CRUSTACEANS AS SYMBIONTS: AN OVERVIEW OF THEIR DIVERSITY, HOST USE, AND LIFESTYLES

J. Antonio Baeza

Abstract

The adoption of a symbiotic lifestyle is a major adaptation in the marine realm. Protection against environmental stress, escape from natural enemies, and nourishment are the major benefits obtained by symbiotic crustaceans from hosts. Hosts also represent a mating and nursery ground for symbiotic crustaceans. Costs and/or benefits experienced by hosts are diverse but may be subtle and challenging to measure. Costs suffered by hosts include physical injury, reduced feeding/growth rates, decreased fecundity and lifespan, and feminization, including castration, of male hosts. Some rhizocephalans are capable of altering host behaviors. The life cycles of symbiotic crustaceans vary widely. At one extreme, juveniles recruit directly into hosts from parental brooding chambers in crustaceans with direct/abbreviated development. Many symbiotic crustaceans with indirect development spend their larval life in the pelagic environment and establish themselves in/on their hosts during the first post-larval stage. At another extreme, the most complex life cycles occur in parasitic copepods and rhizocephalan cirripeds. Such life cycles involve one or two hosts and subtle or considerable changes in body morphology relative to that of their closest free-living relatives. The species richness of various symbiotic clades is higher than that of their closest free-living relatives. Whether the symbiotic lifestyle favors adaptive radiations in crustaceans is an outstanding and open question.

INTRODUCTION

The adoption of a symbiotic lifestyle (symbiosis here is defined sensu De Bary [1879] as dissimilar organisms living together) is one of the most important environmental adaptations in marine organisms (Ross 1983, Vermeij 1983). Symbiotic associations in the marine realm usually comprise...
small organisms (hereafter *symbiotic guests*) and large partners that serve as hosts. Symbiotic relationships can be characterized in terms of the costs and benefits experienced by the partners (i.e., parasitism, commensalism, mutualism), the degree of interdependency among the associates (i.e., facultative or obligate symbiosis), the number of species used by one or both entities involved in the symbiotic interaction (i.e., generalists vs. specialists), and the location or physical area in or on hosts exploited by symbiotic guests (endosymbionts, ectosymbionts, mesosymbionts, cohabitants; Bush et al. 1997, Thiel and Baeza 2001).

In marine crustaceans, some degree of dependence between pairs or among small assemblages of species has evolved multiple times independently in tropical, subtropical, and temperate habitats.

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**Fig. 7.1.** Two examples of symbiotic crustaceans. (A) The caridean shrimp *Lysmata pederseni*, a socially monogamous and protandric simultaneously hermaphroditic species inhabiting the vase sponge *Callyspongia vaginalis*. Photo courtesy of Raphael Ritson-Williams. (B) The isopod *Cymothoa exigua*. This species causes the degeneration of most of the tongue of its host fish, the snapper *Lutjanus guttatus*. From Brusca and Gilligan (1993), with permission from the American Society of Ichthyologists and Herpetologists.
Species of caridean shrimps, pentastomids, tanaulocarids, crabs, amphipods, isopods, mysids, cirripeds, and copepods (among others) from dissimilar monophyletic clades have been reported to engage in symbiotic associations with other macroinvertebrates, including sponges, corals, sea anemones, oysters, sea urchins, and ascidians, and with reptiles and mammals (Bruce 1976, Castro 1976, Ross 1983, Tappe and Büttner 2009; Fig. 7.1).

Crustaceans are among the most diverse marine invertebrates (Brusca and Brusca 2003), and the studies conducted during the past decades in symbiotic representatives of this species-rich group have revealed most impressive morphologies (Schmitt et al. 1973, Fransen 2002), colorations (Limbaugh et al. 1961), nourishment tactics (Ďuriš et al. 2011), reproductive strategies (Shuster and Wade 1991), social systems (Duffy et al. 2000), parent–offspring interactions (Thiel 2003), and modes of interspecific communication (Vannini 1985, Becker et al. 2005).

This chapter reviews the diversity of symbiotic crustaceans. An overview of the cost and benefits experienced both by crustaceans and their partners and the life cycle of symbiotic crustaceans is provided.

SYMBIOTIC CRUSTACEANS AND THEIR HOST PARTNERS

The systematic arrangement laid out by Martin and Davis (2001) is used as a main framework to explore the incidence of symbiosis in the Crustacea. This review revealed no instances of symbiosis in members from the classes Remipedia (remipedes) and Cephalocarida (horseshoe shrimps). Their anchihaline lifestyle (Remipedia) and/or meiofaunal habitat (Cephalocarida) might prevent the evolution of symbiosis in these clades (Neiber et al. 2011).

In the morphologically and ecologically diverse class Branchiopoda (cladocerans or “water fleas” and fairy, brine, tadpole, and clam shrimps), members from all orders but one are free-living. Only a few species in the order Diplostraca, suborder Cladocera, family Chydoridae, have been considered parasites of freshwater cnidarians (Hydra spp.). For instance, Anchistropus minor and A. emarginatus have strong hooks on the first pair of limbs that are used for shredding ectodermal cells from regions of polyps other than their cnidocyte-rich tentacles (Hyman 1926, Fryer 1968). However, some authors considered these species to be predators because they are lethal to their “hosts” and can quickly destroy an entire population of Hydra in short periods of time (Van Damme and Dumont 2007).

In the diverse class Malacostraca, this review revealed no instances of symbiosis in the subclass Phyllocarida (leptostracans). However, in the subclass Eumalacostraca, the symbiotic lifestyle is pervasive in the superorder Eucarida, order Decapoda (e.g., shrimps, brachyuran crabs, squat lobsters, hermit crabs) and in the superorder Peracarida (e.g., amphipods, isopods, mysids).

In the order Decapoda, groups that have adopted a symbiotic lifestyle include stenopodid shrimps (Infraorder Stenopodidea) in the family Spongicolidae (e.g., Globospongicola) that live entrapped in the atrium of deep-water hexactinellid sponges (Saito and Takeda 2003, Saito and Komai 2008; Fig. 7.2A). In the infraorder Caridea, pontoniid shrimps (superfamily Palaemonoidea, subfamily Pontoniidae) from diverse genera engage in obligatory ecto- or endosymbiotic associations with a wide variety of hosts, including, sponges, hydrozoans, sea anemones, jellyfish, black corals, sea pens, echinoderms, mollusks, and ascidians (Bruce 1982, De Grave 1999, Fransen 2002, 2006).

