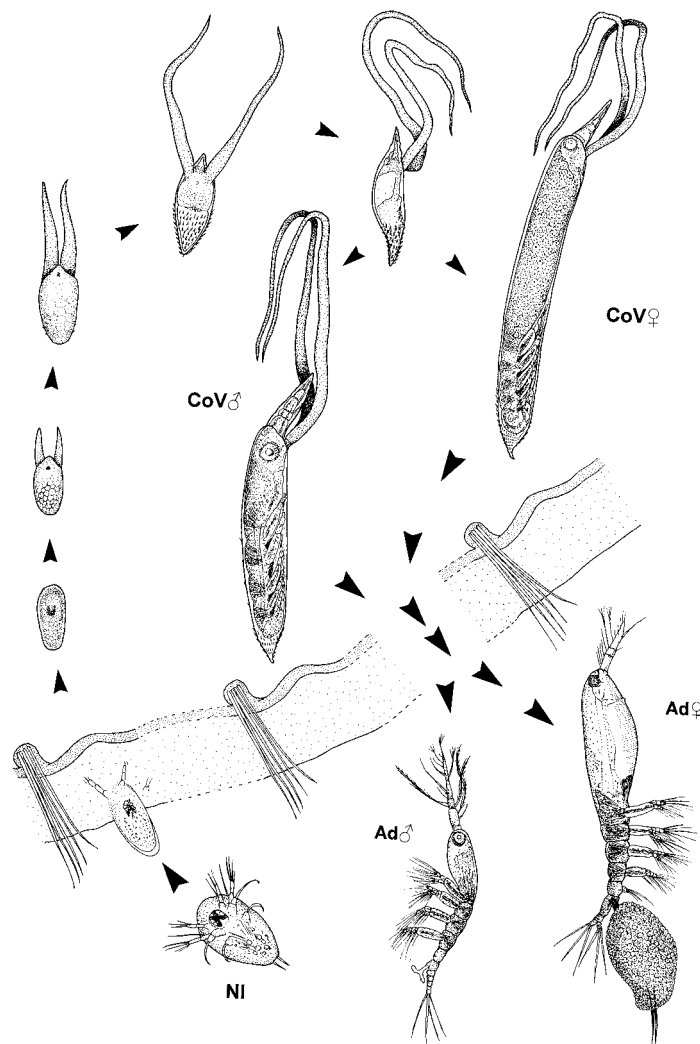


Figure 4.6 Life cycle of the Monstrilloida, comprising a free-living phase consisting of the non-feeding adults and the first nauplius stage released by the female, and an endoparasitic phase during which development from infective nauplius to fifth copepodid stage takes place. Abbreviations: NI, infective first nauplius stage; CoV, copepodid stage 5; Ad, adult; host, host body wall.

nauplii that locate a host, either a polychaete or a mollusc, and burrow into its tissues. Once within the host's blood system the nauplii transform into a sac-like body bearing paired, root-like anterior processes. Development through the copepodid phase, up to the fifth stage takes place within the host. Once development is complete the monstrilloid leaves its host as the final copepodid stage and undertakes a single moult into the adult. Adults of both sexes live in the marine plankton community but lack mouthparts, presumably serving as a dispersal and reproductive phase in the life cycle. A family of cyclopoids, the Thaumatopsyllidae (once classified as monstrilloids), has a similar life cycle, with parasitic nauplii inhabiting the gut of brittle stars and non-feeding adults living in the plankton. The copepodid phase in *Thaumatopsyllus paradoxus* comprises the full five stages preceding the adult, and the entire phase from final nauplius to adult is completed without further food intake.

Modifications of the copepodid phase

The first copepodid (Fig. 4.5C) is relatively uniform in structure and is characterised by the presence of two functional pairs of biramous swimming legs, each with one-segmented rami. In general, the copepodid phase provides a gradual transition from the copepodid body form, which is common to all podopleans, to adult morphology, however transformed. In more derived families successive copepodid stages show increasing levels of modification in body form and limb structure, as compared to their free-living relatives. In almost all copepod parasites the first copepodid is a free-swimming stage, the few exceptions include the monstrilloids and the brittle star parasite *Parachordeumium amphiuræ*, which hatches directly as an infective second copepodid, having passed through the first within the egg.

A common modification to the copepodid phase is the specialisation of the later stages as particular larval forms. In most siphonostomatoid fish parasites, for example, the first copepodid produces a chitinous frontal filament soon after settlement on the host. This filament is secreted by an anteriorly located gland and anchors the developing larva securely to its host. These are chalimus larvae (Fig. 4.5D) and the basic life cycle of the caligid sea lice contains four chalimus stages followed by either one or two pre-adult stages. Pre-adults secrete a frontal filament during moulting, but it is temporary and after moulting caligid pre-adults detach and are motile. Frontal filaments and chalimus larvae are present in most families of fish parasitic siphonostomatoids for which the larvae are known. However, none is present in the Lernanthropidae (Raibaut 1985). Elsewhere in the Copepoda a similar chitinous filament is found in the Nicotoidae, attaching the developing larva to the exoskeleton of its crustacean host (Hansen 1897).

In the tunicate parasite *Gonophysema* the infective copepodid larva settles on the host then undergoes a metamorphic moult into an onychopodid larva (Fig. 4.5E). This larva is reduced to a simple elongate sac-like body provided with grasping antennae that are used to attach to the host. The onychopodid then penetrates the skin of the tunicate and begins a transformation into the amorphous, lobate adult (Bresciani and Lützen 1961).

The basic copepodid phase, as primitively retained in siphonostomatoids (e.g. *Cancerilla*), comprises five stages plus the adult. The presence of pre-adults, as true moult stages, is a feature of many fish parasites. Either one pre-adult (e.g. in *Caligus clemensi*) or two pre-adult stages (e.g. in *Lepeophtheirus salmonis*) may be interpolated into the basic life cycle, and represent an addition to the ancestral copepod life cycle. The addition of a stage or stages is remarkable, given the general pattern of abbreviation and loss of stages exhibited across the parasitic copepods. It appears to be shared by only certain families of fish parasitic siphonostomatoids, but its presence in related families has yet to be confirmed. Reports of additional copepodid stages or of pre-adults in cyclopid families are doubtful and are more likely to represent growth stages than moult stages.

The infection process

The infective copepodid larva is typically small, in the order of 0.3 mm to 0.7 mm body length, but the oceans are enormous, potential hosts are patchily distributed and many of them are highly mobile. Clearly, overcoming the problems of locating a host and successfully infecting it are critical to the completion of the life cycle in parasitic copepods. Infection biology has been studied in a few fish parasites, especially sea lice. The probability of encounter between a copepodid and a potential host is increased by aggregation of larvae at the appropriate part of the environment. For example, copepodids of *Lepeophtheirus pectoralis*, a parasite of flatfish, become negatively phototactic after some hours and tend to sink to the sea bed where they would be more likely to encounter hosts. In contrast, copepodids of *Lepeophtheirus salmonis*, a salmonid parasite, tend to aggregate around the subsurface halocline in coastal waters, a depth horizon at which salmonids are known to cruise. Infective larvae in close proximity to fish hosts

have been shown to respond to mechanical signals generated by the locomotory or respiratory motions of the potential host. The primary sensory interface between the copepodid and its environment is the paired antennules and their array of chemosensory, mechanosensory and bimodal setation elements. In addition, *L. salmonis* larvae also respond to visual signals, exhibiting bursts of high velocity swimming in a modified shadow reflex. Caligid copepodids have a nauplius eye consisting of three ocelli, the two dorsal ocelli being provided with a spherical lens as well as a reflective tapetal layer. The optical properties of such an eye probably allow the formation of a simple image. Final attachment to the host appears to be a chemosensorily-mediated behaviour and this may form the basis for host recognition, but the details of this mechanism are unresolved.

Many marine invertebrate hosts provide sessile targets for infective stages, although copepods also utilise motile invertebrates from scyphozoans to cephalopod molluscs. As in the fish parasites, the infection process has been studied in relatively few species. Infective stages of the *Sabelliphilus sarsi* locate their sessile polychaete host by responding to chemical cues emanating from the host. On this basis larvae are able to distinguish between different polychaete species.

In shallow coastal seas host densities may be relatively high and the environment exhibits a complex physico-chemical structure that may be exploited by the aggregation behaviour of the infective larvae. In the deep ocean the more structured waters lie close to the bottom and only three families of parasitic copepods are routinely found, the Chondracanthidae, Lernaeopodidae and Sphyrriidae, primarily on bottom-living rather than pelagic host fishes. In the vast open pelagic biome away from the effects of the coast and the sea bed, the likelihood of an encounter with potential hosts is lowest of all. Only two species of copepods, *Cardiodectes medusaeus* and *Sarcotretes scopeli*, are commonly found in the pelagic. Both species exhibit low host specificity, occurring on several different host families (Boxshall 1998) and this may be a factor in their success.

Two-host life cycle

Some pennellids, such as *Sarcotretes scopeli*, retain a direct life cycle, while others have an unusual life cycle involving two different hosts. After a brief planktonic phase, primitively comprising two nauplius stages, the infective copepodid larva locates the first host. This may be a fish, as in the case of *Lernaeocera* (Fig. 4.2K), or a gastropod mollusc, as in the case of *Cardiodectes*. Development through the attached chalimus stages to the sexually mature adults takes place on the gills or in the mantle cavity of the first host. Mating takes place on the first host, after which the mated adult female, which is still basically cyclopiform in shape, leaves the first host and finds a second, usually a fish but occasionally a marine mammal. Once attached to the second host the female embeds and commences a profound metamorphosis involving considerable increase in body volume. The post-metamorphic female then produces egg strings while on the second host, using stored sperm to fertilise the eggs as they are extruded. The advantages of the two-host life cycle have not been fully analysed but must presumably outweigh the apparent disadvantage of requiring two separate host infection events to complete the cycle.

Effects on hosts

Attachment

Parasitic copepods damage their hosts directly by their attachment mechanisms and by their feeding activities. Attachment by means of clawed limbs is typical for ectoparasites and penetration of the skin by the claws causes local lesions, the pathology of which varies according to site and other factors. On the skin of fishes attachment can cause pressure necrosis and epidermal erosion and the host tissue responses can include swelling, hyperplasia, proliferation of fibro-

blasts, fibre production and cellular infiltration. Any surface lesion may also render the host susceptible to secondary infections. Attachment to gill filaments typically results in hypertrophy of the gills and fusion of secondary lamellae, with consequent loss of respiratory surface area. For some fish parasites, such as *Ommatokoita elongata*, the preferred site on the shark host is the cornea of the eye. This species and other eye parasites, such as *Lernaenicus sprattae* (the eye maggot of sprat), cause blindness and this may have a profound impact on the host, given that 84% of the Greenland shark, *Somniosus microcephalus*, carried *Ommatokoita elongata* in both eyes (cf. Kabata 1979).

Feeding

Most parasitic copepods feed by rasping at the surface of the host using their mandibles. Dislodged fragments of host tissue are taken directly into the mouth or oral tube and carried into the gut for digestion. In siphonostomatoids such as the entomolepidids, the distal part of the oral tube forms a long, narrow siphon which is used for piercing host tissues or cells to withdraw fluids (Boxshall 1990a). In caligids the oral tube is movable, being erected by special muscles during feeding (Fig. 4.5F–G) and held flat against the body when not feeding. Once erected the mandibles contained within the oral tube extend through the distal opening and scrape at the host's epidermis in concert with the strigil, a toothed ridge on the labium. Feeding activity produces surface lesions where the epidermis has been removed and, in cases of heavy or prolonged infestation, deeper lesions result, with damage to the dermis and blood vessels. Deeper lesions often result in haemorrhaging and can cause anaemia.

In many pennellids and sphyriids the entire head is permanently embedded in a fixed position in the host and feeding appears to be mainly on host fluids. Blood feeders, such as *Cardiodectes*, have evolved systems for sequestering excess iron derived from feeding. *Cardiodectes medusaeus* synthesises ferritin crystals and stores them as large aggregates within the cephalic holdfast. Fish infected with large blood-feeding parasites commonly show signs of anaemia, such as reduced packed cell volume, reduced haemoglobin levels, the presence of numerous immature erythrocytes and altered white blood cell counts.

A surprising variety of copepods possess a system of rootlets which penetrate host tissues. In the case of chitonophilids, herpyllobiids and their relatives, and the nicothoids *Rhizorhina* and *Nicorhiza*, these rootlets appear to be absorptive in function, extracting nutrients from the host and transporting them to the ectosoma where the reproductive organs are located. The rootlet system in the siphonostomatoid *Nicorhiza* is derived from the modified oral tube, but in the other families the homology of the rootlets is unknown. The elaborate body processes found in some endoparasites, such as *Echiurophilus fizei*, splanchnotrophids, anthecherids and some genera of Chordeumiidae and Lamippidae, may also function as nutrient absorbing systems. The structure of the body integument provides evidence of modification to facilitate absorption of nutrients through the body surface. For example, in *Antheacheres* and *Linaresia* the thin integument consists of only epicuticle, the procuticle having been lost. Vesicles may be present within the cuticle and the underlying epidermal cells may have modified apical surface provided with microvilli (Bresciani 1986).

Economic importance

Infestation by any parasitic copepod may result in loss of condition of the host. For example, *Pectenophilus* can attain prevalence rates of 100% on its host the Japanese scallop, *Patinopecten yessoensis*, in aquaculture facilities. It causes significant loss of condition in cases of heavy infestation. This in turn may result in reduced growth rates, reduced reproductive effort and greater mortality. Caligid sea lice, especially species of the genera *Lepeophtheirus* and *Caligus*, are serious pests in fin-fish aquaculture: in salmonid farming in both northern and southern hemispheres

and in brackish water tilapia culture facilities in southern Asia (Boxshall and Defaye 1993, Pike and Wadsworth 1999) (see pp. 378–391). Caligid sea lice can cause severe economic losses due to the reduced growth of infected fish, to the costs of chemotherapy and to mortality. The economic effects of parasitisation of fishes by copepods include reduced marketability. Farmed fish with unsightly lesions have reduced value. Integrated parasite management, which may include routine inspections for sea lice, chemotherapy, separation of year classes, fallowing and use of cleaner fish, is widely employed but sea lice levels remain problematic in some areas and have been implicated in raising infestation levels in adjacent populations of wild salmonids. Effects on the host are generally less pronounced in wild fish, although the redfish, *Sebastes*, with large and obvious parasites like *Sphyrion lumpi* embedded in its flanks is problematic for filleting and processing, and has reduced market value.

Important references

Some important books on parasitic copepods are available. They include Kabata (1979) who gives a very detailed and beautifully illustrated account of copepods infecting British fishes, and Boxshall and Halsey (2004), *An Introduction to Copepod Diversity*.

The volume edited by Boxshall and Defaye (1993) focuses on the biology and control of sea lice on wild and farmed fish.

