Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates

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Abstract

The symbiotic associates of hermit crabs (excluding parasites and flora) are reviewed worldwide. The review includes species found on the shells occupied by hermit crabs (epibiotic species), species boring into these shells (endolithic species), species living within the lumen of the shell (either free-living or attached to the shell), species attached to the hermit crabs themselves, and hypersymbionts. In total over 550 invertebrates, from 16 phyla are found associated with over 180 species of hermit crabs. Among these associates, 114 appear to be obligate commensals of hermit crabs, 215 are facultative commensals, and 232 are incidental associates. The taxa exhibiting the highest number of associates are arthropods (126), polychaetes (105), and cnidarians (100). The communities of species associated with *Dardanus arrosor*, *Paguristes eremita*, *Pagurus bernhardus*, *Pagurus cuanensis*, and *Pagurus longicarpus* are the best studied and harbor the most diverse assemblages of species. While trends in biodiversity of hermit crab assemblages do not follow predicted patterns (e.g., hermit crabs within the Indo-West Pacific do not harbor more species than those from temperate regions), this is suggested to reflect a lack of sampling rather than a true representation of the number of associates. Hermit crabs date to at least the Cretaceous and provided a niche for a number of groups (e.g., hydractinians, bryozoans, polydorids), which were already associates of living gastropods. Apparently hermit crab shells initially supplied a substrate for settlement and then these symbiotic relationships were reinforced by enhanced feeding of symbionts through the activity of the hosts. Through their use and recycling of gastropods shells, hermit crabs are important allogenic ecosystem engineers in marine habitats from the intertidal to the deep sea. Hermit crabs benefit from some symbionts, particularly cnidarians and bryozoans, through extension of shell apertures (alleviating need to switch into new shells) and by providing protection from predators. However, hermit crabs are also negatively impacted (e.g., decreased reproductive success, increased predation) by some symbionts and a review of egg predators is provided. Thus, the symbiotic relationships between hermit crabs and many associates are difficult to characterize and often exhibit temporal changes

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depending on environmental and biological factors. Research on the biology of these symbionts and the costs/benefits of their associations with hermit crabs are analyzed. While some associates (e.g., *Hydractinia* spp.) have been studied in considerable detail, for most associations little is known in terms of the impacts of symbionts on hosts, and future experimental studies on the multitude of relationships are suggested.

1. Introduction

Hermit crabs are decapod crustaceans most of which have noncalcified abdomens requiring protection from predation. Inhabiting empty gastropod shells serves to protect most of the more than 800 described species of hermit crabs within the Superfamily Paguroidea, nearly all of which are marine (McLaughlin, 1983, 2003). Hermit crabs are best known from intertidal areas where they are conspicuous and ecologically important scavengers and predators (Whitman et al., 2001). A small percentage of hermit crabs use bivalve and scaphopod shells, hollowed cylinders of wood (Lemaitre, 1995; McLaughlin and Lemaitre, 1997; Forest, 1987) or hollowed-out fragments of stone (Pope, 1953; Mayo, 1973), while others live in immobile domiciles provided by calcareous tubes of polychaetes or vermetid gastropods (Markham, 1977; Gherardi and Cassidy, 1994; Gherardi, 1996; Rodrigues et al., 2000), corals (McLaughlin and Lemaitre, 1993), or sponges (Forest, 1987). Some, such as the fully calcified coconut crab, *Birgus latro* (Linnaeus, 1767), exist without a shell for most of their terrestrial lives, although shells are utilized by megalopae and young crabs (Reese, 1968; Greenaway, 2003).

The adaptation of most hermit crabs to a life in empty gastropod shells has been studied in detail. Shell attributes such as type, weight, size, and internal volume affect the reproduction, growth, predator avoidance and behavior of hermit crabs (Markham, 1968; Vance, 1972; Fotheringham, 1976; Bertness, 1981a,b; Elwood et al., 1995; Angel, 2000; Benvenuto and Gherardi, 2001; Yoshino et al., 2002; Gilchrist, 2003). In addition, shell availability limits hermit crab populations in certain areas (Kellogg, 1976; but see Barnes, 1999) and may account for the coexistence of multiple hermit crab species in intertidal areas (Abrams, 1980, 1981, 1987a,b; Gherardi and Nardone, 1997). The biology and behavioral ecology of hermit crabs have been reviewed (Hazlett, 1981; Lancaster, 1988; Elwood and Neil, 1992).