In the Infraorder Brachyura (true crabs), the symbiotic lifestyle is also widespread. In the superfamly Trapezioidea, most genera (e.g., Trapezia, Tetralia) are obligate ectosymbions of hydrozoan stylasterid corals, gorgonian and alcarycanecous corals, scleractian corals, and antipatharian corals (Castro 1976, Castro et al. 2004). Also, crabs in the superfamly Cryptochiroidea are obligate
Fig. 7.2. Diversity of symbiotic crustaceans. (A) *Globospongicola spinulatus*, a stenopodid shrimp (Stenopodidea) in the family Spongicolidae that lives entrapped in the atrium of deep-water hexactinellid sponges. From Komai and Saito (2006), with permission from Publications Scientifiques du Muséum national d’Histoire naturelle, Paris. (B) *Tunicotheres moserii*, a pea crab (Brachyura, Pinnotheroidea) with abbreviated development living in the atrial chamber of various ascidians in the Caribbean. From Campos (1996), with permission from The Crustacean Society. (C) Dorsal (left) and ventral (right) view of the whale-lice *Cyamus ovalis* (Cyamidae) that attach to the skin of the right-whale *Balaena acutalis*. From lwasa (1934), with permission from Hokkaido Imperial University. (D) *Hyperia galba*, an amphipod (Peracarida) developing obligate symbiosis with gelatinous zooplankton. From Sars (1899). (E) Dorsal view of the female (left) and micrography of the male (in ventral view right) of *Orthione griffenis* (Bopyridae), a parasitic isopod of thalassinid mud shrimps found in the north Pacific. From Williams and An (2009), with permission from Oxford University Press. (F) *Ceratothoa gaudichaudii* (Cymothoidea), an associate of various pelagic fish in the southeastern Pacific. From Brusca (1981), with permission from John Wiley and Sons. (G) Dorsal view of the adult male (left) and adult female (right) of *Gnathia maxillaries*. From Sars (1899). (H) Praniza larva of *Gnathia maxillaris*, an ectoparasite of the marine fish *Blennius pholis*. From Sars (1899). Scale bars or magnifications: A and B = 2 mm; C = 4.2X; D and E = 1 mm; D, G, and E, not available.
symbionts of scleractinian corals. These crabs live in self-constructed “galls” or open “pits” that they excavate in corals. The interiors of these structures are lined with living coral tissue (Scotto and Gore 1981). Last, the superfamly Pinnotheroidea (pea crabs) is recognized for its symbiotic lifestyle. Most species from the 55 currently recognized genera (e.g., Zaops, Pinnotheres, Tunicotheres) have developed some degree of dependence with a wide variety of hosts, primarily bivalves, gastropods, equinoderms, polychaetes, equiurid worms, and ascidians (Schmitt et al. 1973; Fig. 7.2B). Some species even use burrows constructed by other crustaceans as a refuge (e.g., Austinixa patagonensis in burrows of the ghost shrimp Sergio mirim; Harrison 2004).

In the species-rich superorder Peracarida, many members from the orders Isopoda and Amphipoda have adopted a symbiotic lifestyle. Species from the other orders (e.g., Cumacea, Tanaidacea, and others) are almost invariably free living. One notable exception is Heteromysis harpax (order Mysida), which forms family groups in the interior of gastropod shells occupied by hermit crabs (Vannini et al. 1994).

In the order Amphipoda, members from the suborder Caprellidea, family Cyamidae (whale-lice) cling to the external surface of whales and dolphins (Gruner 1975) (Fig. 7.2C), whereas many species in the suborder Hyperidea are obligate symbionts of cnidarians, salps, and other gelatinous zooplankton (e.g., Hyperia galba; Sars 1899, Laval 1980, Vinogradov et al. 1996; Fig. 7.2D). Other amphipods symbiotic within sponges and tunicates pertain to the families Dexaminiidae and Leucothoidae. Another 22 species from seven different families are also considered ecto- or endosymbiotic or micropredators of sea anemones (Vader 1983).

In the order Isopoda, the suborder Epicaridea is exclusively symbiotic (parasitic, see below) with other crustaceans. The diverse family Bopyridae inhabit the visceral cavity, branchial chamber, or abdominal surfaces of a diverse number of benthic decapods and pelagic mysidaceans and euphausiaceans (Kensley and Schotte 1989; Fig. 7.2E). In turn, the suborder Flabellifera is mostly free-living but a few groups within this clade have adopted a symbiotic lifestyle. Among them, the family Cymothoidae is recognized for its obligatory relationship with fishes (Bunkley-Williams and Williams 1998; Fig. 7.2F). Also, a few species in the family Corallanidae have been collected from the gills of bony fishes, nurse sharks, and rays (e.g., Alcirona insularis, Excorallana tricornis tricornis) or from the surface of corals (e.g., E. tricornis tricornis). Also in the Flabellifera, members of the family Aegidae might be considered symbiotic because they temporarily attach to marine fishes (or rarely humans) to feed on their blood (e.g., Rocinela signata). However, specimens from this family are most frequently captured by relatively deep bottom trawls (Brusca 1983). Last, various members from the family Sphaeromatidae are found under chitons (e.g., Dynamenella perforata) or use sponges for breeding (e.g., Paracerceis sculpta; Shuster and Wade 1991). In the suborder Gnathiidae, adult specimens do not feed and are found in cavities available in the mud, dead barnacles, corals, or sponges (Kensley and Schotte 1989). However, the early ontogenetic stages temporarily attach to fish (Lester 2005; Fig. 7.2G,H). Symbiosis is absent or is much less common in the suborders Anthuridea, Asellota, Oniscoidea, Microcerberidea, and Valvihera. However, a few species from these clades have been collected from the surface of corals or sponges (Asellota: Ioperis coraliola from the corals Oculina arbuscula, Madracis sp., and the sponge Agelas sp.) or from crinoids (Valvihera: Astacilla regina; Kensley and Schotte 1989).

In the species-rich and morphologically diverse but comparatively poorly studied class Maxillopoda (e.g., barnacles, copepods, tongue-worms, fish-lice), the symbiotic mode of life is pervasive. In the subclass Thecostraca (barnacles and allies), symbiosis is obligatory in three major taxa, the infraclasses Ascothoracida and Facetotecta and the subclass Rhizocephala in the infraclass Cirripedia (Høeg et al. 2005). Members from the Ascothoracida are ecto- and endosymbiotic with cnidarians and echinoderms (Fig. 7.3A–C). Laboratory observations suggest that the enigmatic Facetotecta are endosymbiotic too, having an invasive stage similar to that of rhizocephalan cirripeds. However, the natural hosts of this group are not known (Grigyer 1987,
Fig. 7.3.
Diversity of symbiotic crustaceans. (A) External view of the brittle star *Ophiocen sericeum* infected with *Ascothorax ophiocrenis* (Ascothoracida). The arrow points at the endosymbiont. From Wagin (1946), with permission from John Wiley and Sons. (B) Male (m) and female (f, dorsal view) of *Ascothorax ophiocrenis* after extraction from the host. From Wagin (1946), with permission from John Wiley and Sons. (C) Male of *Ascothorax ophiocrenis* after separation from the female. From Wagin (1946), with permission from John Wiley and Sons. (D) *Sacculina carcini* (Rhizocephala), an endoparasite of various brachyuran crab. Notice the extreme body modification. From Haekel (1899). (E) *Coromula reginae* (Thoracica), a sessile barnacle that lives attached to the right whale *Eubalaena glacialis*. From Haekel (1899). (F) The copepod *Cryptopontius thorelli* (Siphonostomatoida), ectoparasitic on the sponge *Petrosia ficiformis*. From Haekel (1899). (G) Inner view of the oral pole of the sea urchin *Hygrosoma petersii* showing calcified galls containing the copepod *Pionodesmotes*
In turn, members from the Rhizocephala are highly modified and commonly use decapod crustaceans as hosts (Fig. 7.3D) and, less frequently, have been retrieved from species of Cumacea (Peracarida), Stomatopoda, and few free-living barnacles in the subclass Thoracica (Cirripedia). Also in the Cirripedia, members from the superorder Acrothoracica excavate burrows in calcareous material, including corals, crinoids, or gastropod shells used by hermit crabs (Williams and McDermott 2004). In turn, sessile cirripeds in the superorder Thoracica, superfam-
ily Coronuloidea, attach to the body of whales (e.g., Coronula reginae, Scarf 1986) and turtles (e.g., Chelonibia testudinaria, Frick and Ross 2001; Fig. 7.3E).