Isopoda (isopods)

RJG Lester

Introduction

Parasitic isopods are typically marine, and usually inhabit the warmer seas. Their body form (Fig. 4.7) varies from an easily recognisable isopod to a relatively amorphous sac recognised as an isopod only from the less modified male found within the folds. Though free-living isopods tend to be detritivores, parasitic forms feed on host blood or host haemolymph. Their mouthparts form a cone with maxillipeds that tear at the flesh and tiny pointed mandibles that pierce into the tissue to penetrate blood vessels or blood sinuses. The gut, particularly the hind gut, is quickly filled, often swelling the body, then the contents are slowly transferred to the midgut glands for digestion. Thus the parasites tend to be intermittent feeders. They can be a major drain on the host, frequently affecting reproductive performance and sometimes affecting growth rate.

Most parasitic isopods are ectoparasites. There are three major groups: cymothoids, epicaridians and gnathiids. Cymothoids are parasites of fish, both as immature forms and adults. Epicaridians are parasites of Crustacea, again as immatures and adults. Gnathiids are larval parasites of fish, the adults being free living and non-feeding. Genetically, the cymothoids and epicaridians appear to be closely related whereas the gnathiids appear to have evolved from a different isopod line.

Cymothoidae

Morphology and diversity

These are the isopods commonly seen on teleosts in tropical and subtropical waters, attached to the body surface, in the mouth or on the gills (Brusca 1981, Bunkley-Williams and Williams 1998; Lester and Hayward in press; Fig. 4.7A). They resemble free-living isopods except for their hook-like legs. The stages normally found are the non-swimming, permanently attached mature females, often with a small male nearby.

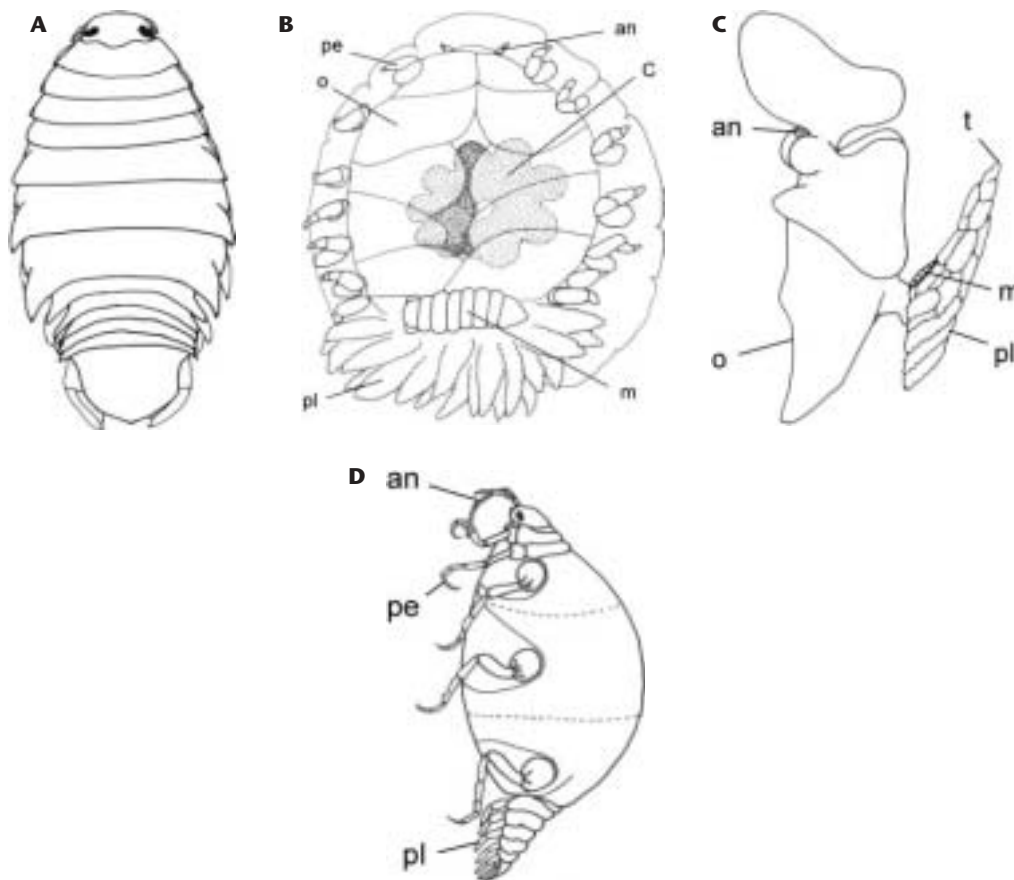


Figure 4.7 Parasitic Isopoda – variation in body form of adult females. A. A cymothoid, *Nerocila orbigny*. B. A bopyrid, *Eipipenaeon ingens*, a parasite of prawns, itself parasitised by the cryptoniscid *Cabirops orbionei*. C. An entoniscid, *Pinnotherion vermiforme* from within a pea crab, *Pinnotheres* sp., itself parasitising a mussel, *Modiolus modiolus*. D. A gnathiid, *Paragnathia formica*. Abbreviations: an, antenna; C, cryptoniscid; m, male; o, oostegite; pe, pereopod; pl, pleopod; t, tip of abdomen. Figures: redrawn from Bruce (1987); drawn from unpublished photograph taken by L Owens; modified from Giard and Bonnier (1893); modified from Monod (1926), respectively.

Though most adult isopods on fish belong to the Cymothoidae, there are parasitic forms in other families. The Aegidae, distinguished from Cymothoidae by having less modified pereopods, includes the notorious *Alitropus typus*, which parasitises fishes in India and south-east Asia in fresh and brackish waters. The parasites attack fish to feed but retain their free-swimming capability as adults. Unlike cymothoids they do not appear to be protandrous hermaphrodites.

Tridentellid and corallanid isopods are mostly free living but have a few representatives that are parasites of fish, such as the corallanid *Argathona macronema* which is common in the nasal passages of serranids and lutjanids on the Great Barrier Reef. Some corallanids are parasitic on Crustacea. Those belonging to the genus, *Tachaea*, are parasites of freshwater shrimps in Asia and Australia, and are usually found attached to the outside of the cephalothorax.

Life cycle

Gravid females release eggs into a brood pouch or ‘marsupium’ formed from their ventral oostegites. Here the eggs embryonate, hatch and undergo two or more moults to form the ‘manca’ or

'pullus II' stage. These are released from the brood pouch, sometimes more or less simultaneously as a result of contractions from the parent. The parent then moults, feeds, digests the meal and eventually produces the next batch of eggs. Several batches may be produced during her life span. The mancae have only six pairs of legs (compared to seven in juveniles and adults), large compound eyes and heavily setose pleopods with which they swim extremely rapidly. After a short free-swimming period they are parasitic and need to find a fish to take their first meal within one to two days or they will die. In genera such as *Anilocra* and *Nerocila* the mancae then leave the fish, moult, reattach to another fish, and so on until they complete their juvenile moults, the number of which has not been determined for any species, and approach adulthood. In other species such as the gill-inhabiting forms (e.g. *Mothocya*, some *Livoneca* spp.), the 'tongue biters' (e.g. *Ceratothoa* spp.) and the tissue dwellers (e.g. *Ourozeuktes* spp.) the mancae or an early juvenile stage move to the preferred site and remain attached to the fish.

Cymothoids are protandrous hermaphrodites. The first male to parasitise a fish changes into a female. Males attaching to the same fish remain as males. It seems likely that a pheromone or neurohormone is released by the female which inhibits further development of the males. Whether this is through the host's blood as suggested by Raibaut and Trilles (1993), through the host's mucus as suggested by Trilles and Hipeau-Jacquotte (1996) or through the water is not clear. Egg development apparently depends on the presence of a male, for each batch. Fertilisations occur immediately after the female has moulted in some species. In some skin-inhabiting forms males are rarely found. They presumably remain free-swimming and stay with females only long enough for fertilisation to occur. In others the small males are permanently attached alongside females and have lost the ability to swim. In gill-inhabiting species such as *Enispa convexa*, non-swimming males are found on the same fish as females, though not necessarily in the same gill cavity, and move back and forth to fertilise the females, presumably again in response to a female pheromone. In 'tongue biters' such as *Ceratothoa imbricata*, juveniles and one or more males occur on the gills and the adult female in the mouth. In tissue-inhabiting forms such as *Ourozeuktes*, small males are found in the pouch with the female. Male cymothoids are usually narrower than females and the ratio of length to width has been used as a measure of femininity, the Montalenti Index (Montalenti 1948). There is usually a strong correlation between parasite length and host length, in some cases because the fish are parasitised when small and the parasites live for many years and in other cases where the parasite apparently grows to fill the available space and then stops.

Effects on hosts

Cymothoids harm the fish in several ways. Mancae feed voraciously and easily kill fry and fingerlings through the tissue damage they cause. Permanently attached adults stunt the growth of fish and retard or inhibit reproduction, probably because of the nutritional drain though more subtle mechanisms such as through hormonal changes have not been ruled out. Those in the gill chamber are usually associated with stunted gills, partly from pressure atrophy and partly from damage associated with feeding and attachment. They have also been frequently associated with anaemia. Those in the mouth affect the development of oral structures and may completely replace the tongue, as in *Ceratothoa oestroides*. Menhaden infested by the buccal parasite, *Olenicira praegustator*, school separately from uninfested fish of the same age. The tissue-inhabiting forms such as *Ourozeuktes* spp., which form a pouch from a depression in the skin, cause pressure atrophy of adjacent muscle and visceral organs. Though cymothoids penetrate the skin with their pereopods and mouthparts, and the tissue-inhabiting forms maintain a small opening to the outside, little secondary infection occurs.

In Mediterranean mariculture, infections of *Nerocila orbignyi* (Fig. 4.7A) on the gills of sea-caged bass, *Dicentrarchus labrax*, and bream, *Sparus aurata*, are associated with poor growth.

Bragoni *et al.* (1984) recommended using fine mesh nets near aquaculture cages to keep out mullet believed to be the source of the parasite. To avoid the parasite *Emetha audouini*, cages containing sea bass were moved away from the shore into deeper water with a stronger current (Papapanagiotou *et al.* 1999).

Salmon farms in Chile and Australia have been plagued by tongue biters, *Ceratothoa* spp. In Chile the problem became less acute when the numbers of the normal host *Trachurus murphyi* declined. In Australia, infections disappeared when the fish were treated with fresh water to control amoebic gill disease.

Epicaridea

Morphology and diversity

Though there has been relatively little morphological diversity among the Cymothoidae, isopods with *Tachaea*-like ancestors have radiated as Epicaridea (the 'Bopyridae' *sensu lato* of Dreyer and Wagele 2001), which are parasites of Crustacea. Indeed, Kuris (1974) estimated that 3% of all crustacean species were parasites of other Crustacea. The Epicaridea contain the bopyrids, dajids, entoniscids and cryptoniscids. All known life cycles involve two hosts, both of which are Crustacea.

Bopyridae conform to the isopod pattern of distinct segmentation, seven pairs of pereopods, and with a brood pouch formed from oostegites (Fig. 4.7B). Adult females occur in the gill chamber (e.g. subfamily Pseudioninae), or less commonly attached to the pleon (e.g. Athelginae), of shrimps and crabs. Adult males are much smaller than the females and are usually found attached between her pleopods. Females feed on host haemolymph by piercing a blood sinus usually on the inside wall of the gill cover or 'branchiostegite'. The parasite may take up to 25% of the shrimp's haemolymph in one day though presumably as in cymothoids this rate of uptake is not continuous. The male apparently has no contact with the shrimp. Whether males are hyperparasites on the female, or do not feed at all, is not known.

Life cycle

Eggs released into the brood pouch, embryonate and hatch into an 'epicaridium' larva with styli-form suctorial mouthparts and six pairs of clawed pereopods. They swim rapidly, do not feed, and last for one to two weeks while they seek their first host, a copepod, frequently a calanoid. Once attached to the side of the copepod they pierce the exoskeleton, feed and within a few days moult to the 'microniscus' stage (Fig. 4.8). Unlike the biphasic ecdysis of most isopods (posterior first), epicaridia apparently moult in one piece. The micronisci remain attached to the copepod for several weeks during which they enlarge to 10 times their original size. They are frequently found on copepods in fresh zooplankton samples but quickly drop off when the samples are preserved. Micronisci transform into free-swimming larvae called 'cryptonisci' (not to be confused with the family Cryptoniscidae, see pp. 143–144). The change apparently occurs without a moult by expanding folds in the cuticle (Anderson and Dale 1981). The cryptonisci then leave the copepod and seek a definitive host.

In *Leidya distorta*, a parasite of the fiddler crab, *Uca uruguayensis*, the cryptoniscus settles between the gill lamellae and after moulting one or more times migrates to the roof of the branchial chamber and matures into a female. Other cryptonisci and males were found attached to various parts of the maturing females (Roccatagliata and Jorda 2002). In *Probopyrus pandicola*, a parasite of shrimp, female cryptonisci may penetrate into the tissues and become endoparasites for up to two weeks, during which they can cause host mortality, before appearing in the gill chamber. Males are not endoparasitic and are attracted straight to the female (Anderson 1990). Gender appears to be environmentally determined in *Epipenaeon* species, the first

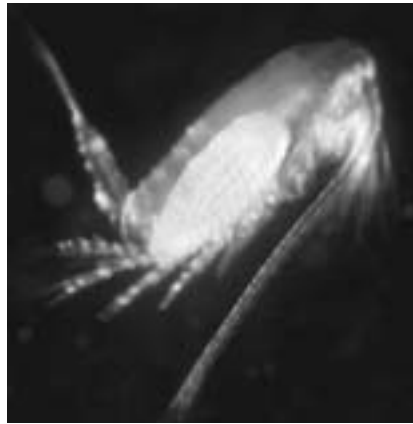


Figure 4.8 A microniscus (larval epicaridean) attached to a copepod at Heron Island, Australia. L Newman, photo.

cryptoniscus to attach to a shrimp becomes a female, subsequent ones become males. In *Parapenaemon* species gender seems to be genetically determined as about equal numbers of male and female cryptoniscus settled on adult females whereas in *Epipenaemon ingens*, an environmentally determined species, virtually all the settled cryptoniscus were males (Owens and Glazebrook 1985). In many species it appears that the definitive host is infected when a juvenile and remains infected for life. When the host moults, the parasites crawl through a split in the carapace and immediately reattach at the same location. In many species, the release of epicaridea and the moult of the parent is synchronised with the moult of the shrimp and will occur a few days prior. After the shrimp has moulted the male moves into the female brood pouch, presumably for insemination, and within several hours, a new batch of eggs is laid (Cash and Bauer 1993).

A female in the gill chamber of a shrimp or crab causes the chamber to be greatly enlarged. In those bopyrids that do not survive as long as the host, signs of the branchial enlargement frequently remain. The swelling caused by bopyrids is a problem in commercial shrimp fisheries where mechanical sorters select small parasitised shrimps with much larger unparasitised shrimps, and as a consequence staff have to be employed to remove the parasitised shrimps from the premium grades (Owens 1993).