In many regions gastropod shells inhabited by hermit crabs provide a substrate for epibiotic and endolithic species to attach and bore into, respectively. In addition, hermit crabs often harbor associates that live within the lumen of the shell (either free-living or attached to the shell) and others that attach to the hermit crabs themselves, both externally and internally. Taxonomic studies of symbiont species are abundant, yet certainly not complete and the ecological relationships between these associates and their hermit crab hosts remain largely unknown. Only a few studies have documented the biocoenosis or complete community of species associated with particular hermit crabs and their shells

(Samuelsen, 1970; Karlson and Shenk, 1983; Jensen and Bender, 1973; Cuadras and Pereira, 1977; Stachowitsch, 1977, 1980; McDermott, 2001; Reiss et al., 2003), although some partial reviews exist (Balss, 1924; Gordan, 1956; Lancaster, 1988; Ates, 2003). Gastropod shells and associated species can affect the brood size of hermit crabs and therefore can potentially have significant effects on the fitness of these species (Wilber, 1989). Hermit crab choice of gastropod shells can be affected by epibionts (Brooks and Mariscal, 1985a,b; Hazlett, 1984; Conover, 1979; McClintock, 1985; Caruso et al., 2003; Turra, 2003). In addition, mating behavior can be influenced by gastropod shells and perhaps attached associates (Hazlett and Baron, 1989).

Through their use of gastropod shells, hermit crabs influence the abundance and distribution of a diverse assemblage of invertebrates and thus provide a good example of ecosystem engineers (Jones et al., 1994, 1997). The acquisition of an empty gastropod shell by a hermit crab brings the shell in a sense ''back to life'' in that it has returned to its original mobile state (in some cases even fossil shells are used; Barnes, 2001; McDermott, unpublished data). This capacity to securely inhabit shells is the result of a long evolutionary process that fashioned a morphological compatibility between hermit crabs and snail shells (Cunningham et al., 1991; Schram, 2001). Furthermore, these shells exhibit different characteristics from when they were part of the living gastropod (e.g., shell secretion ceases, periostracum becomes eroded, the lumen is empty). Thus, in many ways the shells become new substrates, usually more conducive to attachment, penetration, and lumen invasion by symbionts. Therein some of these obligate or facultative associates reproduce and complete at least part of their life cycles as a result of hermit crab shell use. These organisms derive a variety of other benefits from hermit crabs and in some cases the symbiotic relationship is mutualistic, with hosts positively affected (e.g., protection from predators).

Ecosystem engineering is a broad, general concept for habitat modification and/or creation by organisms (Jones et al., 1994, 1997; Thomas et al., 1998; Coleman and Williams, 2002; Wilby, 2002; Gutiérrez et al., 2003; Berkenbusch and Rowden, 2003) and while hermit crabs are not engineers on the same scale as some other species [e.g., beavers (Wright et al., 2002) and gophers (Reichman and Seabloom, 2002)], hermit crabs on a world-wide basis influence whole communities of associates in a range of habitats from terrestrial to the deep sea. Specifically, hermit crabs are allogenic engineers (i.e., those engineers that transform ''living or non-living materials from one physical state to another''; Jones et al., 1997, p. 1949). As ecosystem engineers hermit crabs put discarded gastropod shells that would otherwise likely be buried in the sediments back into circulation (Gutiérrez et al., 2003). Species with analogous roles in marine habitats include the cockle, *Austrovenus stutchburyi* (Finlay, 1927) that provides a stable substrate along the shores of New Zealand (Thomas et al., 1998; Lafferty et al., 2000; Mouritsen and Poulin, 2003). The shell of the cockle is colonized by a variety of invertebrates, thus forming a community of species (obligate and facultative) that would otherwise not be able to persist in this habitat. The cockle provides an example of an autogenic ecosystem engineer (those engineers that ''directly transform the environment via endogenous processes''; Jones et al., 1997, p. 1949). Similarly, the bivalve *Donax variabilis* provides a substrate for the hydroid *Lovenella gracilis* in wave-swept environments (Manning and Lindquist, 2003). Hermit crabs provide a stable but mobile substrate and thus prevent