In the class Maxillopoda, subclass Copepoda, symbiosis is obligatory in three orders, the Monstrilloida, Poecilostomatoida, and Siphonostomatoida. In the Monstrilloida, the naupliar, pre-
adult, and adult phases are planktonic but during their postnaupliar and juvenile phases, they are endosymbiotic with gastropods, polychaetes, or, rarely, with equinoderms (Suárez-Morales 2011). Members of the Poecilostomatoida are usually ectosymbiotic and find refuge on the buccal cavity of mollusks and equinoderms or gills of bony fishes. However, three genera (Claviosaldis, Echinirus, and Echinococcius) in this clade have adopted an endosymbiotic lifestyle living in the esophagus of sea urchins (Dojiri and Cressey 1987). Members of the Siphonostomatoida parasitize invertebrates and fishes (Barel and Kramers 1977; Fig. 7.3F–H). One order, Calanoida, is mostly free-living. However, several species from this order have adopted a symbiotic lifestyle. The other two orders, Cyclopoida and Harpacticoida, contain relatively large and moderate numbers of symbiotic species, respectively.

Last, the most aberrant symbiotic species pertain to the class Maxillopoda, subclasses Tantulocarida and Pentastomida. Tantulocarids are minute parasites of deep-sea benthic crusta-
ceans that exhibit a highly modified adult form (Boxshall and Lincoln 1983; Fig. 7.3I, J). Pentastomids (tongue-worms) are larger parasites than tantulocarids, have a worm-like body shape, and dwell on the respiratory tracts of reptiles, birds, and mammals, including humans (Lavrov et al. 2004, Tappe and Büttner 2009; Fig. 7.3K). Much less aberrant, the Branchiura (fish lice) live on the external surface of marine and freshwater fish and amphibians (Fig. 7.3L). Examples are Argulus coregoni infecting the rainbow trout Oncorhynchus mykiss (Bandilla et al. 2005) and A. ambystoma infecting the salamander Ambystoma dumerili (Poly 2003).

**BENEFITS TO SYMBIOTIC CRUSTACEANS DERIVED FROM HOSTS**

Protection against environmental stress and/or escape from natural enemies (e.g., predators and competitors) appear to be the major benefits that symbiotic crustaceans obtain from their respec-
tive hosts (Table 7.1). This is certainly true for endosymbiotic species developing obligatory sym-
bioses. Highly modified crustaceans inhabiting host cavities (e.g., pea crabs and rhizocephalan cirripeds; Figs. 7.2 and 7.3) would probably die within minutes or hours if deprived from their host.

![Fig. 7.3.](Continued)

*phormosonae* (Poecilostomatoida). From Koehler (1898) in Jangoux (1987). (H) Section through gall harboring a female of *Pionodesmotes phormosonae* and also showing the outer pore of the gall (P). From Bonnier (1898) in Jangoux (1987). (I) Female of *Microdajus langi* (Tantulocarida) attached to the gnathid *Leptognathia breviremis* (shown in ventral view). From Boxshall and Lincoln (1987), with permission from Royal Society. (J) Juvenile tantid peracarid with two early stage female *Microdajus langi*. From Boxshall and Lincoln (1987), with permission from Royal Society. (K) Various exceptionally preserved specimens of fossil Pentastomida (from CORE; available at http://www.core-orsten-research.de). (L) Dorsal (left) and ventral (right) view of *Argulus quadristriatus* (Branchiura), symbiotic with the marine fish *Psammoperca waigiensis*. From Devaraj and Hansa (1977). Scale bars. H = 1 mm; J = 200 micrometers; K = 500 micrometers, M = 2 mm.
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</table>

**Class Ostracoda**

| Sc. Myodocopa         |            | Fish                     | Ec  | HostT| P    | ?   | ?    | ?    |

| O. Myodocopida        | Rare       | Fish                     | Ec  | HostT| P    | ?   | ?    | ?    |

The existence and extent of the symbiotic lifestyle (Symbiosis: Rare, Frequent, Obligatory) in each major clade, the hosts (Hosts) most commonly used by symbiotic crustaceans in each clade, the location or physical area in/on hosts exploited by symbiotic guests (Location: endosymbionts [En], ectosymbionts [Ec], cohabitants [Coh]), the type of nourishment and/or mode of acquisition of food by symbiotic crustaceans (Food: food not acquired directly from hosts but obtained via, for example, filter feeding [I], direct from hosts [D], including the consumption of host's tissues, waste or mucus produced by hosts [HostT]), the type of symbiotic relationship characterized in terms of the costs and benefits experienced by the partners (Type: parasitism [P], commensalism [C], mutualism [M]), the number of host species used by symbiotic crustaceans (Specificity [along the generalist—specialist continuum] from low specificity [L] to moderate [M] and high [H] specificity), the extent of mobility during the life cycle of symbiotic crustaceans (Mobility: from None to low [L] to moderate [M] to high [H] mobility), and the sociobiology of symbiotic crustaceans (Sociability: unstructured, including species living in aggregations [Unstr], family groups composed by a female and offspring or reproductive (e.g., male–female) pairs [Fam], structured, including pair-living species that do not interact with offspring, and polygamous species [Str]) are shown. These are general classifications for each clade, and several of these should be considered tentative considering the lack of studies. See text for details.