Effects on hosts

Bopyrids may cause a slight decrease in host growth (Somers and Kirkwood 1991), or in the case of male shrimp, a slight increase, and may cause small changes in the host's secondary sexual characters but the most dramatic changes are in the host's reproductive capability. Both partial and total sterilisation of parasitised female shrimps and crabs have been reported by many authors. Males are less affected. When the parasites are removed, females recover, sometimes partially and often totally. The parasites cause a major energy drain. *Probopyrus* on *Palaemonetes* takes 10% of host's energy intake and reduces egg production by 50% (Anderson 1977).

The metabolic activity of parasitised copepods and shrimps is reduced and their activity decreases (Anderson 1975a,b, Bergery *et al.* 2002). This affects the rate at which parasitised shrimps capture food (Bass and Weis 1999) and limits their migration capability (Somers and Kirkwood 1991). Infected shrimp showed a reduced tolerance to salinity stress (Moles and Pela 1984). The gills of infected crabs and shrimps are flattened and sometimes deformed from pressure atrophy. The efficiency of oxygen uptake is reduced because of hydrodynamic changes in the gill chamber (Schuldt and Rodrigues-Capitulo 1987).

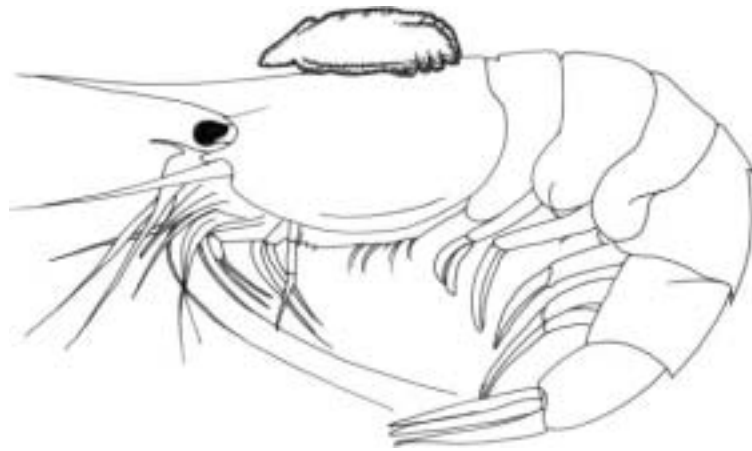


Figure 4.9 An adult dajid, *Holophryxus acanthephyrae*, on its prawn host. Figure drawn from Jones and Smaldon (1986).

Thus bopyrids partially or totally remove the reproductive capability of females without seriously affecting host moulting and growth. Most theories suggest that this is the result of either excessive blood loss or a direct effect of the parasite on the host's hormones. For the latter to occur, bioactive compounds from the parasite must pass to the host. Adult female bopyrids attract many cryptoniscids, possibly using pheromones and it is conceivable that these also inhibit the sexual maturation of the host. Alternatively, the parasite could inject material into the host to prevent clotting of the haemolymph and this could include compounds active against ovarian development. However, there are few reports of inflammation or melanisation associated with the feeding sites, suggesting little if any foreign material is injected. Cymothoid isopods on small fish also inhibit sexual maturation, apparently solely through nutritional drain, and perhaps this is the most likely explanation here.

Dajids have only five pairs of pereopods and females have a brood pouch formed from oostegites. They occur on mysids, euphausiids and prawns often on the cephalothorax facing to the rear with their mouthparts penetrating directly into the shrimp's pericardium (Brandt and Hanssen 1994, Fig. 4.9). How they cope with the host's moult is not known. Their epicaridian larvae are found on copepods.

Adult female entoniscids have lost most signs of pereopods but do retain oostegites that form the brood pouch (Fig. 4.7C). They are internal parasites of decapods, generally enclosed by a host sheath in the host's visceral cavity. Males occur within the pleopods of the female parasite or elsewhere within the crab. Epicaridean larvae are released to the outside through a small opening in the host's branchial chamber which is kept open by the tip of the parasite's abdomen. The larvae apparently pass through a microniscus stage on a copepod before transforming to a cryptoniscus (Trilles 1999). The cryptoniscus seeks a decapod, may penetrate through a weak point in the gills and after an internal phase a developing female makes the small opening to the outside. An entoniscid may constitute up to 12% of the weight of an infected crab and generally causes sterility. Some are encapsulated and killed by the crab's internal defence mechanisms.

Adult female cryptoniscids are typically without pereopods or oostegites (see C in Fig. 4.7B). They parasitise barnacles (including Rhizocephala), ostracods and other isopods, often occurring as hyperparasites. *Hemioniscus balani* is a worldwide parasite of barnacles in temperate waters. The female attaches to the barnacle's ovaries and removes ovarian fluid thus sterilising

the ovary though not affecting sperm production. Epicaridian larvae develop within the female parasite which eventually ruptures and frees the larvae (Blower and Roughgarden 1989). In *Lirioopsis* sp. the anterior lobe of the mature female is buried in the host and the parasite presumably feeds on the barnacle's haemolymph. *Clypeoniscus hansenii* lies within the brood pouch of the isopod *Idotea pelagica* and feeds on its eggs after they have been laid (Sheader 1977). Like other cryptoniscids, *Cabirops orbionei* sterilises its host, the bopyrid parasite, *Epipenaeon ingens* (Fig. 4.7B). As a result it has been proposed as a possible biological agent to control the bopyrid (Owens 1993). Cryptoniscids are thought to use copepods as first intermediate hosts.

Gnathiidae

Morphology and life cycle

Gnathiids are a small, relatively homogeneous group of isopods that are parasitic as juveniles on teleosts and elasmobranchs (see pp. 266–278; Lester and Hayward, in press). Adult males develop formidable jaws, adult females (Fig. 4.7D) resemble juveniles. The adults do not feed. They are found in small groups in marine cavities such as in mud banks, in dead barnacles or coral, or in sponges. Typically a cavity will contain a male and a group of females. Young females appear to find the cavity in response to a pheromone produced by the male. Other males that enter the cavity are either inhibited from maturation, as in *Gnathia calva*, or ejected by the resident male (Wagele 1988). Females mature in the cavity. Eggs are brooded in the ventral brood pouch and they hatch to produce a 'zuphea' or unfed juvenile. These leave the cavity, swimming rapidly using their setose pleopods and seek a fish to which they attach using their hooked pereopods. They tear their way into the tissue, eventually pierce a blood vessel and engorge themselves on the host's blood. In doing so, the hind gut becomes greatly distended and is accommodated by the folded carapace of their three mid segments expanding rather like a concertina so the parasites, now called 'praniza' become dilated in the mid section and may appear reddish. After several hours or days depending on species and temperature, the praniza leave the host and enter a cavity in the substrate where they digest the meal and eventually moult to the second zuphea stage. This is repeated twice more until the third stage praniza leaves the fish to seek a cavity in which to mature. In their behaviour on fish and their free-living, egg-laying stage, they are reminiscent of terrestrial ticks.

On teleosts, praniza may remain for only a few hours while they feed. Praniza on elasmobranchs, however, may remain for weeks. A good way to identify praniza is to keep them in clean sea water until one moults into an adult male, which can be identified. If an adult male and several females are kept together, the females will eventually become gravid and produce a new generation of zuphea.

The prevalence of gnathiids is often underestimated because many species leave their host immediately the host is captured, and others only feed on fish at night. However, gnathiids may be so abundant on coral reefs as to form the main component of the diet of cleaner fish (see pp. 266–278).

Important references

Trilles and Hipeau-Jacquotte (1996) presented a comprehensive account of parasitism in the crustaceans. Lester and Hayward (in press) reviewed fish parasitic isopods. A monograph on the Gnathiidae is by Monod (1926), and one on the Epicaridea is by Trilles (1999). Bunkley-Williams and Williams (1998) wrote a synopsis of isopods associated with fishes. Raibaut and Trilles (1993) reviewed the sexuality of parasitic crustaceans. Among interesting papers dealing with specialised aspects is Dreyer and Wagele (2001), who used molecular and morphological evidence to postulate that bopyrids which parasitise crustaceans evolved from fish parasites.

Branchiura (fish lice)

Geoff Boxshall

Introduction

The Branchiura comprises about 175 species classified in four genera placed in a single family, the Argulidae, but only the genus *Argulus* occurs in the marine environment. Branchiuran fish lice range in length from a few millimetres to about 30 mm and they have strongly flattened bodies, with a low profile when attached to their hosts.

Morphology

The body (Fig. 4.10A) comprises a head of five limb-bearing segments and a trunk, divided into a thoracic region carrying four pairs of strong swimming legs, and a short abdomen. Fish lice have paired compound eyes located in a blood sinus below the cuticle in the anterolateral part of the head. The head has well-developed carapace lobes, which form as posterior extensions of the dorsal head shield, and they typically cover the legs on either side of the body. In some species they may extend further to cover the abdomen. These carapace lobes contain highly branched gut caeca and have two specialised areas ventrally, which have traditionally been referred to as 'respiratory areas' although they appear to be involved in regulating the internal body fluids (Haase 1975).

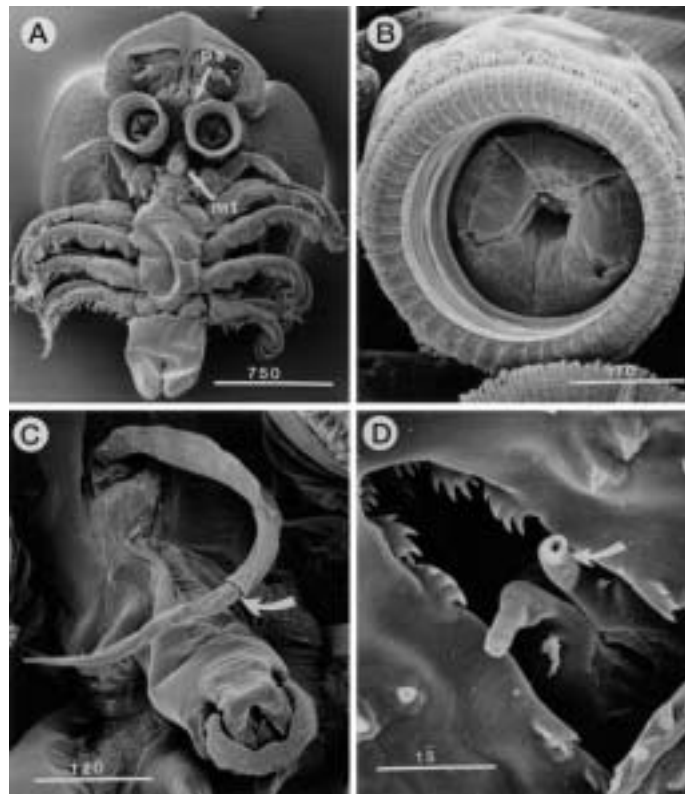


Figure 4.10 Scanning electron micrographs of *Argulus*. **A.** Ventral view of adult, with mouth tube (mt) and pre-oral poison spine (ps) arrowed. **B.** Sucker derived from modified maxillule. **C.** Mouth tube and everted poison spine, with groove separating distal spine from proximal sheath arrowed. **D.** Mouth opening showing paired labial spines (arrowed). After Gresty *et al.* 1993.

Branchiurans have nine pairs of limbs in total. Anteriorly on the ventral surface of the head lie the short antennules and antennae. Both are provided with claws and function as organs of attachment to the host. The claw of the antennule is located proximally and the cylindrical distal segments carry arrays of short setae which are probably sensory. Branchiurans have a tubular sucking mouth equipped with rasping mandibles located at the tip of the mouth tube. In *Argulus* there is a retractable poison stylet located just in front of the mouth tube (Fig. 4.10A, C). This stylet is absent in two of the freshwater genera, *Chonopeltis* and *Dipteropeltis*. The maxillules are developed into powerful muscular suckers (Fig. 4.10B) in the adults except in the freshwater genus *Dolops*, which retains clawed maxillules into the adult phase. The maxillae are uniramous limbs with spinous processes on the basal segments and small claws at the tip. The four pairs of thoracic swimming legs are biramous and directed laterally. Dorsally, the first and second legs commonly carry an additional process, the flagellum, originating near the base of the exopod. The third and fourth legs are usually modified in the male and are used for transferring sperm to the female during mating. The abdomen contains the paired testes in the male and the paired seminal receptacles, where sperm are stored until needed to fertilise eggs, in the female. The abdomen terminates in paired abdominal lobes separated by the median anal cleft, in which lies the anus and the minute, paired caudal rami.

Life cycles

The sexes are separate and in most branchiurans males transfer sperm directly to the females using a variety of modified structures on the third and fourth thoracic legs. The sperm are elongate and filiform in structure, and they are motile. The fine structure of the sperm has been used to link the Branchiura with the Pentastomida (Wingstrand 1972), a close phylogenetic relationship that is also supported by molecular sequence data (Abele *et al.* 1989). Only the life cycle of *Argulus* is well known; little is known of the other genera or of marine species. In freshwater species, after taking a meal, a mature female *Argulus* will leave its host and begin to lay eggs in rows on any hard, submerged surface. Up to 1200 eggs are laid at any one time and cemented to the substrate. The abandoned eggs hatch after between 12 days and 80 days according to species, but development time is also very dependent on temperature. Eggs within a string tend to hatch within a week. These eggs hatch into free-swimming larvae equipped with setose swimming antennae and mandibles, plus rudiments of the maxillules, maxillae and first two pairs of swimming legs. These larvae function as a dispersal phase and moult into the second stage, in which strong claws have replaced the setae on the antenna and the setose palp of the mandible is lost (Gresty *et al.* 1993). The first larval stage lasts about six days and moults occur at intervals until maturity. Branchiurans are parasitic from the second larval stage onwards but appear to leave the host and then find a new host at intervals throughout development. Changes during the larval phase are gradual, mainly involving the development of the thoracic legs and reproductive organs, except for the maxillule, which undergoes a profound metamorphosis around the fifth larval stage (Rushton Mellor and Boxshall 1994) changing from a long limb bearing a powerful distal claw into a short but powerful circular sucker. This is one of the most remarkable transformations known for any arthropod limb.

Effects on hosts and ecological importance

Branchiurans are primarily ectoparasites of fishes, but have occasionally been reported from the tadpoles of amphibians. They live mainly in freshwater habitats, both running and static water, and may occur at high density in artificial water bodies such as reservoirs, ornamental fish ponds and fish farms. A few species of *Argulus* infest estuarine and coastal marine fishes but they do not occur in oceanic waters. Infestations with *Argulus* have been reported from marine fish-farming facilities in Chile and Canada and can cause mortality in farmed salmonid stocks.

Branchiurans attach to the skin of their fish hosts and feed on its blood and external tissues. They have rasping mandibles, which scrape tissues into the opening at the tip of the tubular sucking mouth. In *Argulus* the poison stylet is used to inject a secretion into the host. The secretion may contain digestive enzymes to begin to break up host tissues before ingestion. Paired labial stylets lying within the opening of the mouth tube (Fig 4.10D) are also secretory and may produce secretion with a similar pre-digestive function. Host blood is also taken and is digested within paired, lobate gut caeca that lie within the carapace lobes (Overstreet *et al.* 1992).