Note: No symbiotic species have been reported in the class Remipedia, class Cephalocarida, orders Anostraca and Notonopora in the class Branchiopoda, subclasses Phyllocarida and Hoplocarida in the class Malacostraca, subclass Syncarida in the subclass Eumalacostraca, order Spelaecarida, Thermochoanacea Lophogastridea, Mictacea, Tanaidacea and Cumacea in the subclass Pincarcida, order Euphausiacea and Amphipodacea in the subclass Eucarida, subclasse Mystacocarida in the class Maxillopoda, order Gelyllida, Misoophidiida, Mormorillida and Platycopoida in the subclass Copepoda, and orders Halocyprida, Platycopida and Podocarida in the class Ostracoda.
individuals (killed by predators or adverse environmental conditions). Also, many ectosymbiotic crustaceans most likely gain protection against environmental stress and/or escape from natural enemies by dwelling on or near the surface of their respective hosts. Admittedly though, the actual number of experimental studies that have formally tested for the positive effect of hosts on the survival of ectsymbiotic crustacean guests is most limited (Thiel and Baeza 2001).

Other than shelter, hosts provide a suite of other resources and services to symbiotic crustaceans. Among them, hosts represent an indirect or direct food source. The porcelain crab *Allopetrolisthes* [a.k.a. *Petrolisthes* *spinifrons* and its sea anemone hosts represent an example of the indirect function played by hosts in the nourishment of symbiotic crustaceans. By clinging to sea anemones, porcelain crabs gain access to exposed sites in the intertidal and subtidal zones that are favorable for suspension-feeding (Valdivia and Stotz 2006; Fig. 7.4A). In turn, various other symbiotic species acquire food directly from their hosts, and, in many instances, hosts represent the only source of nourishment for symbiotic crustaceans. Examples include members from the Branchiura (e.g., *Argulus* spp.; Fig. 7.3L) that suck blood and/or tissue fluids by puncturing the skin of their fish and amphibian hosts. Modified mouth parts, including a styliform proboscis and mandibles with cutting edges, most likely aid in feeding (Wilson 1944). Similarly, cymothoid isopods apparently feed principally on blood, but they may consume the mucus, epithelium, and subcutaneous tissues of their host (Bunkley-Williams and Williams 1998, Leonardos and Trilles 2003; Fig. 7.4B,C).

An extreme body modification in symbiotic crustaceans for acquiring nourishment from hosts is seen in the Rhizocephala (Cirripedia), which lack the rudiments of an alimentary canal and other organs and systems. These aberrant cirripeds infiltrate their hosts with a highly ramified system of rootlets with a microstructure that suggests it is used for the absorption of nutrients directly across the integument, as in a gut epithelium (Bresciani and Høeg 2001; Fig. 7.4D). Last, brachyuran crabs symbiotic with corals (superfamily Trapezioidea) use modified pereopods to “steal” mucus produced by the host colony (Knudsen 1967). Similarly, pea crabs (Pinnotheroidea) use chelipeds, pereopods, and modified mouth pieces to “steal” mucus strings that are rich in food filtered by their bivalve hosts (*Calyptraeotheres* sp.; Chaparro et al. 2001). In most symbiotic crustaceans, the mechanism of food acquisition is not known or is poorly understood.

Hosts represent a mating ground for symbiotic crustaceans, too. For instance, numerous symbiotic crustaceans, including true crabs (McDemmott 2005), porcelain crabs (Ng and Nakasone 1993), caridean shrimps (Fransen 2002, Baeza 2010), and cymothoid isopods (Bunkley-Williams and Williams 1998) inhabit hosts as male-female pairs (in gonochoric and sequentially hermaphroditic species) or hermaphrodite-hermaphrodite pairs (in protandric simultaneous hermaphroditic shrimps; Baeza 2010; Fig. 7.1). In all these species, symbiotic individuals mate in the interior (body cavities), on the body surface, or in the vicinity of host individuals. In various species of pea crabs (Pinnotheroidea), females live solitarily in the mantle cavity of mollusks. Males appear to continuously roam among hosts in search of receptive females that are quickly mated and soon abandoned (Ocampo et al. 2012).

The highly modified Rhizocephala represent a remarkable example of extreme body and sexual system modification. Females can harbor one or two minute males (or male tissue; see Høeg et al. 2005) in specialized receptacles located in the externa, a pouch-like structure that protrudes from the host’s body. Once established, these males become permanently embedded in the female tissue (Glenner et al. 2010). In these, as well as in many other obligate symbionts (e.g., pinnotherid crabs or bopyrid isopods), males are thus substantially smaller than the comparatively large females.

Last, in the isopod *P. sculptra*, males set up territories in sponge cavities large enough to permit the cohabitation of several females at the same time (Fig. 7.4E). These females are inseminated during the breeding season (Shuster and Wade 1991). Also in this isopod, three genetically determined male morphs featuring dissimilar mating strategies coexist in the same population (Shuster and Wade 1991).
Fig. 7.4.
Benefits to symbiotic crustaceans derived from hosts. (A) The porcelain crab *Allopetrolisthes* (a.k.a. *Petrolisthes*) *spinifrons* perching on its sea anemone host with their usual posture (left) and when feeding with the third maxillipeds extended during filter feeding (right). From Valdivia and Stotz (2006), with permission from *Journal of Crustacean Biology*. (B) The parasitic isopod *Mothoeca epimerica* (Cymothoidea) attached between the first and second branchial arches of its host, the sand smelt *Atherina boyeri*. From Leonardos and Trilles (2003), with permission from Inter-Research. (C) Branchial cavity of the host after the removal of the parasite. From Leonardos and Trilles (2003), with permission from Inter-Research. (D) The root system in various species of Peltogasteridae (Rhizocephala) used for the absorption of nutrients directly across the integument as in a gut epithelium. From Bresciani and Hoeg (2001), with permission from John Wiley and Sons. (E) Alpha male of the isopod *Paracerceis sculpta* guarding a territory (a sponge cavity) harboring two females. Beta (left) and gamma (right) males can be seen closer to the territory. From Shuster (2007), with permission from Oxford University Press. (F) Female of the amphipod *Peramphithoe femorata* on the kelp *Macrocystis pyrifera*. The female has built a nest that is used by herself and her offspring. From Cerda et al. (2010), courtesy of Ivan A. Hinojosa. Scale bars: B and C = 2 mm.
In addition to shelter, food, and a mating arena, hosts might, directly or indirectly, be used as nurseries by symbiotic crustaceans. For instance, in the enigmatic pea crab *Tunicotheres moserii*, dwelling in the atrial chamber of various ascidian species in the Caribbean, females exhibit abbreviated development and retain embryos, larvae, postlarvae (megalopae), and the first crab instars within their brood pouches (Hernández et al. 2012). Interestingly, early ontogenetic stages of *T. moserii* do not make use of the space available within the atrial chamber of the ascidian hosts. Offspring remain protected within the abdominal “brood chamber” of females and abandon females (and hosts) during the first crab instar. In contrast, in various endosymbiotic amphipods and isopods with abbreviated or direct development, embryos that develop and hatch as advanced larvae or juveniles recruit to and remain in the parental dwelling (hosts) for relatively long periods of time (Thiel 2003). A similar situation occurs in eusocial shrimps symbiotic with sponges (Duffy et al. 2000). Figure 7.4F shows the amphipod *Peramphithoe femorata* on the kelp *Macrocystis pyrifera*. In this species, females build a nest used for protecting the offspring. The lifestyle of herbivore crustaceans living on algal hosts is treated in a separate chapter by Veijo Jormalainen (see Chapter 18 in this volume). It is generally assumed that growing offspring remain in the parental dwelling because the chances of finding unoccupied hosts are very limited, and the risk of falling prey to predators is high (Duffy 2007, Thiel 2007, Hernández et al. 2012). Whether larvae and/or juveniles are actively or passively fed, defended, and groomed by parental individuals in these species remains to be addressed.

**COSTS AND BENEFITS DERIVED BY HOSTS FROM SYMBIOTIC CRUSTACEANS**

Costs and/or benefits to hosts resulting from their interaction with symbiotic crustaceans might be obvious in cases where crustaceans are obligate symbionts, but are much more subtle and challenging to measure in facultative symbionts. Costs are usually severe for organisms that host highly modified endosymbiotic crustaceans. Effects of the Rhizocephala on their hosts include castration, morphological and behavioral feminization of male hosts, diminished growth rate, and full arrest of the molt cycle (Høeg et al. 2005). Some rhizocephalans also appear capable of altering the behavior of their hosts, which can be beneficial for these crustacean symbionts but detrimental to the hosts. For instance, males of the swimming crab *Charybdis longicollis* infected with *Heterosaccus dollfusi* are less aggressive than uninfected males during agonistic encounters. Diminished aggressiveness in males might avoid injury and enhance the life expectancy of the host and parasite (Innocenti et al. 2003) while likely reducing the reproductive success of the hosts. Also, the presence and feeding activities of pea crabs (*Pinnotheroidea*) cause gill injuries and reduce feeding rates and body condition, among other issues, and ultimately impact the growth rate and reproduction of host individuals (Stauber 1945, Bierbaum and Shumway 1988, Narvarte and Saiz 2004, Sun et al. 2005; Fig. 7.5A). In some hosts, the mere presence of crab symbionts appears to be sufficient for halting female reproduction, as demonstrated by implantation of crab mimics (Chaparro et al. 2001; Fig. 7.5B–E).

The effect of ectosymbiotic crustaceans on hosts can also be deleterious and severe. For instance, symbiotic copepods in the family Caligidae are known to affect the growth, fecundity, and survival of their fish hosts (Johnson et al. 2004 and references therein). These copepods may also serve as vectors of viral and bacterial diseases to cultured fishes (Nylund et al. 1994). Feeding and attachment of isopods from the family Cymothoidae also cause diverse effects on their fish hosts, including behavioral changes, skin and/or gill damage (Figs. 7.1 and 7.4B,C), and increased basal metabolism, which ultimately affect condition (body weight and size), growth rate, and life span (Adlard and Lester 1994, Ostlund-Nilsson et al. 2005). Some species are reported to cause anemia.
Fig. 7.5.
(A) The effects of the endosymbiotic pea crab *Pinnotheres novaecelandiae* on the green-lipped mussel *Perna canaliculus* include lower total wet weight and meat yield, as well as changes in shell dimensions. From Trottier et al. (2012), with permission from Elsevier. (B) The endosymbiotic pea crab *Tumidotheres maculatus* in the mantle cavity of the bivalve *Ostrea puelchana*. The white arrow points at the pea crab, from Doldan et al. (2012), with permission from Latin American Journal of Aquatic Research. (C–E) The effect of the pea crab *Calypttraeotheres* sp. on the reproduction of the slipper limpet *Crepidula fecunda*. From Chaparro et al. (2001), with permission from Elsevier. (C) Shows the percentage of brooding females after removal of egg capsules and introduction of a pea crab. (D) Shows the same response by *C. fecunda* after removal of egg capsules and introduction of a pseudo-pea crab (a pinnotherid-sized piece of Parafilm). (E) Shows the percentage of brooding females after elimination of a pinnotherid (* = no incubation occurred; for experiment details, see Chaparro et al. (2001)). (F) *Trapezia* crab defending its coral host, *Pocillopora damicornis*, from a crown-of-thorns starfish. From Pratchett et al. (2000), with permission from Springer. (G) Effect of the vermetid snail *Dendropoma maximum* and the symbiotic crab *Trapezia serenei* on the growth rate of *Pocillopora cf. verrucosa* (means ± 1 SE). From Stier et al. (2010), with permission from Springer; see Stier et al. (2010) for experiment details. Scale bars: B = 10 mm.
Symbiotic associations also result in benefits to hosts, although these are less commonly reported. The caridean shrimp *Alpheus lottini* and crabs from the genus *Trapezia* defend their coral hosts (*Pocillopora elegans*) from predatory sea stars *Acanthaster planci* in the tropical east Pacific (Glynn 1980). Similarly, the shrimp *Alpheus cf. armatus* defends its sea anemone host *Bartholomea annulata* from the predatory worm *Hermodice carunculata* (Polychaeta) in the Caribbean (Smith 1977). In the Indo-Pacific, crabs from the genus *Trapezia* and *Tetralia* also defend their coral colonies from predatory sea stars (Pratchett et al. 2000; Fig. 7.4F) and remove the mucus produced by the vermetid gastropod *Dendropoma maximum* that also dwells among the host corallites. The mucus of this snail is deleterious to corals (Stier et al. 2010), and mucus removal by crabs positively affects the growth rates of their hosts (Fig. 7.5G). *Trapezia* and *Tetralia* crabs can and do discard sediments deposited on the coral surface of their host individuals and are effective at removing grain sizes that damage coral tissues (Stewart et al. 2006). In temperate regions (northwestern Atlantic), the herbivorous crab *Mithrax sculptus* removes algae and invertebrates growing on or near the coral *Oculina arbuscula* and thus prevents algae from overgrowing and killing the host coral (Stachowicz and Hay 1999).

Other subtle benefits to hosts are difficult to identify. The shrimp *Ancylomenes yucatanicus* excretes ammonia, which represents a source of bioavailable nitrogen to symbiotic zooxanthellae contained in the tissue of the host sea anemone *Condyllactis gigantea* (Spotte 1996). Whether other symbiotic crustaceans represent a potential source of regenerated nitrogen for other host species (e.g., sea anemones and corals harboring symbiotic zooxanthellae) remains to be addressed.

These examples highlight the difficulties of establishing the costs and benefits experienced by symbiotic partners. Some symbiotic crustaceans appear to be clearly parasitic; for example, endosymbiotic copepods, tantulocarids, rhizocephalan cirripeds considering their aberrant form and the extremely negative effects experienced by their respective hosts. Potential benefits (e.g., increased growth rate) generated by these symbiotic crustaceans cannot out-balance the costs for hosts (e.g., permanent castration). In most cases, though, examining (and quantifying) the totality of the costs and benefits experienced by all partners of a symbiotic relationship is challenging. Characterization of these partnerships as parasitic, commensal, or mutualistic is often hard to sustain because little or no empirical information is available (characterizations in Table 7.1 are tentative for most cases). Many more studies examining the totality of the costs and benefits experienced by symbiotic partners, ideally measured in terms of fitness proxies (e.g., offspring production), are needed in order to better evaluate the evolution of these associations.