Important references

Overstreet *et al.* (1992) reviewed the fine structure of Branchiura, and Gresty *et al.* (1993) the fine structure and function of the cephalic appendages of *Argulus japonicus*. Rushton-Mellor and Boxshall (1994) described the developmental sequence of *Argulus*.

Tantulocarida (tantulocarids)

Geoff Boxshall

Introduction

Tantulocaridans are tiny ectoparasitic crustaceans that spend most of their lives attached to the external surface of their hosts, a wide range of other crustaceans. All tantulocaridans are marine and they occur at all depths, from shallow coastal waters to the deep ocean, and in all temperature regimes from polar to tropical. The Tantulocarida is a small group comprising 28 species placed in 20 genera and four families, but its true diversity is undoubtedly underestimated as these parasites are often overlooked because of their minute size. It is classified in the class Maxillopoda and is regarded as most closely related to the Thecostraca (barnacles and relatives) with which it shares a similar body plan and the positions of the genital openings in both sexes (Huys *et al.* 1993).

Morphology

The adult asexual female consists of a minute head, a neck of varying length, and a sac-like trunk full of eggs or developing tantulus larvae, and it may attain lengths of up to 2 mm. It attaches to the exoskeleton of its host by means of a tiny oral sucker, only 12 µm to 15 µm in diameter. This stage has no limbs at all and no genital apertures, and it appears to release mature larvae by rupturing of the wall of the trunk sac. The sexual female, where known, is smaller, less than 0.5 mm in body length, and consists of a large cephalothorax and a five-segmented post-cephalic trunk. The cephalothorax carries a pair of sensory antennules but no mouthparts. A few large eggs lie within the cephalothorax which also carries a conspicuous median genital opening, interpreted as a copulatory pore (Huys *et al.* 1993). The first two of the trunk segments each carry a pair of biramous thoracic legs, which appear to be used for grasping, and the fifth segment bears the elongate caudal rami. The adult male resembles the sexual female in size and basic body plan, with a large cephalothorax and six-segmented trunk, but it has more limbs: vestigial sensory antennules, six pairs of biramous swimming legs, a well-developed median penis and caudal rami. Adults of both sexes develop within posteriorly located, sac-like expansions of the trunk of the still-attached preceding tantulus larva.

Knowledge of tantulocaridan biology is fragmentary. They spend most of their lives attached to their hosts, which include isopod, tanaid, amphipod, cumacean, ostracod and copepod crustaceans. The tantulus larva functions as the infective stage in the life cycle and has been found living free in marine sediments (Huys 1991). The sexual adults have never been collected away from the host, but probably inhabit the hyperbenthic zone, just above the sea bed.

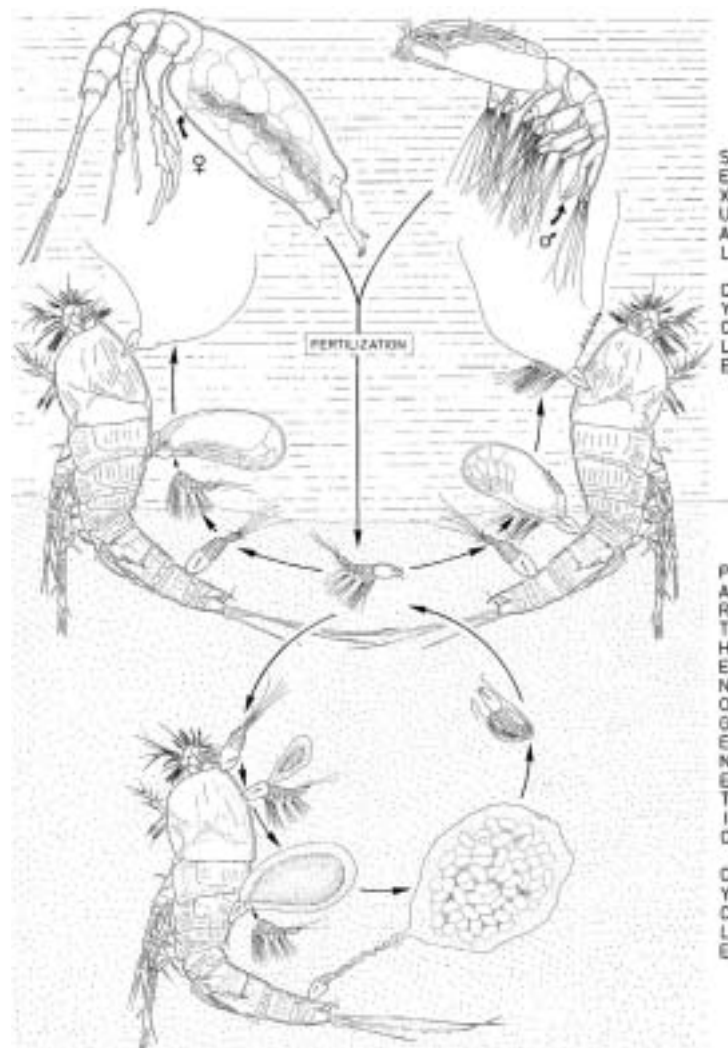


Figure 4.11 The double life cycle of the Tantulocarida. Composite Figure based largely on stages of *Itoitantulus misophricola* known from copepod hosts. The sexual cycle comprises the free-living, non-feeding sexual adults, which mate and the female then releases larvae. The parthenogenetic cycle contains only the tantulus larva and the sac-like, limbless asexual female. From Huys *et al.* (1993); reprinted with permission from The Crustacean Society.

Life cycles

Tantulocaridans have a bizarre double life cycle (Fig. 4.11), with a sexual phase and an asexual phase. The asexual phase is common and the sexual phase is rare. Sac-like asexual females release fully formed tantulus larvae (Boxshall and Lincoln 1987), which are capable of infecting a new host and developing directly into another asexual female, without mating and without even moulting. This tantulus larva, ranging from 85 μm to about 180 μm in length, comprises a head, which has an oral disc but lacks any cephalic limbs, and a trunk of eight segments. The first six trunk segments carry biramous swimming legs equipped with reduced endites. After release from the mother, infective larvae spend time in the sediment before encountering a suitable benthic or hyperbenthic host. Host location and attachment mechanisms are poorly

understood as these forms lack eyes and antennae, the main sensory interfaces of other crustaceans. After successfully locating a host the larva punctures the host cuticle using its oral stylet. The cephalic musculature that operates the stylet then degenerates. The tantulus larva develops into an asexual female and the post-cephalic trunk of the larva is shed, so the female remains attached to the host by the adhesive oral disc of the preceding larval stage. The trunk of the female expands to accommodate the growing larvae until they are released.

In the sexual phase, the cycle again begins with the infective tantulus larva attaching to its host by its oral disc. A sac-like expansion forms on the trunk, within which either a sexual adult male or adult female then develops. The precise location of this expansion varies according to family. Developing adults are supplied with nutrients from the host, transported via an umbilical cord originating in the still-attached larval head. Fully formed adults develop within the sac, which is attached to the host only by the oral disc of the larva. On reaching maturity these sexual adults are released by rupturing of the sac wall. They have never been observed alive, but it is assumed that the male, which has well-developed swimming legs and paired clusters of chemosensory aesthetascs representing the antennules, actively searches out and locates the receptive female. The male has a large penis and presumably inseminates the female via the mid-ventral copulatory pore. The fertilised eggs develop within the expandable cephalothorax of the female until ready to hatch as a fully formed tantulus or other larva.

Effects on hosts and ecological importance

Tantulocaridans exhibit varying degrees of host specificity: for example, members of the family Deoterthridae occur on cumacean, isopod, tanaid, amphipod, ostracod and copepod hosts, members of the Microdajidae on tanaid hosts only, members of the Doryphallophoridae on isopods only, and members of the Basipodellidae on copepods only. They attach to the host's outer surface by their adhesive oral disc but they do not appear to suppress the host's moulting (Boxshall and Lincoln 1987). Nutrients are obtained from the host via the puncture in the cuticle, made by means of the oral stylet, which is protruded through a pore in the centre of the disc. There is evidence of an absorptive rootlet system extending from the oral disc of the tantulocaridan and penetrating through the tissues of the host (Boxshall and Lincoln 1983, 1987), but this awaits confirmation.

Important references

The group was established and the main asexual cycle elucidated by Boxshall and Lincoln (1983, 1987). The free-living larval phase was studied in most detail by Huys (1991) who also reviewed available information on the group. The life cycle was completed by the discovery of the sexual female (Huys *et al.* 1993).

Ascothoracida (ascothoracids)

Mark J Grygier and Jens T Høeg

Introduction

The Ascothoracida comprise about 100 species of parasitic crustaceans divided among six families in two orders. All Ascothoracida are marine parasites and occur from the intertidal to the deep sea (5000 m). Hosts are various echinoderms (excluding regular urchins and sea cucumbers) and cnidarians (i.e. gorgonians, zoanths, scleractinian corals, antipatharians). Their body is enclosed by a carapace that is fundamentally bivalved, but often modified and enlarged for brooding and possibly food absorption in females. The most speciose genera are *Dendrogaster* (about 30 species in seastars) and *Baccalaureus* (about 11 species in zoanths).

Grygier (1996b) provides a comprehensive entry to the literature. Many largely inaccessible Russian works were summarised by Wagin (1976) in the only book-length review devoted to this group.

Phylogenetic relationships of the Ascothoracida and the evolution of parasitism

The monophylum Thecostraca comprises the Cirripedia (with the orders Acrothoracica, Rhizocephala and Thoracica), the Ascothoracida and the Facetotecta. The Ascothoracida and Rhizocephala (see pp. 154–165) are parasitic. The Facetotecta occur throughout the marine waters of the world as γ -nauplii and γ -cyprids; adults are completely unknown, but they are also believed to be parasitic (Grygier 1996a). The likely sister group to the Thecostraca is the Tantulocarida (see pp. 147–149), parasitic on Crustacea (Høeg and Kolbasov 2002, Pérez-Losada *et al.* 2002). Thus a major clade of Crustacea consists of an assortment of parasitic taxa, along with the filter-feeding barnacles (the Acrothoracica and the speciose Thoracica). Morphology and phylogeny indicate that parasitism evolved convergently in the Tantulocarida, Ascothoracida and Rhizocephala. The Ascothoracida, which in contrast to the Cirripedia are a fundamentally non-sessile group (e.g. *Synagoga*), appear to be a relict group that has survived through adoption of a parasitic mode of life.

No ascothoracidans are known as fossils, but several trace fossils (excavations and galls) dating back to the Cretaceous on echinoderm and anthozoan hosts have with considerable confidence been attributed to the Ascothoracida. Although none is yet recorded, fossil galls formed by Petrarcidae in scleractinian corals should be easy to recognise.

Morphology and diversity

Compared to the parasitic Cirripedia Rhizocephala, the Ascothoracida are surprisingly diverse in morphology, biology and host range. The basic body plan comprises a bivalved carapace, with diverticula of the gut and gonads, which encloses the main body. The cephalon has grasping antennules and an oral cone and the 11-segmented trunk has six pairs of biramous thoracic legs, male genitalia and caudal rami (Fig. 4.12). This body plan remains evident in adult females of the family Synagogidae (especially *Synagoga* and *Waginella*). In other families females tend to



Figure 4.12 *Synagoga paucisetosa* (from Grygier 1990); this ectoparasite deviates but little from the free swimming α -cyprid (ascothoracid larva). Scale = 500 μ m.

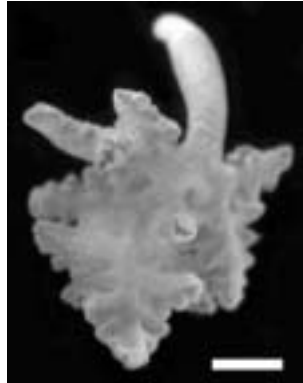


Figure 4.13 *Dendrogaster ludwigi*, a parasite in seastars, with the carapace modified into a heavily ramified mantle enclosing the brood chamber. Scale = 1 mm.

have reduced trunk appendages and abdomen and a large brood chamber formed from the carapace, which may sometimes be lobed or branched (Fig. 4.13). Size ranges from about 1.5 mm in some species of Petrarciidae (in galls in coral polyps) to over 16 cm in some species of *Dendrogaster* (filling the inside of the seastar host). Most studies have dealt with taxonomy and morphology. Thorough studies on life cycles and on demography and ecology are very few, notably Wagin (1947), Brattström (1947, 1948), and Grygier (1991).

Host relations

Some ascothoracidans are ectoparasites, and *Synagoga* may even be capable of swimming from host to host. Many are mesoparasites, either located in a cavity of the host that is connected to the outside (e.g. bursae of brittlestars) or in a cyst or gall with an opening to the outside, as in *Gorgonolaureus* and allies on gorgonians and Ctenosculidae on seastars. True endoparasites seem to include Petrarciidae in galls in scleractinian corals and *Dendrogaster* and allies in seastars. *Ulophysema* is initially an endoparasite in its urchin host, but by inducing a hole in the test becomes a mesoparasite (Figs 4.14, 4.15). Parasites of cnidarians may occupy individual polyps, or nodules formed from several polyps; in corals, so-called external galls involve a proliferation of the coenenchyme in general.

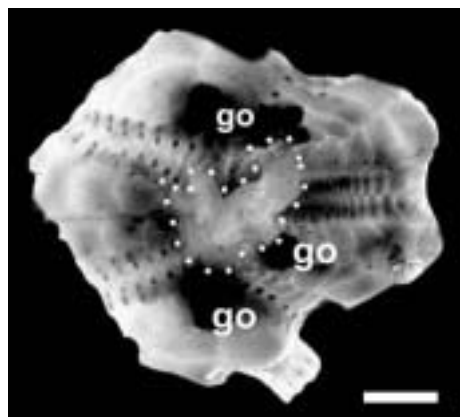


Figure 4.14 *Ulophysema oeresundense*, adult female (outlined), attached to the inside of the host echinoid test (broken open and viewed from the ventral side). Scale = 1 mm; go, gonad.