Other than the more evident cases of parasitism, the associations between crabs in the genus *Trapezia* and scleractinian corals (e.g., *Pocillopora* and *Acropora*) are some of the few symbiotic relationships that have been well studied in terms of the costs and benefits experienced by all partners. *Trapezia* crabs were first considered to be parasites because of their feeding habit on coral tissue and mucus from polyps (Knudsen 1967, Stimson 1990). Although not formally quantified, the crab's feeding behavior most likely represents a cost to their hosts in terms of fitness. However, crabs actively defend their colonies from predatory sea stars, remove mucus produced by other organisms that is deleterious to corals, and discard sediment and remove sand grains that damage colony tissues (Glynn 1980, Stewart et al. 2006, Stier et al. 2010). These activities imply that these same crabs provide considerable benefits to their coral hosts. The *Trapezia–Pocillopora* partnership is now considered to be mutualistic, with net benefits for both crabs and coral colonies (Stewart et al. 2006, Stier et al. 2010). Another putative example of a mutualistic symbiosis is that between the shrimp *Alpheus cf. armatus* and the sea anemone *B. annulata* in the Caribbean (Smith 1977). Last, mutualistic interactions also include caridean “cleaner” shrimps that remove parasites from fish hosts (Limbaugh et al. 1961, Becker and
Grutter 2004) and shrimps in the genus *Alpheus* symbiotic with goby fishes (Karplus and Thompson 2011). Nonetheless, *Alpheus* shrimps do serve as hosts and provide shelter to fishes rather than being symbiotic guests.

**LIFE CYCLE OF SYMBIOTIC CRUSTACEANS**

Matching their taxonomic diversity, the life cycle and the timing of establishment of the symbiotic partnership vary widely in symbiotic crustaceans. At one extreme, amphipods (e.g., Hyperide and Caprellidea: Cyamidae [whale-lice], among others), mysids (*H. harpax*), caridean eusocial shrimps (e.g., *Synalpheus* spp.), and a few brachyuran crabs (e.g., *T. moserii*) that exhibit direct or abbreviated development have a simple life cycle, with benthic juveniles recruiting directly into the host dwelling from parental brood chambers. These juveniles might remain on the same host for the rest of their life (e.g., *Synalpheus regalis*; Duffy et al. 2000) or might leave the parental dwelling momentarily in search of new hosts from the same or different species where they can reestablish themselves (Thiel 2003). At the other extreme, the most complex life cycles occur in parasitic copepods and rhizocephalan cirripeds.

In between extremes, many symbiotic crustaceans with indirect development spend their early (larval) life in the pelagic environment. Once they have reached the first postlarval stage, these species actively search for and settle in/on hosts to establish a permanent or semipermanent association with their partners where they grow, mature, and reproduce. Many symbiotic partnerships involving decapod crustaceans fit the life cycle just depicted (e.g., caridean shrimps *Lysmata* spp.; porcelain crabs *Polyonyx* spp.; almost all brachyuran crab symbionts, including coral crabs in the genus *Trapezia* spp.; and pea crab in the genera *Austinixa*, *Pinnixa*, and *Pinnaxodes*, among many others). However, several other symbiotic crustaceans with indirect development deviate from this pattern. For instance, in the fish lice *Argulus* spp., the only genus in the Branchiura for which the life cycle is well studied, females leave their hosts and temporarily visit hard submerged surfaces to deposit their eggs. These eggs hatch into a first swimming larval stage well-equipped for dispersal, with setose antennae and mandibles and rudiments of the maxillules, maxillae, and first two pairs of swimming legs. The second larval instar is the first parasitic ontogenetic stage, and the setae on the antenna are replaced by strong claws at this time (Gresty et al. 1993, Møller et al. 2007). The successive larval stages appear to leave and find new hosts at intervals, and most morphological changes during larval development are gradual. An exception occurs between the fourth and fifth larval stage, when the maxillule experiences a metamorphosis, changing from a long limb with a powerful distal claw into a short but powerful circular sucker (Boxshall 2005). Various molts succeed each other until maturity is reached, and copulation usually appears to take place on the external surface of the hosts (Rushton-Mellor and Boxshall 1994, Pasternak et al. 2000).

Another example of indirect development is that of cymothoid isopods. Parental females in this group release offspring from their brood pouches as a modified "manca" (also called a "pullus II" stage) that swims efficiently thanks to heavily setose pleopods. These larvae need to find a fish to take their first meal within 1–2 days; otherwise, they die (Lester 2005). This life cycle contrasts to that of free-living peracarids with direct development, where juveniles assume an adult lifestyle shortly after emerging from the female's brood pouch (Thiel 2003).

These examples highlight the fact that many symbiotic crustaceans exhibit free-living dispersive stages early during their ontogeny. However, the opposite holds true in several other groups. For instance, in gnathid isopods (Gnathiidae), adult specimens do not feed and are found in cavities available in mud banks, dead barnacles, coral colonies, or sponges. In turn, recently hatched unfed juveniles or "zuphea" stages are those that seek a fish host to which to attach and feed on their blood. Due to the volume of blood consumed, the body of the zuphea expands. At this point, the zuphea becomes a "praniza." The praniza leaves the host, finds shelter in the benthos, digests its meal, and molts. After molt, the new
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Zuphea searches again for another host fish on which to feed. This cycle is repeated twice, until the third praniza finds a cavity in which to mature (Upton 1987a,b, Kensley and Schotte 1989, Lester 2005).

The most complex life cycles occur in parasitic copepods and rhizocephalan cirripeds. Such life cycles involve one or two hosts and subtle or considerable changes in body morphology and modification of the life cycle relative to that of their closest free-living relatives. For instance, the life cycle of parasitic copepods is abbreviated compared to that of their free-living counterparts that exhibit six naupliar dispersive stages and five copepodid stages preceding the adult phase. In parasitic copepods, the naupliar stages are usually lecithotrophic, the first copepodid is the ontogenetic stage that, most commonly, establishes the symbiotic relationship, and symbiotic partnerships usually involve a single host (Boxshall 2005). However, there are remarkable exceptions and deviations from the basic life cycle depicted above. For instance, Lernaeocera branchialis (family Pennellidae) features a life cycle that involves two nauplius stages and two, instead of a single, host species. Adult postmetamorphosis females that live on whiting (Merlangius merlangus) produce eggs that take 13 or more days to hatch as a nauplius I larva that passes through a nauplius II larval stage before turning into infective copepodids. These nonfeeding copepodids attach to the gills of the flounder Platichthys flesus, where they pass through all their developmental stages (four additional copepodid stages) to adulthood and copulation in a minimum of 25 days (Whitfield et al. 1988, Brooker et al. 2007).

A second remarkable example of a complex life cycle in symbiotic copepods is that of the Monstrilloidea, characterized by most larval and all but the last juvenile (copepodid) phases being endosymbiotic and by a free-swimming pelagic adult phase that does not feed (Suárez-Morales 2011). In this group, eggs attached externally to the body of the parental females hatch into lecithotrophic nauplii that locate, attach, and burrow into the tissue of a mollusk or polychaete host. Once in the hemolymph of the hosts, the infective naupliar stage metamorphoses into an endoparasitic sac-like second naupliar stage that forms a protective sheath around its body but has two root-like processes for absorbing nourishment from the host. Development and transition among ontogenetic phases takes place within the host. Hosts are abandoned at the copepodid stage that, after a single molt, becomes a free-living adult, lacking all cephalic appendages other than the antennules (Huy et al. 2007, Suárez-Morales 2011).

Epicaridean isopods (bopyrids, dajids, entoniscids, and cryptoniscids) are also recognized because of their complex life cycles. All known life cycles in this clade involve two crustacean hosts (Williams and Boyko 2012). For instance, in the bopyrid Orthione griffenis, symbiotic with the mud shrimp Upogebia pugettensis in the northeastern Pacific, parental females brood eggs in their brood pouch. These eggs develop and are released as a nonfeeding “epicaridium” larva that swims efficiently and seeks a copepod (usually a calanoid) host. The epicaridium attach to the copepod, perforate the exoskeleton, and feed on this intermediate host with the aid of its clawed pereopods and styliform suckorial mouthparts. Within days, the epicaridium metamorphoses into a “microniscus” larva that remains attached to the intermediate host, grows considerably, and metamorphoses into a cryptoniscus larva that leaves this intermediate host and swims until finding its second and definitive host (U. pugettensis). In this second, terminal host, the cryptoniscus metamorphoses into the first juvenile stage or bopyridium. In O. griffenis, the first bopyridium that parasitizes a host becomes a female, and subsequent isopods become males and live on the female (Williams and An 2009; Fig. 7.6). Thus, the life cycle of O. griffenis includes environmental sex determination, which has also been suggested for other bopyrids (Reinhard 1949). However, the sex in most other epicarideans is genetically determined (Williams and Boyko 2012). The life cycle of dasids, entoniscids, and cryptoniscids is not as well known as that of bopyrids.

The Rhizocephala also have a remarkably complex life cycle. An example is that of Loxothylacus panopaei, symbiotic with the brachyuran crab Rhithropanopeus harrisii in the northwestern Atlantic (Glenner 2001). In this species, free-swimming male and female nauplius larvae are released from
The nauplii develop into cyprids after 2 days. The male cyprid detects and settles at the mantle opening of a recently emerged externa on another host and metamorphoses into a dwarf male (a trichogon) that migrates through the mantle cavity and becomes inserted into one of the two receptacles of the virgin externa. Here, it will shed its cuticle, become established, and begin spermatogenesis. The externa will mature and begin to produce larvae only when a dwarf male has become established. In turn, female cyprids locate uninfested host crabs and settle on the gill lamella in the branchial chamber. Underneath the carapace of the cyprid, a kentrogon stage develops, which uses a cuticular-reinforced stylet to penetrate the integument of the gills to inject a "vermigon" into the open, blood-filled space of the gill lamella. The vermigon starts developing a rootlet branching system 10–12 days after injection into the host, and, after another month, the parasite finally protrudes a virgin externa through the integument of the host at the ventral part of the abdomen (Glenner 2001; Fig. 7.7).
The life cycle of the rhizocephalan cirriped *Loxothylacus panopaei*, from Glenner (2001), with permission from John Wiley and Sons. Solid lines illustrate developmental changes; dashed lines represent migration. (A) The externa (ex) underneath the abdomen of the host *Rhithropanopeus harrisii*. (B) The externa releases free-swimming male and female nauplius larvae. After 2 days, the nauplius larvae develop into cyprids. (C) The male cyprids detect and settle at the mantle opening of a recently emerged externa (I). The settled cyprid metamorphoses into a dwarf male, which becomes inserted into one of the two receptacles of the virgin externa. (D) Female cyprid locates host crabs and settles on the gill lamella (D1) in the branchial chamber. (E) A kentrogon (ken) develops underneath the carapace of the cyprid. hcu, cuticle of the gills; cc, carapace of the cyprid. (F) The cuticular-reinforced stylet penetrates the integument of the gills and injects a vermigon into the open blood-filled space of the gill lamella. Abbreviations: st, stylet; vg, vermigon. (F1) A median section of the vermigon in the area of the ovary anlage. Four cell types are represented: the a and b cells of the ovary anlage (ac, bc), the central core cells (ccc), and the cells of the epidermis. (G) Rootlet (branching) of an internal parasite 10–12 days after having been injected into the host. (G1) Median section of the rootlet (rl) in the area of the ovary anlage. The primordial mantle cavity (amc) has already developed. (H) After about a month, the virgin externa (ex) can be seen through the integument of the host at the ventral part of the abdomen. (H1) Vertical section though the virgin externa of H. The externa is about to erupt through the cuticle of the host. Abbreviations: amc, mantle cavity; ov, ovary; ch, cuticle of the host. (I) The recently emerged externa on the abdomen of the host. To continue its development, the virgin externa has to receive at least one dwarf male in one of its two receptacles. (I1) A vertical section through the externa as depicted in I. A cyprid has settled at the opening to the mantle cavity. A dwarf male (a trichogon) will develop underneath the carapace of the cyprid and migrate through the mantle cavity to the opening of one of the two receptacles. Here, it will shed its cuticle, become established, and begin spermatogenesis. (J) Having received dwarf males, the externa (ex) will now mature and begin to produce larvae.
Last, the Tantulocarida deserve to be mentioned, considering their exceptional life cycle, which includes a rare sexual and a common asexual (parthenogenetic) phase. Asexual females produce a tantulus larva with a well-defined cephalothorax and trunk (Fig. 7.8A,B). This larva spends time in the benthos seeking a suitable host (a peracarid, copepod, or ostracod) to which it attaches with an oral stylet that punctures the host’s cuticle. The larva sheds its trunk and develops into a new asexual (parthenogenetic) female without mating (Boxshall and Lincoln 1987; Fig. 7.8C). The new trunk of this female expands to accommodate the growing asexual larvae until they are released. In turn, during the sexual phase, the tantulus larva attaches to the host but does not shed the trunk. Instead, a sac-like expansion forms on the larval trunk from which sexual adult males or females develop. Once adults attain sexual maturity, the walls of the sac-like expansion rupture, releasing these adults to the external environment. The remaining portion of the sexual cycle is not well known. However, sexual dimorphism is pronounced in this group; males exhibit well-developed swimming appendages and paired clusters of chemosensory aesthetascs.