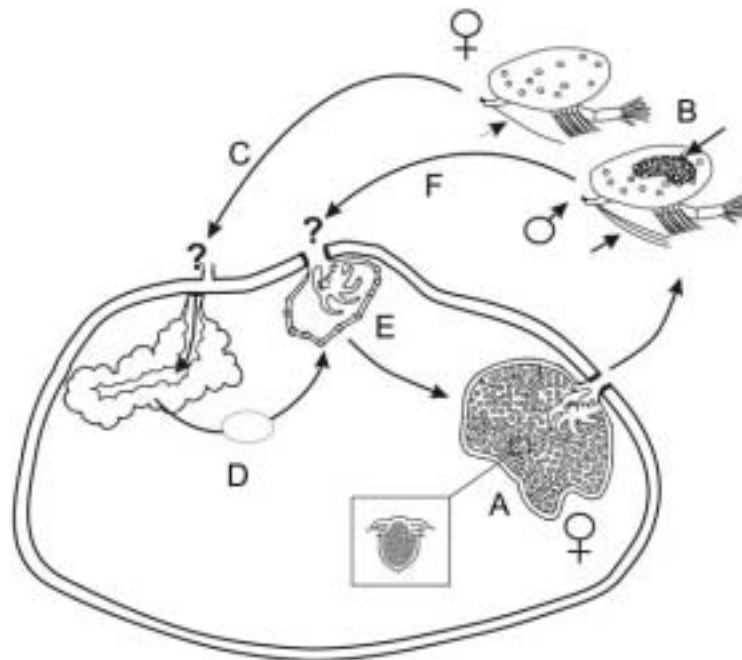


Figure 4.15 Life cycle (in part tentative) of *Ulophysema oeresundense* infesting the heart urchin *Echinocardium cordatum*. After Michael Hartmann, MSc Thesis, Univ. Copenhagen. The adult parasite is internal. **A.** The larvae are brooded in the mantle cavity until the second a-cyprid instar is released into the plankton through the parasite-induced pore in the test of the host. **B.** Male and female larvae differ morphologically, male a-cyprids having three (females one) antennular aesthetascs and testes with mature sperm (arrows). **C.** Females possibly enter the host through a gonopore, eventually breaking into the host's body cavity. **D.** In the host's body cavity the females are free but covered in ciliated host cells. **E.** The female eventually attaches by its apertural region to the host's test and produces a hole to the exterior, which could allow male a-cyprids to fertilise the female. **F.** Male a-cyprids fertilising the female. Young females without such a hole for the entry of males never contain developing embryos or larvae.

Many of the parasites of echinoderms (*Ascothorax*, *Ulophysema* and *Dendrogaster*) have been implicated in host castration. Little is known of feeding. Primitively, they undoubtedly feed by the piercing-sucking mouth apparatus. The ultrastructure of the cuticle of *Ulophysema* is suggestive of absorptive feeding in the manner of rhizocephalan barnacles, but whether this is its primary mode of food intake and occurs in other ascothoracidans remains unknown.

Life cycle and sexual system

Sexes are separate except for the hermaphroditic Petrarcidae. Sex determination seems to be genetic, and in some species male and female larvae differ morphologically (e.g. in the armature of chemosensory aesthetascs, just as in most Cirripedia Rhizocephala). Primitively, larval development comprises six naupliar instars followed by one or two cypris-like stages (a-cypris), homologous to the single cypris instar of the Cirripedia and the γ -cypris of the Facetotecta. Lecithotrophy is common, but some species have planktotrophic nauplii. The a-cypris, also known as the ascothoracid-larva, attaches by its grasping antennules rather than by glandular secretions as in cirripede cyprids (Figs 4.16, 4.17). In species with two a-cyprid instars, only the second is the actual settlement stage. Many species have an abbreviated ontogeny, and the entire naupliar phase is sometimes brooded, or even embryonised.

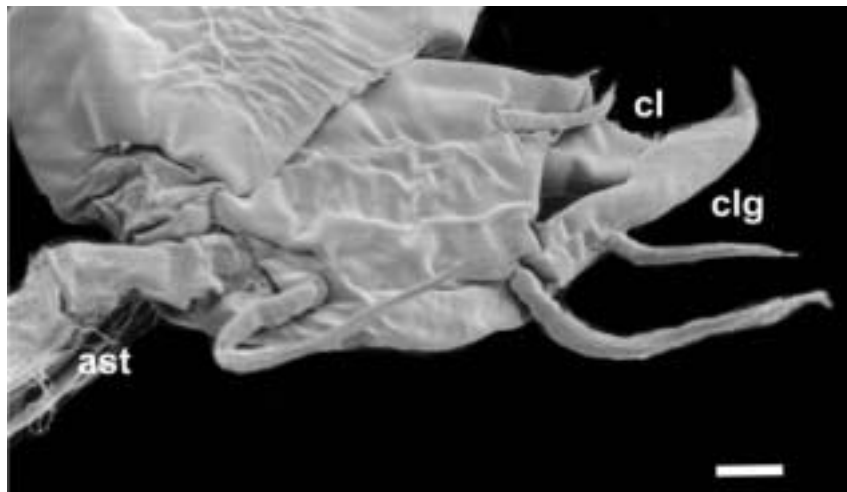


Figure 4.16 Terminal part of antennule of a-cyprid of *Ulophysema oeresundense* with chemosensory aesthetascs (ast); attachment is purely mechanical using the claw (cl), which is retractable into the claw guard (clg). Scale = 10 μ m.

No complete life cycle has been worked out for any ascothoracidan, and neither host infection nor copulation has ever been witnessed directly (seminal receptacles are in the female's legs, but absent in Dendrogastridae). The two best-known species are *Ulophysema oeresundense* (see Brattström 1948) and *Bacallaureus falsiramus* (see Itô and Grygier 1990). *Ulophysema oeresundense* (Fig. 4.15) has two brooded naupliar instars and two a-cyprid stages, the latter being released into the plankton. *Bacallaureus falsiramus* has six naupliar stages and a single a-cyprid stage. Its manner of host infestation (in *Zoanthus* sp.) is unknown, but like its congeners the female becomes a mesoparasite, with the carapace aperture open to the outside. The dwarf male

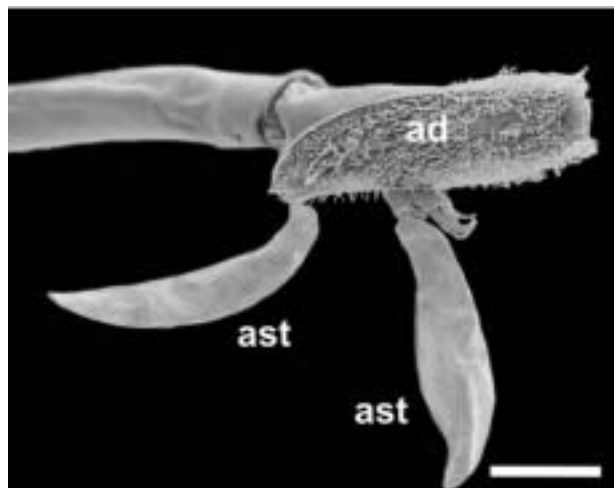


Figure 4.17 *Briarosaccus callosus* (Cirripedia Rhizocephala), male cyprid, terminal part of antennule; attachment is by a cement secretion from the attachment disc (ad). Both the ascothoracidan (a-cyprid in Fig. 4.16) and rhizocephalan (cyprid) antennules carry large chemosensory aesthetascs (ast), assumed to assist the location of a host (females) and a female parasite (males). Scale = 10 μ m.

sits close to the aperture, and larvae presumably escape this way. Dwarf males of *Dendrogaster* live within the mantle cavity of the female, presumably feeding upon it; how they arrive there is unknown, but self-production of an initial brood of males by the female has been suggested. Females of *U. oeresundense* are not permanently associated with males, but male a-cyprids have testes with mature sperm, and they possibly fertilise the females through the pore induced by the latter in the test of the host echinoid (Fig. 4.15). In agreement with this hypothesis, females of *U. oeresundense* that are free in the host's body cavity never contain developing embryos or larvae. In no highly modified species has metamorphosis from the last larva to juvenile been observed, although the transformation from bivalved to sac-like carapace form has been supposed to take place in one moult in *Ulophysema* and *Dendrogaster*. In *Parascothorax* a 'post-larval' stage of both the female and male has been distinguished and second-stage a-cyprids ready to moult to the male stage have been observed.

Ecology and epidemiology

Few species have been thought to be abundant enough for meaningful ecological and particularly demographic study. There are two main exceptions. One is *Ulophysema oeresundense*, parasitising Scandinavian heart urchins (Brattström 1947), including up to 20% of *Echinocardium cordatum* in the Sound connecting the Baltic Sea and the Kattegat. The other is *Parascothorax synagogoides*, parasitising the brittlestar *Ophiophthalmus normani* in the bathyal basins off California, with prevalence varying among basins (0.5–9.0%), multiple infestations being more frequent than chance would predict, and brood sizes varying from 3 to 183 (Grygier 1991). Male a-cyprids apparently join females before the cysts induced by the latter become closed; as many as five males may accompany a female. Grygier (1991) is perhaps the only demographic study ever published of a deep-sea invertebrate parasite; this paper also makes a comparison with known ecological information on two species of confamilial *Ascothorax*.

Hyperparasitism of ascothoracidans by cryptoniscid isopods is not uncommon, occurring in four of the six families; parasitic castration of the ascothoracidan was noted in the case of *P. synagogoides*.

Important references

Comprehensive accounts of the Ascothoracida are by Wagin (1976, in Russian) and Grygier (1996b). Itô and Grygier (1990) described the larval development of an ascothoracid. Grygier (1996a) gave a detailed account of the Facetotecta. The phylogenetic relationship of the Ascothoracida and Cirripedia and the phylogenetic position of the Facetotecta were analysed using morphology by Høeg and Kolbasov (2002) and on the basis of 18S rDNA sequences by Pérez-Losada *et al.* (2002).

Cirripedia Thoracica and Rhizocephala (barnacles)

Jens T Høeg, Henrik Glenner and Jeffrey D Shields

Introduction

The Rhizocephala comprise about 250 species, which is about one-quarter of all cirriped species. Rhizocephalans are parasites of other Crustacea, principally Decapoda. Adult Rhizocephala are sessile, in contrast to the related Ascothoracida, discussed in the previous Section (see pp. 149–154), which are fundamentally (primitively) mobile. Adult females have lost all obvious crustacean morphological traits and consist of a sac-like part attached to the crab host (Fig. 4.18) with outgrowths of tissue (rootlets) extending cancer-like into the host's body. The males are reduced to dwarfs and live within the parasitic female. Only the larvae are free living and

they closely resemble those of other barnacles. Rhizocephalans are particularly fascinating because they induce marked behavioural changes in their hosts that can benefit host survival. They also have considerable economic importance causing mortality and castration, thus reducing the profitability of crustacean fisheries.

Thoracica

Nearly all parasitic Cirripedia belong to the Rhizocephala, which parasitise Crustacea. The few parasitic cirriped species that do not belong to the rhizocephalans possess rudimentary thoracopods and are tentatively included in the Thoracica. These are *Rhizolepas*, with a few species infecting polychaetes, and *Anelasma squalicola*, which infects dogfish. Neither of these genera is related to the Rhizocephala. Both are ectoparasites in which a body with rudimentary thoracopods (cirri) is attached by means of a peduncle that sends nutrient-absorbing roots penetrating into the host. *Anelasma* is hermaphroditic and close in morphology to a filter-feeding barnacle, retaining both mouth appendages and a gut, albeit these structures may not be functional. The dogfish host seems always to carry at least two *Anelasma* together, attached at the dorsal fin. More recently additional thoracican barnacles have proven to be ectoparasites including the family Microlepadidae on diademid echinoids, *Koleolepas* on sea anemones inhabiting hermit crab shells and Hoekiini barnacles on corals. Unlike *Rhizolepas*, *Anelasma* and the rhizocephalans, all of these species feed on the host as micropredators, using their appendages and mouth for food intake (Grygier and Newman 1991, Ross and Newman 1995, Yusa and Yamato 1999, Yusa *et al.* 2001). Whale barnacles (Thoracica: Coronuloidea), although deeply anchored within the dermis of their cetacean hosts, feed exclusively by filtration and do not absorb nutrients from the host.

Effects on hosts

Most epizootic Thoracica are better known as fouling agents rather than parasites because they do not penetrate into their host or otherwise cause physical damage. However, at sufficiently high densities, infestations of balanid and pedunculated barnacles may become physiologically deleterious. *Chelonibia patula* is an acorn barnacle symbiotic on turtles, whales and other crustaceans. Heavy infestations on crabs can burden the host by hampering movement and increasing its vulnerability to predation (e.g. Overstreet 1983). The pedunculated *Octolasmis* spp. infest the gills of decapod hosts. Oxygen uptake, lactate levels, pH and other blood parameters do not differ between infested and uninfested blue crabs infected with *O. muelleri*, but infested hosts show an elevation in heart rate and ventilation rate as if in a constant state of exercise (Gannon and Wheatly 1992, 1995). Heavily fouled crabs may indicate the presence of other disease agents, senescence or anecdyosis, and they probably do not survive long in nature.

Economic importance

The thoracican barnacles are not known to cause significant economic impacts to crustacean or other fisheries. However, heavily fouled hosts are not typically selected for high grading and may end up in lesser valued processed foods rather than as whole product. Heavily fouled hosts may indicate the presence of other disease agents or senescence and, thus, they are often culled from further use.

Rhizocephala

The Rhizocephala are a bizarre, highly modified group of barnacles that are barely recognisable as Crustacea. While the morphology and life cycle of these intriguing parasites is now well described, their ecology and coevolution with their hosts is only just beginning to be understood.

Most rhizocephalans parasitise brachyuran and anomuran crabs. A few are parasites on caridean shrimp, stomatopods, peracarids and even other barnacles. None are found on palinuran lobsters or astacidean crayfish, which is surprising given the broad range of infections in disparate host taxa.

Most infect more than a single host, and many of these do not appear to be cryptic species (Murphy and Goggin 2000). The well-studied *Sacculina carcini* infects more than 10 crab species from several genera (Øksnebjerg 2000). Larval female cyprids can settle on species that never harbour adult parasites, with far reaching implications for the colonisation of new hosts (i.e. habitats) (Thresher *et al.* 2000). However, a few rhizocephalans are specialists, using only a single host species or genus.

Rhizocephalans are found from the deep sea to the pelagic and into high intertidal habitats. They extend into brackish waters, but only a few species occur on truly freshwater or semiterrestrial crustaceans, leading to marked changes in life history (Andersen *et al.* 1990).

Several reviews have dealt with the taxonomy, morphology or life cycle of the Rhizocephala (Høeg and Lützen 1985, Høeg 1992, 1995, Høeg and Lützen 1995, 1996, Øksnebjerg 2000, Walker 2001). The ecology of only a few species has been studied. Høeg (1995) and Høeg and Lützen (1995) reviewed the literature until about 1992. Later important references are Hochberg *et al.* (1992), Alvarez *et al.* (1995), Hines *et al.* (1997) and Tindle *et al.* (2004) on species of *Loxothylacus*, Alvarez *et al.* (2001) on *Lernaedodiscus porcellanae* and Werner (2001) on *Sacculina carcini*.

Systematics and evolution

The Rhizocephala consists of two monophyletic suborders, the Kentrogonida with more than 230 species and the Akentrogonida with 30–40 even more highly specialised species. More than 120 species belong to the genus *Sacculina*, including the 'classic' *S. carcini*, but molecular evidence indicates that the genus is polyphyletic. Species level systematics is very problematic, but scanning electron microscopy promises to offer characters for comparatively easy identification (Rybakov and Høeg 2002).

These parasites must have evolved from sessile filter-feeding cirripedes, but the details of this process, including the intercalation into the life cycle of an internal migratory phase, the vermigon, remains largely unexplained (Glenner and Høeg 2002). While other barnacles are well represented in the fossil record, there are no fossils of Rhizocephala (Conway Morris 1982); thus molecular techniques will be needed to further study their evolutionary and coevolutionary patterns.

Morphology, life cycle and reproductive ecology

The adult parasite has lost virtually every arthropod trait, including segmentation, appendages, sense organs, excretory organs and gut. It consists of an external reproductive body, the externa, connected to a nutrient-absorbing system of rootlets infiltrating the host, the interna. Specialisation lies mainly in their sexual systems and the advanced level of behavioural control exercised by these parasites upon their hosts.

A typical rhizocephalan life cycle includes several life history stages (Figure 4.19).

Larval development and dispersal

Despite the parasitic life style, larval development of Rhizocephala is virtually identical to that of other Cirripedia (Walossek *et al.* 1996). There are several naupliar instars and a terminal cyprid, the settlement stage unique to all cirripedes. Larval development is entirely lecithotrophic and normally of short duration, lasting two to three days in warm waters, about two weeks at 10°C, but up to 30 days in the arctic. As a probable adaptation to enhance survival or dispersal, several

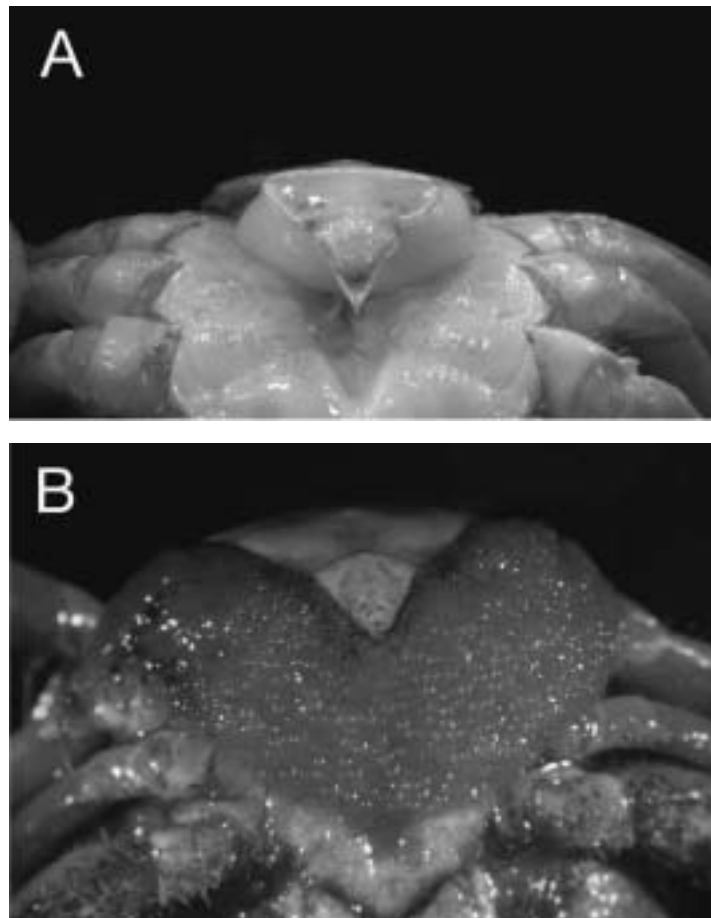


Figure 4.18 A. *Sacculina carcini* infesting the shore crabs *Carcinus maenas* and *C. mediterraneus* in western European and Mediterranean waters. The external reproductive body sits under the abdomen where B. healthy females normally carry their brood, but the host in A. is a feminised male crab.

rhizocephalans release their larvae as cyprids, including most deep sea species, all freshwater and semi-terrestrial species and all members of the specialised suborder Akentrogonida.

Female parasite strategies

Female cyprids probably rely on odour trails in the water column to locate the host (Pasternak *et al.* 2004a,b). At settlement, the cyprids recognise the host by means of carbohydrate or glycoprotein cues in the epicuticle (Boone *et al.* 2003, 2004). The host's behavioural defences can be circumvented by three means: efficient host finding; avoidance of detachment before penetration; and avoidance of the host's immune response coupled with a rapid takeover of host control once injected by the cyprid larva. In general, the female cyprid can locate recently moulted crabs by chemosensory ability. Rhizocephalans settle at specific sites on the host, but always in areas with a thin or soft cuticle to facilitate penetration. The well-studied example of *Lernaeodiscus porcellanae* and its host, the porcelain crab *Petrolisthes cabrilloi*, illustrates the effectiveness of host cleaning defences and parasite countermeasures (Fig. 4.20). Female cyprids settle in the narrow confines between the gill filaments in the branchial chamber to avoid being groomed away by

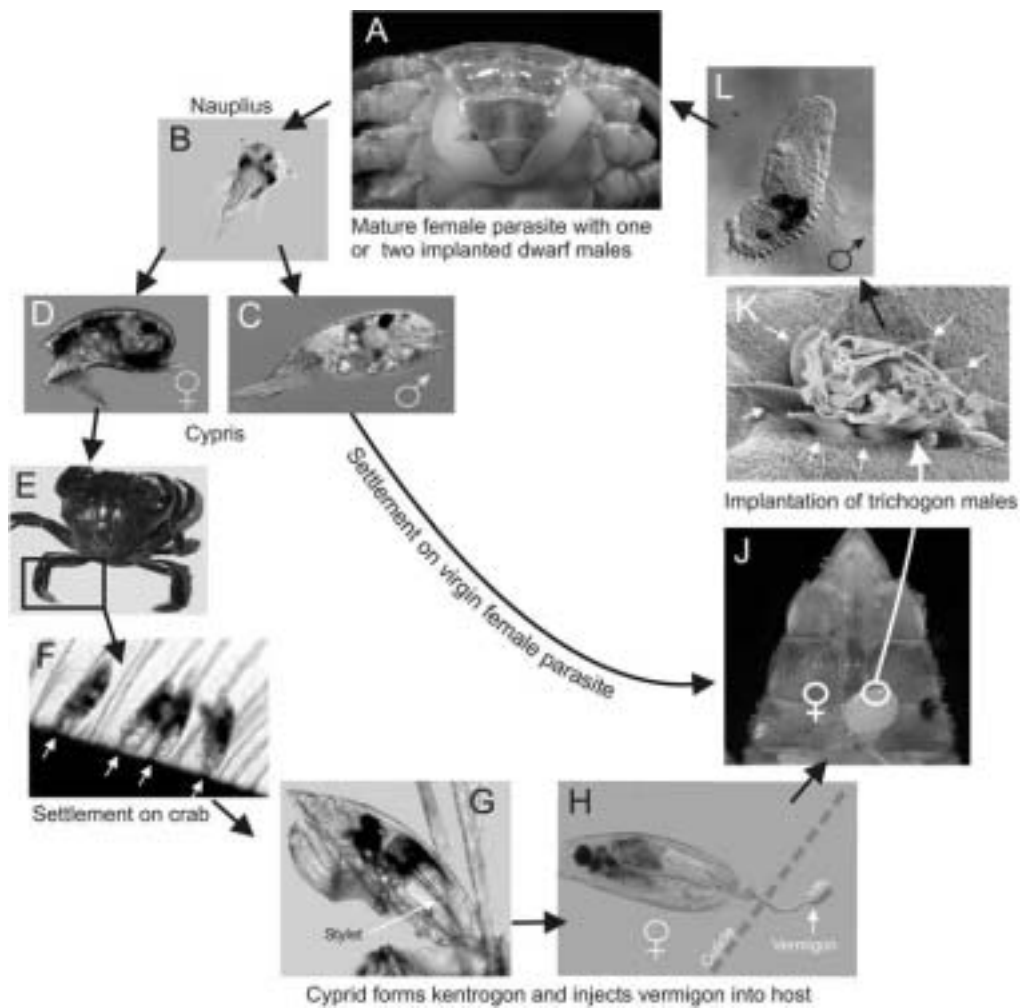


Figure 4.19 Life cycle of *Sacculina carcini* (Kentrogonida) parasitising the brachyuran crab, *Carcinus maenas*. **A.** The parasite is externally manifested by a reproductive body (externa) located on the abdomen and connected with a nutrient-absorbing system of rootlets (interna) inside the host. The parasite is female, but is host to and nourishes two highly reduced dwarf males in a pair of receptacles. A series of broods are released and fertilised by sperm produced cyclically by the resident males. **B.** Larvae are released as nauplii that develop lecithotrophically into cyprids. Female cyprids (**D**) settle on potential host crabs (**E**, **F**). They form a kentrogon (**G**), which uses a hollow cuticular stylet (**G**, arrow) to penetrate the host cuticle and inject a vermigon stage into the hemocoel; the stippled line in (**H**), indicates where would have been the crab cuticle in this *in vitro* preparation. After an internal growth period, the parasite emerges externally as a small, virgin female (**J**). These are the targets for male cyprids (**C**), which accumulate around and fight for access to the narrow opening into the brood chamber. At most two of them will successfully inject a trichogon stage into the chamber and become established in a receptacle as highly reduced sperm producing dwarf males (See also Fig. 4.21). Implantation of one or two males immediately induces the female to grow into sexual maturity. The males produce sperm in synchrony with the cycles of egg production in the ovary of the female. They are nourished by the female and remain with her for the duration of her lifetime. (Based on Delage 1884, Lützen 1984, Høeg 1984, 1987, Walker 1988, Glenner 2001 and previously unpublished micrographs.)

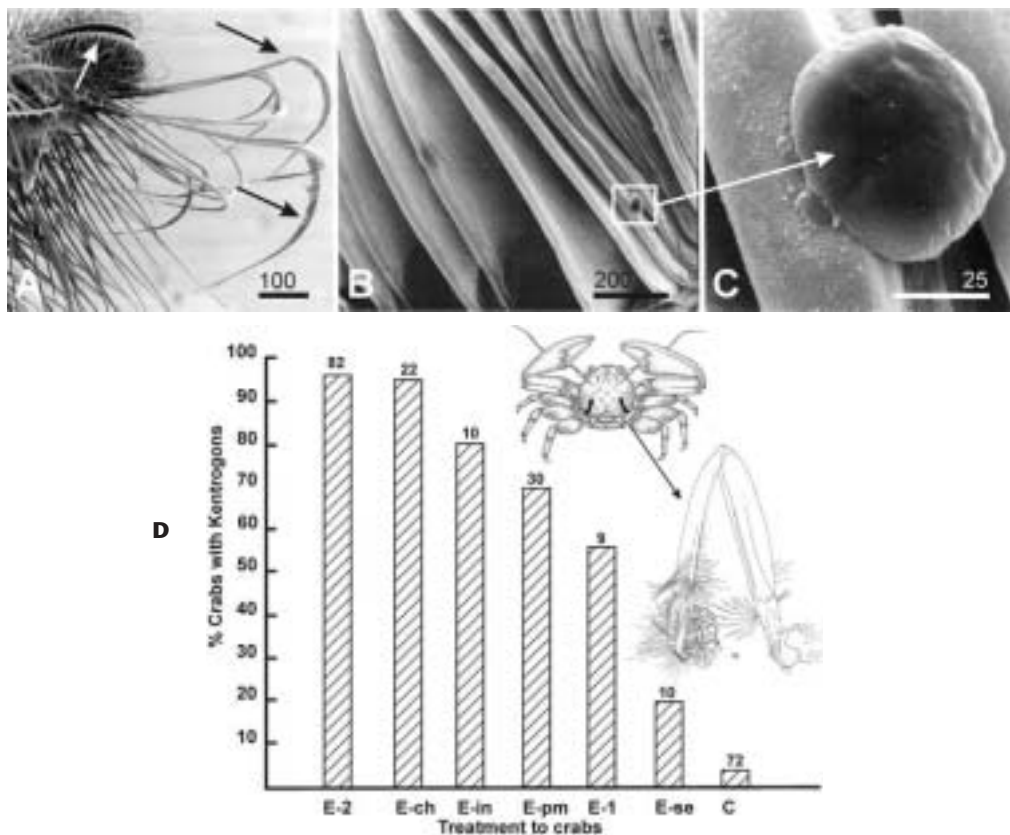


Figure 4.20 Host cleaning defences and parasite countermeasures in the porcelain crab, *Petrolisthes cabrilloi*, and the rhizocephalan, *Lernaediscus porcellanae*. The line drawings depict a crab and an enlarged grooming limb with clusters of setae at the tip. SEM micrographs show the following. **A.** The tip of a grooming limb; the sickle-shaped setae (black arrows) remove parasite cyprids and general debris on the gills, but only the cheliped (white arrow) can remove the scale-shaped and more firmly attached kentrogons. **B.** Several gill filaments with an attached kentrogon (square). **C.** Kentrogon enlarged. All scales in micrometers. **D.** Experiments on gill cleaning efficiency (see details in text). Healthy control crabs can normally groom away all parasite larvae before they manage to invade, while crabs with missing or damaged grooming limbs (E-2, E-ch, E-1, E-se), injured crabs (E-in) and immediate post-moult crabs (E-pm) risk infection because they retain substantial numbers of infective kentrogons after exposure to parasite cyprids. Numbers above bars indicate how many crabs were used for each experiment.

the crab before they succeed to invade. Using the specialised 5th pair of thoracopods (Fig. 4.20D), the crabs can normally groom away most of the settled cyprids before formation of the infective kentrogon (Fig. 4.20C). Removal of cyprids is by means of the sickle-shaped setae at the tip of the grooming limbs (Fig. 4.20A, black arrows). The smaller, firmly attached and low-profiled kentrogons (Fig. 4.20B, C) can only be removed using the chelipeds at the tip of the grooming limbs (Fig. 4.20A, white arrow). As a parasite countermeasure, formation of the better protected kentrogon is very rapid (<1 hour after settlement), thus minimising the period when the larvae are critically exposed as cyprids. Experimental crabs in Figure 4.20D were exposed to female cyprids for 30 minutes and thereafter isolated for 90 hours, followed by counting the numbers of kentrogons on their gills to estimate the efficiency of host grooming. Crabs with both grooming limbs ablated (E-2) cannot remove parasite larvae and are thus very susceptible

to infection. Decreasing numbers of kentrogons due to increasing grooming efficiency is seen in crabs with both grooming chelipeds crushed using forceps (E-ch), crabs injured with a needle prick (E-in), immediate post-moult crabs with soft cuticles (E-pm), crabs with only one grooming limb removed (E-1), and crabs with the sickle-shaped setae removed (E-se). Control crabs (C) can almost completely remove parasite larvae, even at the unnaturally high densities in this laboratory experiment.

In *Sacculina carcini*, settlement at the base of a seta may offer a similar protection against host grooming. Injection of the vermigon (the migratory internal stage) happens within one to three days after settlement and the parasite immediately begins to take over control of the host, one of the first effects being to damage the nervous system by penetration of the parasite's rootlets and by bringing hormonal slavery. How host control is achieved and maintained is little understood and is wide open to a modern molecular approach.