![Fig. 7.8.](image-url)

Life stages in the Tantulocarida. (A) Tantulus larva of *Itoitantulus misophricola* in lateral view. From Huys et al. (1992), with permission from Zoological Science. (B) Live tantulus larva of *Arcticotantulus kristensenii* attached dorsally to an harpacticoid copepod host. From Knudsen et al. (2009), with permission from Magnolia Press. (C) Parthenogenetic female of *A. kristensenii* with embryos inside. Arrow points at the head of the female. From Knudsen et al. (2009), with permission from Magnolia Press. (D) Male in late stage of development of *A. kristensenii* attached to cephalon of an harpacticoid copepod. Cephalic stylet in the larval head (cs) and male antennal aesthetascs (aes) are indicated. From Knudsen et al. (2009), with permission from Magnolia Press. Scale bars: A = 20 micrometers; B = 50 micrometers; C and D = 100 micrometers.
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(Fig. 7.8D). Thus, it is believed that the males actively search for receptive females. Once females are found, males presumably inseminate them using a well developed penis-like intromittent abdominal organ via a mid-ventral copulatory pore. The fertilized eggs develop within the expandable cephalothorax of the sexual females until ready to hatch as a fully formed tantulus or other larva (Boxshall and Lincoln 1987, Huys et al. 1993).

Once symbiotic partnerships have been established, various symbiotic crustaceans appear to be territorial, protecting “their” host individuals against conspecific (or even heterospecifics) via agonistic interactions. Nonetheless, formal experimental studies demonstrating territorial behavior have been conducted in only a few species of the Decapoda that dwell on their hosts either solitarily or as reproductive pairs (Baeza 2010). Whether or not highly modified symbiotic crustaceans (e.g., endosymbiotic rhizocephalans and epicaridean isopods) display territorial behaviors remains to be addressed.

COMPARISON WITH OTHER INVERTEBRATE GROUPS AND FUTURE DIRECTIONS

Symbiosis is common in marine invertebrates. Sponges, cnidarians, ctenophorans, flatworms, nemertean, nematodes, priapulids, echiurid, annelids, mollusks, equinoderms, and tunicates, among others, have been reported to engage in symbiotic associations with other marine vertebrates or invertebrates (Vermeij 1983, Margulis and Fester 1991). Importantly, most of the clades just mentioned are used as hosts by other invertebrates rather than being themselves the symbiotic guests of other organisms. Even so, there are several remarkable groups of invertebrates that do use other organisms as hosts. For instance, in the Porifera, boring sponges are capable of excavating complex galleries in corals (e.g., Cliona spp.). In the Cnidaria, various representatives of the subclass Hexacorallia, order Zoanthidea are epizootic on sponges (e.g., Zoanthus spp.). Three classes of flatworms (Platyhelminthes) are exclusively parasitic (Cestoda, Monogenea and Trematoda) and exhibit complex life cycles. These parasites exhibit considerable body modifications during their life and use one, two, or three hosts to complete their life cycle. Other symbiotic invertebrates include nemerteans parasitic on the egg masses of decapod crustaceans (e.g., Carcinonemertes spp.), the enigmatic Symbion pandora (Phylum Cycliophora) living on the mouthparts of lobsters, and aberrant polychaetes in the order Myzostomida that are endosymbiotic with echinoderms. Still, none of these particular monophyletic clades displays the wide diversity, in terms of morphology, feeding strategies, and life cycles, herein shown to occur in symbiotic crustaceans.

In crustaceans, members from almost all major taxonomic groups have established symbiotic relationships with other marine invertebrates, especially sessile invertebrates. Furthermore, a few crustaceans have established symbiotic partnerships with most unusual partners, including jellyfish, horseshoe crabs, amphibians, reptiles, birds, and mammals. Still others are parasites of humans (Tappe and Büttner 2009). This review demonstrates that the adoption of a symbiotic lifestyle represents a major environmental adaptation in crustaceans.

Many groups of crustaceans not included in this review do serve as hosts and provide shelter to other organisms that, in turn, might benefit them (e.g., caridean shrimps in the genus Alpheus symbiotic with goby fishes, Karplus and Thompson 2011; anomuran crabs harboring sea anemones on “their” shells, Ross 1983; brachyuran crabs masking their bodies with sponges, Guinot et al. 1995). These symbiotic partnerships, in which crustacean act as hosts rather than as symbiotic guests, are not uncommon. This information underscores the fact that the symbiotic lifestyle in decapod crustaceans is even more recurrent than shown in this review. The ecology of crustaceans providing shelter to other marine organisms deserves further attention.
Although the symbiotic lifestyle is pervasive in crustaceans, the incidence of symbiotic partnerships varied among taxonomic groups and was low or null in various clades (e.g., Remipedia, Cephalocarida, Branchiopoda, Cumacea, and Tanaidacea, among others). Various groups in which symbiosis is unusual live in freshwater or have an almost entirely pelagic life cycle. Other groups inhabit deep-sea environments. These habitats, with fewer life forms and less predictable and persistent productivity, might provide crustaceans with few evolutionary opportunities to exploit potential hosts. Yet symbiotic lifestyles cannot be discarded and remain plausible in these environments considering how little we know about their diversity.

Many groups of crustaceans in which symbiosis is the exclusive or predominant lifestyle are species-rich. For instance, in the Decapoda, examples include crabs from the superfamily Pinnotheroidea (302 species) and the superfamily Trapezioida (56 species) and shrimps from the subfamily Pontoninae (562 species). In many cases, the diversity of these symbiotic groups is considerably higher than that of their closest free-living relatives. For instance, in decapod caridean shrimps pertaining to the family Palaemonidae, symbiotic shrimps from the subfamily Pontoninae are more diverse than those pertaining to the predominantly free-living sister family Palaemoninae (562 vs. 372 species, respectively; De Grave 1999). This comparison begs the question as to whether or not the symbiotic lifestyle represents a key innovation favoring adaptive radiations in crustaceans. The adoption of a symbiotic lifestyle is believed to favor adaptive radiations in other groups of marine vertebrates such as shrimp-associated gobies (Thacker et al. 2011), sponge-dwelling gobies (Herler et al. 2009), and other coral-associated fish (Ruber et al. 2003). Studies on the phylogeny and life history of monophyletic clades of crustaceans containing both free-living and symbiotic species is warranted because it will test whether the adoption of a symbiotic lifestyle drives speciation and/or extinction rates (Fransen 2002).

CONCLUSIONS

In summary, symbiotic crustaceans represent a very interesting model group for ecological, behavioral, and evolutionary studies. More detailed ecological studies on several species of ecto- and endosymbiotic crustaceans are needed to evaluate their adaptations and interactions with their respective hosts. Molecular phylogenetic analyses are also needed to conclude about the effect of the symbiotic lifestyle on body, coloration, and color pattern modification. Furthermore, robust and comprehensive phylogenies of several groups may be used to propose and test hypotheses about the evolution of social systems and symbiotic interactions in the marine environment. Last, comparative studies including several species of symbiotic crustaceans are needed to better understand the diversification processes in this interesting clade of symbiotic organisms in particular and in marine invertebrates in general.

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