Male parasite strategies

Unlike the female cyprid, which at settlement meets the hostile environment of the potential host, the male cyprid must locate and inseminate the virgin externa of the female via implantation. However, the male also faces several hurdles mainly due to competition with other males (Fig. 4.21). The male cyprid must not only locate a host crab, but also one already carrying an established virgin parasite. Furthermore, no more than two males can normally be implanted in any parasite, and once a single male is acquired, the female externa immediately begins to mature sexually; the accompanying morphological and physiological changes soon prevent the insemination by other males. Where prevalence is high there is a surplus of male larvae, so males must compete to find the rare virgin. Many male cyprids can land on a female vying for insemination, so only the fastest and strongest ones will successfully inseminate the female (Høeg 1987, 1991). At low prevalences, male larvae are fewer and virgin parasites may remain receptive over extended time periods (Høeg and Ritchie 1985).

When a virgin is found, the cyprid can penetrate no farther than the narrow entrance to the brood chamber, which contains the paired receptacles that will eventually host the one or two successful males (Fig. 4.21B). Only those settled closest to the orifice can inject a trichogon stage into the brood chamber, and once inside (Fig. 4.21C), they must be the first to reach an empty receptacle. Having achieved this, the trichogon sheds its spiny cuticle, thereby blocking access to any subsequently arriving competitors (Fig. 4.21D). This spatial barrier into the brood chamber may serve both to protect against multiple matings and to insure that only the most vigorous males gain access. Male cyprids have more chemosensory organs than females (Fig. 4.17), and the efficiency of these organs is highlighted by the whole process, from locating the externa to entering a receptacle, being able to be completed within minutes. Once established, the male undergoes spermatogenesis and is nourished by the female parasite for the duration of its lifetime (cryptogonochorism). However, the male may still face competition with a potential partner in the other receptacle (Fig. 4.21E). It is, therefore, of benefit to the male that the female commences sexual maturation immediately after insemination by the first male. Which sex controls this process is not known. Apparently a single male suffices to fertilise all of the ova in the broods produced by a female. The presence of two receptacles (i.e. two possible males) may therefore benefit the female either by increasing genetic variability or by insuring continued reproduction should one male accidentally perish.

Sexual biology and reproductive strategies

Unlike most other cirripedes, which are hermaphroditic, rhizocephalans have separate sexes, but the detailed mechanism of the genetically based system for sex determination remains unknown (Yanagimachi 1961). For unknown reasons, male larvae are generally larger than females, but it

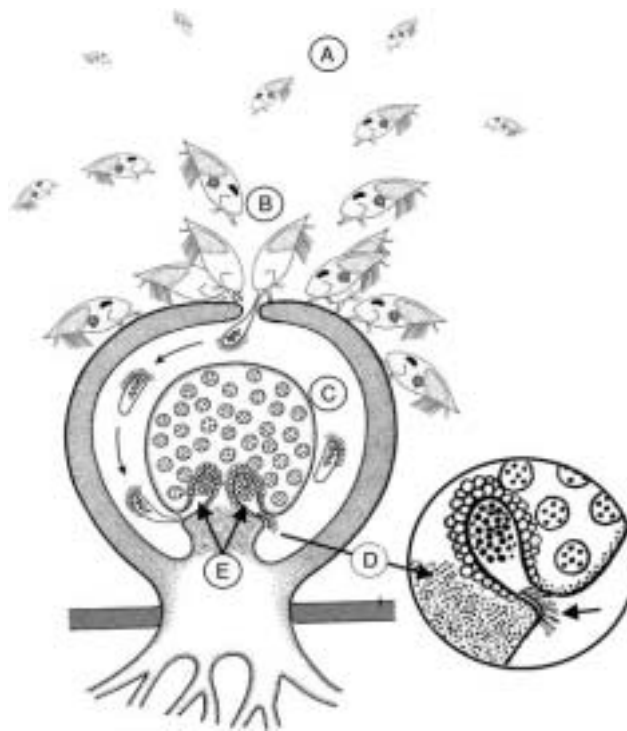


Figure 4.21 The battlefield of the virgin externa: The male larvae faces many obstacles in achieving reproduction. **A.** A cyprid locates a host carrying a virgin parasite externa. **B.** Competition for space around the narrow confines of the aperture and implantation of a trichogon stage into the brood chamber. **C.** The race against time to migrate to the opening of one of two male receptacles. **D.** Blockage of one of two male receptacles (arrow) by the shed cuticle of a previously arrived male. **E.** Competition of an established dwarf male with its male partner in the other receptacle in fertilising the eggs of the female. In this virgin externa, several males have settled close to the aperture and injected trichogons; one is being successfully implanted in the left side receptacle (curved arrows); the right side receptacle is already blocked by a previously arrived male (D) and the trichogons arriving there will eventually perish. Based on Høeg and Ritchie (1985) and Høeg (1987).

may allow them longer time to search for virgin females. The brooded eggs can have any sex ratio, although it is normally wholly or predominantly biased towards one sex. Surprisingly, the sex ratio varies through successive broods for a single externa and follows the yearly cycle of the population. In *S. carcini*, broods are heavily biased to the male sex when virgin females are most frequent (Table 4.2). Adding to the complexity, the mean sizes of both male and female larvae varies with season, again for reasons entirely unknown. In the Akentronida, sex determination and larval ecology remains largely unknown.

The number of males hosted by a single female parasite varies. Kentrogonids with colonial externae, each with two receptacles, can host many males, thereby increasing genetic variability. An extreme case is seen in the akentrogonid and colonial Thompsoniidae, where the female consists of hundreds or thousands of externae, each of which can be fertilised by males.

The adult rhizocephalans have two strategies for host use dictated by their own longevity. Peltogastrid and lernaediscid species that infest anomuran hosts remain on the host for a term approaching the life expectancy of a healthy crab. During this period they regularly release broods of larvae every two to four weeks. These species also allow their hosts to continue moulting and sometimes also to increase in size; they probably do not extract more resources than

Table 4.2 The percentage of juvenile (virgin) females, adult females and male cyprid larvae of *Sacculina carcini* infesting *Carcinus maenas* along the French coast of the English Channel

	Juvenile female parasites (%)	Adult female parasites (%)	Male cyprid larvae (%)
Spring	51	49	86
Late summer	37	63	14
Data combined for 1982, 1983, 1986.			

would otherwise be used in the host's own reproduction. Conversely, sacculinids that infest brachyuran crabs produce a limited series of large broods over a rather short period, one to two reproductive periods, after which they die. The crab host is normally prevented from moulting and therefore becomes deleteriously fouled. Some akentrogonids produce only a single brood during the life time of the parasite and thus display semelparity, an extreme form of this short-term infection pattern.

A more complicated form of the long-term infection pattern is seen in the species with colonial externae. In some species each such externa reproduces only once, but is replaced by regeneration from the root system. The advantages of this system are not well understood, but it spreads the risk of lethal injury over several externae. This is especially advantageous in species, such as thompsoniids, where the externae protrude anywhere on the body of the host and are thus prone to being lost. But colonial externae may also serve as a means to optimise reproductive output. This is directly correlated to externa volume, which is smaller in a solitary externa than the total volume of multiple externae from a similarly sized host (Wardle and Tirpak 1991, Galil and Lützen 1995).

Epidemiology

Single infections are the rule in most species. Multiple (colonial) externae connected to a common root system are frequent or obligatory in some species, but true multiple infections by separate cyprids can occur. Prevalence varies extensively in the Rhizocephala, both within and between species, but few studies have examined more than a single season or differences between host populations. Prevalence ranges from well below 1% to nearly 100% in some populations of *Sacculina carcini* from Mediterranean lagoons. Prevalence often shows wide local variations over short scales. For example, Werner (2001) followed *S. carcini* on *C. maenas* on the west coast of Sweden and found prevalence to consistently vary by an order of magnitude between stations separated by only a few kilometres, the most sheltered sites having the highest abundance. At Roscoff on the French channel coast, prevalence varies from almost nil to 20% over a few hundred metres. The reasons for such variation are often obscured, but host factors such as sex, size, moulting frequency, moult stage and migratory behaviour show correlations with prevalence. For example, blue crabs, *Callinectes sapidus*, have a peak in moulting activity during spring, and most infections occur at this time because the parasite larvae have a preference for post-moult crabs (Tindle *et al.* 2004). Female blue crabs appear more susceptible to infection at this time because they prefer high salinity waters and thus come into contact with the parasite *Loxothylacus texanus* which cannot tolerate low salinities (Boone *et al.* 2004). Environmental factors such as hydrography, salinity, depth and turbulence often show strong correlations with prevalence in several species (e.g. Reisser and Forward 1991, Walker and Lester 1998, Boone *et al.* 2004). In *L. porcellanae* parasitising intertidal porcelain crabs, hosts inhabiting high wave energy environments have more damage to their grooming appendages making them prone to infection (Fig. 4.20), while those in sheltered habitats such as mussel beds suffer less damage and have lower prevalences. In *Loxothylacus panopaei*, prevalence is highest in hosts

living at salinities of 10 parts per thousand (ppt) to 15 ppt and zero at salinities below 10 ppt (Reisser and Forward 1991). Hydrographic features have been associated with increased prevalence of *Briarosaccus callosus* on king crabs, presumably because fjords with shallow sills entrain the water mass thereby retaining high levels of infectious larval stages (Sloan 1984, 1985). Even when prevalence is low, these parasites can linger for extended periods such as in a hermit crab infested by *Clistosaccus paguri* (1–2.5% over three years, Høeg 1982). However, rare host species may limit the spread of their parasites simply as a result of low population densities.

Effects on hosts

Rhizocephalans change the morphology, physiology and behaviour of their hosts so that hosts become nothing but automatons serving only the purpose of the parasite. Almost all Rhizocephala sterilise their host through hormonal or biochemical alteration of the gonads. In most cases, infections cause feminisation of castrated males through the destruction of the androgenic gland, the male sex-determining organ in crustaceans. Castrated hosts are essentially taken over by the parasites and in most cases remain altered for life, becoming sterile competitors in the host population. This is probably the worst competitor any species can face. Shields and Wood (1993) found that male crabs will even attempt to mate with sterile, infected females and feminised males! Because of such sterile matings, the effect of the rhizocephalan to the host population may be even greater than that predicted by prevalence alone, particularly when considering the lengthy pre-copulatory and post-copulatory embraces elicited by receptive crabs.

Parasitic castration also channels metabolic energy otherwise used in host reproduction to the parasite. This is notable because the sterile, infected host reacts to its parasite by cleaning and caring for it as if it were its own offspring. This effect also extends to male hosts which are feminised behaviourally as above, but also morphologically, often acquiring secondary sexual characters of the females such as a broader abdomen used for 'brood protection' in female crabs and the development of female pleopods (Ritchie and Høeg 1981, Innocenti *et al.* 1998). This elaborate 'brood mimicry' is possible because the reproductive body, or externa, of the parasite generally protrudes from within the brood chamber of the host. Some host species will even assist the parasite by exposing the abdomen when the virgin parasite must acquire males and by ventilating it when the mature female releases its broods of nauplii. Additionally, the parasite can arrest the moult cycle of the host (i.e. cause anecdyosis), but, notably, this is not universally so. Species infesting anomuran crabs allow their hosts to continue moulting, thus enabling it to groom and often also to grow. Due to the effect on the moult cycle, infestation by rhizocephalans can affect the size distribution of the host population, normally resulting in large numbers of stunted 'females' in the population, but the pattern may vary both between and within host-rhizocephalan systems (O'Brien and Van Wyk 1985).

Host strategies

Ecologically, the effect of castration is the loss of the reproductive fitness of an infected host. A successful infection immediately begins to take over control of the hormones and behaviour of the host. Host defences may operate at three levels: 1, behaviourally, by evasion of the female cyprids; 2, physically and behaviourally, by preventing the larvae from attaching and penetrating through the carapace; and 3, immunologically, by fighting the internal parasite before it becomes established. Female cyprids probably rely on odour trails in the water column to locate the host and this may be one reason why they prefer settlement on recently moulted crabs, which are presumably either more odiferous or exude a different odour than intermoult crabs (Glennner and Werner 1998). There is no evidence for behavioural evasion by crabs, but host grooming is important in preventing infections. Porcellanid crabs are excellent groomers and normally remove all parasite larvae before they penetrate (about 48 hours after settlement) and

thus avoid becoming infested (Fig. 4.20). Susceptible individuals are those that for several reasons (damage, disease or moulting) are deficient in their grooming effectiveness. Porcellanids react within seconds to the presence of female cyprids by initiating fervent grooming of their gills (the settlement site for their rhizocephalan), yet in the presence of harmless nauplii or male cyprids, no grooming behaviour is elicited and the crabs continue to filter feed. Defensive gill grooming must be a time-consuming behaviour and may perhaps be relaxed in populations where the prevalence of the parasite is low; however, such critical population-level studies on coevolution have not been performed (Nuismer *et al.* 2003). Another question is whether hosts other than porcellanids use grooming to fight rhizocephalan infection.

Immunologically, the host defences must attack and kill the parasite before it takes over hormonal control. In abnormal hosts there is evidence of cellular reactions to the parasite. Melanised internae can be observed in such hosts, and occur in the few normal hosts that survive the loss and death of the parasitic externa (hence, death of the parasite) (Sparks and Morado 1986). Susceptible hosts often show little indication of a defensive response, so the parasite somehow avoids recognition by the host's defences. There are also indications that if parasitism does not succeed, the host may simply die. The same can be seen in abnormal hosts that are artificially infested (i.e. the parasite may be more lethal to them than to their regular host) but experimental studies have used high exposure levels that may have swamped the host's defences leading to host death. Given that rhizocephalan larvae seem to be opportunistic in their choice of settlement targets, survival in an otherwise abnormal host may have important consequences for their ability to spread into a new geographical area.

Economic importance

Rhizocephalans cause castration, anecdyosis, stunting and increased mortality to their crab hosts, and thus, can have direct and indirect effects on crustacean fisheries. Prevalence can reach extraordinary levels in focal outbreaks and the resulting stunting and increased mortality of infected hosts can result in direct losses to a fishery because stunted and moribund animals cannot be marketed. Indirect effects include castration, sterile matings, loss of fecundity and competition with phenotypically identical parasites (Shields and Wood 1993). Fortunately, few commercial fisheries are plagued by rhizocephalans, but they do damage segments of lithodid and portunid crab fisheries. *Briarosaccus callosus* infects numerous lithodid king crabs from the Antarctic to the Arctic. In the golden king crab, *Lithodes aequispina*, prevalences reached 48% in the fjords of British Columbia (Sloan 1984). In the blue king crab, *P. platypus*, prevalences reached 76% in the fjords of south-eastern Alaska (Hawkes *et al.* 1986). Interestingly, the red king crab, *Paralithodes camchaticus*, hosts *B. callosus* in its native range, but the population introduced into the Barents Sea and now spreading rapidly southwards along the Norwegian coast is without this parasite.

Two important portunid fisheries are also impacted by rhizocephalans. *Sacculina granifera* infects *Portunus pelagicus* with prevalences reaching 40% (Shields and Wood 1993). Infected crabs are frequently stunted and their hepatopancreas turns a vivid green that can impart a poor flavour to the flesh (Bishop and Cannon 1979). *Loxothylacus texanus* on *Callinectes sapidus* can reach prevalences of 30% to 70% in the lagoons around the Gulf of Mexico. All of these rhizocephalans stunt their hosts, producing individuals too small for sale which are left to accumulate in the fishing grounds as 'shorts', serving as foci for transmission to new hosts (Meyers 1990). Human activities such as culling stunted, parasitised crabs back into the water or moving animals between locations (culling while underway) may contribute to the spread of these parasites.

Recent models have suggested that parasitic castrators can regulate populations of crustaceans (Blower and Roughgarden 1989a,b, Kuris and Lafferty 1992). Such systems may be

considered hydrodynamically or demographically closed for purposes of immigration (e.g. Sloan 1984, Cowen *et al.* 2000). Thus, the potential impacts of rhizocephalans on the connectivity between fecundity, larval dispersal and juvenile recruitment represent an exciting area for productive research. As an example, the portunid crab *Charybdis longicollis* has recently spread through the Suez into the eastern Mediterranean and created an important fishery. It was later accompanied by its natural rhizocephalan and the dynamics and spread of this host-parasite system is now being monitored (Galil and Lützen 1998). (For commercial effects see also p. 364.)

Important references

Walker (2001) wrote a brief Introduction to the Rhizocephala. Important comprehensive contributions on the group are given by Bresciani and Høeg (2001, root system), Høeg (1992, microscopic anatomy; 1995, biology and life cycle), Høeg and Lützen (1995, life cycle and reproduction), Høeg and Lützen (1996, general account and taxonomy) and Glenner (2001, up-to-date life cycle). O'Brien and Van Wyk (1985) gave an account of the effects of parasitic castrators (isopods and rhizocephalans) on growth of crustacean hosts. Høeg and Lützen (1985) reviewed Scandinavian rhizocephalans and Øksnebjerg (2000) the taxonomy, biogeography and ecology of rhizocephalans of the Mediterranean and Black seas. Walker (1988) described the larval development of *Sacculina carcini* in some detail. An early but thorough discussion of parasitism by rhizocephalans is that by Veillet (1945). Important papers on parasitic Thoracica are by Grygier and Newman (1991), Yusa and Yamato (1999), Yusa *et al.* (2001) and Ross and Newman (1995).

Amphipoda (amphipods)

Jørgen Lützen

Introduction

Two of the four suborders of Amphipoda, the Hyperiidea and the Caprellidea, contain species with a parasitoid or parasitic life style. Species of the first suborder typically have a large cephalothorax (head and first thorax segment) with very large eyes. The second suborder contains the whale lice which are dorso-ventrally flattened and whose pleon (most posterior part of the body) is strongly rudimentary. These two suborders are discussed separately in the following.

Hyperiidea

Morphology and diversity

The suborder Hyperiidea includes a group of marine pelagic parasitoids that are associated with gelatinous zooplankters such as medusae, siphonophores, ctenophores and thaliaceans. The current view based on a comparison of hyperiid and gammarid amphipods is that hyperiids represent a polyphyletic group of descendants of different lineages of benthic gammaridean ancestors and that the structural similarities uniting recent hyperiids have arisen as a result of their association with planktonic hosts. The structure of hyperiids is poorly adapted to a pelagic life style and differs only slightly from gammarid amphipods (Fig. 4.22A). The maxillipeds have no palps, and in many, but far from all, species the compound eyes are large to huge, sometimes covering the entire cephalon. Species with large eyes may select their hosts visually. The body ranges from almost spherical to an elongate shape. The eggs are brooded in a female brood pouch as in other amphipods. The total number of species amounts to 254 (Thurston 2000) in 22 families.

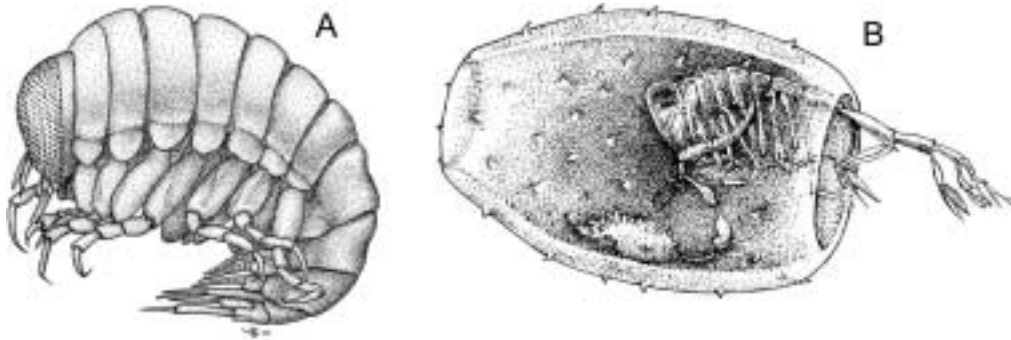


Figure 4.22 Hyperiidea from the North Atlantic. **A.** Lateral view of female *Hyperia galba*, an associate of the scyphozoan *Aurelia aurita*. **B.** *Phronima sedentaria*, female nursing its young in a pyrosome barrel.

Most species occur mainly in the open ocean, and occur most abundantly within the tropical or warm temperate zones, less so in coastal waters. Some species occupy panoeceanic distributions within their preferred temperature ranges, while others apparently are limited to one ocean, or even part of an ocean. Several species extend their distribution into the Polar regions or penetrate into the mesopelagic, bathypelagic and abyssopelagic layers. Benthic representatives are completely lacking.

Hosts

Some genera or families are almost exclusively restricted to a particular type of host, such as *Lestrigonus* and *Hyperia*. A few families are associated with siphonophores. Members of the family Lycaeidae are less specific, as their hosts include medusae, siphonophores, pteropods, heteropods and salps. In several genera and families a parasitic habit has not yet been established, but because these hyperiids do not in any essential respect differ from the rest, they are nonetheless believed to have a similar life style.

At the onset of their existence, hyperiids are obligatorily associated with gelatinous zooplankton which is used as a nursery, shelter and food reservoir for the developing young. Later in life the association becomes looser, but the adults still depend on zooplankton as the principal food source.

Adult hyperiids are only partly pelagic and between bursts of swimming seek out gelatinous zooplankton on which to prey or to rest, or using it as a shelter and a means of transport. Laboratory or field observations have shown that some adult hyperiids are able to consume zooplankton within a short time. Undigested nematocysts are frequently found in the gut contents or faecal pellets of species known to associate with cnidarians. *Hyperia galba* has been observed to feed upon and even sometimes destruct the gonads of its scyphomedusan host although it is believed that it mainly consumes the planktonic matter collected by its host and merely occasionally eats the tissue. Adults of *Vibilia* feed exclusively on the food strand of the salp hosts, while those of *Lycaea* feed on salp tissues (Madin and Harbison 1977).

Life cycles

Following mating, which has only been observed rarely and takes place on a host plankton, adult males, which are better swimmers than females, most likely maintain a free-swimming predatory life style, although still preying on zooplankton. The ovigerous females probably stay permanently upon the host while brooding the eggs. The brood size of hyperiids ranges from half a

hundred to several hundred eggs. Compared to gammarids of similar size the egg number is often greater by an order of magnitude. This is attained by reducing the size of the eggs.

The early part of the life cycle comprises one or a few specialised stages that are passed while still in the brood pouch. Compared to gammarids, the eggs hatch at a precocious stage. The earliest stage is the 'pantochelis' larva which is provided with four cheliform pereopods and has unsegmented and limbless metasome and urosome. The pantochelis stage metamorphoses into a 'protopleon' larva (often divided into three substages) 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, which resembles a miniature adult, and corresponds to the hatching stage of gammarids. The metamorphosis of the last protopleon stage 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 from host to host to deposit a single or a few larvae upon each host specimen, the number being obviously limited by the host size and capacity as a food source for the developing juveniles. Examples of how the larvae are transferred to the host, often involving a complex and stereotyped behaviour of the female, are given by Laval (1980). In *Lestrigonus schizogeneios* the female penetrates the host's subumbrella (a hydromedusa), splits a gonad with its mouth parts and inserts the larvae deeply into the organ. As they grow older, the juveniles abandon the gonad and start to feed upon the prey trapped by the host. Oviparous females of *Vibilia* deposit the pantochelis larvae on the surface of salps with the specialised 7th pereopods. When the larvae moult a few hours later, the ensuing protopleon larvae enter the branchial cavity and start to eat its wall or to feed on the collected suspended matter. If the host cannot support the number of young as they grow up, they probably leave it to invade another salp in the chain.

Species of the family Phronimidae excavate solitary salps or pyrosomes into 'barrels' open at both ends and in which they hide and which they use as a nursery for their young. The female *Phronima sedentaria* (Fig. 4.22B) enters a salp and consumes or removes all internal organs and finally scrapes the internal wall of the resulting barrel smooth with the mouthparts and pereopods 1 and 2. The larvae are demarsupiated into the barrel where they soon bunch together into a tight cluster which slowly moves around on the inner barrel wall. The female exhibits maternal care, as it 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 the brood. Both sexes of *P. sedentaria* live in barrels. The pereopods are used to maintain the position of the animal within the barrel and beating of the pleopods propels the combined barrel-hyperiid through the water.

Effects on hosts and ecological importance

Juveniles and adults of many hyperiids produce visible damage to their hosts as they eat the tissue and vital organs such as the gonads. In chain salps, the defence against this is their rapid growth and faculty of regeneration. Even so, by physically damaging the host or depriving it of its food, hyperiids most likely have long-term effects on growth, longevity and reproduction of salps. In medusae, the harm is roughly proportional to the size of the hyperiid in relation to that of the host (Madin and Harbison 1977). The growth of medusae of *Phialidium* becomes seriously impeded as the subadult hyperiids steal their food, and when the medusa is not adequately fed, it is eventually consumed itself.

Members of the Hyperiididae seem to be immune to the stings of the host medusae, but the involved mechanism has not been studied. Species of the globularly shaped Platyscelidae and Parascelidae shield themselves from the nematocysts of their siphonophore host by rolling up into a tight ball. Some hyperiids mimic in colour or shape the body of the host, or some of its

organs (e.g. the nucleus of salps). It is likely that this helps them to escape the attention of predators such as fishes which detect their prey visually.

Among the marine crustacean zooplankton, hyperiid amphipods rank third in abundance following copepods and euphausiids, but quantitatively they make out only a small part of the zooplankton biomass, and their ecological significance is accordingly relatively limited. However, in Polar seas they may contribute significantly to the food for fishes, diving birds, whales and seals.

Vinogradov *et al.* (1996) has written a book about the world hyperiidean fauna. Laval (1980) has surveyed many aspects of hyperiid biology such as host associations, feeding, reproduction and demersupiation.

Caprellidea

Morphology and diversity

Among the 300 or so species of this suborder, the Cyamidae (whale lice) (Fig. 4.23) form a very homogeneous family with about 30 species. At every stage of the life cycle all species are obligatory parasites on whales, dolphins and porpoises. One species parasitised the now extinct sirenian, the North Pacific Steller's sea cow, *Hydrodamalis stelleri*. The body is short and broad, dorsoventrally flattened, the cephalothorax anteriorly pointed and usually coalescent with the first pereon segment, while the abdomen is reduced to a minute process. Two pairs of the pereopods (3 and 4) are absent and merely represented by four clavate or corkscrew-shaped gills. The pereopods 1, 2, and 5–7 are broad, flattened prehensile appendages with which the whale lice cling firmly to the skin of the hosts. The mandibles, maxillules and maxillae are furnished with



Figure 4.23 Caprellidea, Cyamidae, whale lice. A heavy infection by *Cyamus ovalis* on skin of the Northern right whale, *Eubalaena glacialis*, from East Iceland.

setae and short spines by which the parasites excavate shallow pits in the skin, and ingest small pieces of the tissue. Some species are stationary and restricted to, for instance, the crevices of the flippers and lips, the surroundings of the nostrils and the genital and anal openings, or to the edges of wounds. Other slowly crawl around on the whale's body from one place to another.

The adult length ranges from 8 mm to 27 mm. The females, which are generally broader but shorter than the males, have a brood pouch made up of four oostegites ventrally on segments 3 and 4. The number of eggs produced over a single spawning season varies from 50 to a few hundred, but may reach more than 1000 in the larger species.

Life cycle

The life cycle has been studied in *Cyamus scammoni*, parasitic on the gray whale, *Eschrichtius robustus*, which spends the summer in high latitudes of the Pacific Ocean, but winters in lagoons in Baja California. The eggs are laid over an extended period during summer, and egg-laying has been completed and the eggs are fertilised before the whales reach the winter destinations. The juveniles are released from the brood pouch as miniature adults with clawed pereopods and immediately attach themselves firmly to the host's skin. When the whales return homewards in February the young female *C. scammoni* reach 6 mm to 8 mm, the males 8 mm to 10 mm. In March both sexes have attained maturity at a length of 10 mm to 12 mm and 14 mm to 18 mm, respectively, and the females start egg laying during early summer. It is estimated that eight to nine months are required to complete the life cycle.

Whale lice are unable to swim and a planktonic phase in their life cycle is totally absent. It is, therefore, believed that new hosts become infected only when they come into intraspecific bodily contact with an already parasitised individual, for instance during sexual intercourse and social interactions, at birth or when a female nurtures her young. Some whale lice parasitise several species of whales (e.g. 12 species by *Isocyamus delphini*). The care-giving (epimeletic) behaviour exhibited by many whales towards individuals of their own species, if extended to those of other species, may help to explain how whale lice are able to spread between host species.

Effects on hosts

Infestations by whale lice are usually not very heavy except in the humpback whale, *Megaptera novaeangliae*, and the gray whale. When abundantly present on the skin of these species, they may greatly damage even the largest of the whales.

Martin and Heyning (1999) have published a key to the genera of the whale lice and a checklist of the species and their hosts. The systematics of the family has been reviewed by Gruner (1975). Studies on biology of individual species were presented by Leung (1976) and Balbuena and Raga (1991).

Important references

Vinogradov *et al.* (1996) published an extensive monograph of hyperiid amphipods of the world oceans, and Gruner (1975) provided a catalogue of whale lice. A discussion of the taxonomy of pelagic amphipods including parasitic ones is by Thurston (2000). Madin and Harbison (1977) discussed the associations of hyperiids with salps, and Martin and Heyning (1999) presented a key to the genera of Cyamidae, as well as a checklist of cyamids and their hosts. Laval (1980) reviewed hyperiid amphipods as crustacean parasitoids associated with gelatinous plankton. Important papers dealing with more specific aspects are by Balbuena and Raga (1991), who discussed the ecology and host relationships of the whale louse *Isocyamus delphini* parasitising long-finned pilot whales, and by Leung (1976), who described the life cycle of *Cyamus scammoni*.