organisms from being buried and also provide access to positive conditions (e.g., well oxygenated water, food supply, protection from predators). Hermit crab assemblages could also be considered examples of facilitation (Bruno et al., 2003) in which hermit crabs extend the range of associates through these positive interactions.

The purpose of the present study is to provide a review of species associated with hermit crabs. In addition, potential benefits and costs derived by these associates and their impacts on hermit crab hosts are analyzed (including a review of known and suspected egg predators of hermit crabs) based on experimental studies. A discussion of hypersymbiotic relationships and a table of known examples among hermit crabs are provided. Finally, the evolutionary relationships between hermit crabs and their associates are examined.

This review identifies critical aspects of the life history of hermit crab associates that are in need of experimental studies. A wide range of research topics from the initial association of symbionts with hermit crab hosts (e.g., cues for metamorphosis) to their interactions with other symbionts in the hermit crab assemblages (e.g., predation) remain to be explored. The accurate characterization of their symbiotic relationships with hosts requires further studies. The impacts that associates have on hermit crab behavior (e.g., shell choice) are particularly amenable to laboratory and field experiments since extensive background and quantitative models exist (Elwood and Neil, 1992). In addition, this study will serve as a baseline for future field investigations on the diversity patterns of hermit crab assemblages from different geographic regions. Hermit crab biocoenoses would provide an important model system to test hypotheses on the biotic diversity of marine invertebrates associated with hard substrates and their role as ecosystem engineers.

2. Analysis

The present review, which includes obligate, facultative, and incidental species associated with hermit crabs, was gleaned from the literature since 1864 (inception of the Zoological Record). Symbionts of the atypical ''free-living'' lithodid paguroids (Lithodidae) are not included in this review. We have used the following definitions in the construction of our list of hermit crab associates: obligate associates are found associated only with hermit crab hosts (although different species of hermit crabs may act as hosts), facultative associates may occur with hermit crabs as well as other hosts or substrates, and incidental associates are found only occasionally with hermit crabs. Cases in which facultative symbionts exhibit a predilection for hermit crab shells over other substrates are discussed. The distinction between obligate, facultative, and incidental associates of hermit crabs is based on our knowledge of the literature, and where vital life history information is lacking, we have left the question of the category open. We follow Starr (1975) and Overstreet (1983) in defining symbiosis, hypersymbiosis, commensalism, parasitism, and mutualism. Strict endo- or ecto-parasites of hermit crabs such as entoniscid and bopyrid isopods, rhizocephalans, and fungi are not included in this review (see Overstreet, 1978, 1983; Høeg and Lützen, 1985, 1992; Trilles, 1999; Markham, 2003). However, associates previously defined as commensals but with tendencies toward parasitic behaviors are included (e.g., egg predators of hermit crabs). Flora are not listed, although coralline algae and other forms often cover hermit crab shells, providing

additional substrates for endolithic species (see Hazlett, 1984; Smyth, 1989; Zuschin and Piller, 1997). Fossil records of species associated with hermit crabs and their shells are noted in the Discussion but are not systematically reviewed in the present analysis (for reviews of fossil associates see Walker, 1988, 1989, 1992, 1995; Morris et al., 1991; Taylor, 1994). The higher taxa used in the text and tables generally follow Brusca and Brusca (2003). We attempted to provide currently accepted names for all host and symbiont species; those species of unknown taxonomic status and/or questionable identity were noted but left as originally designated. Within the text, taxonomic authority and date are provided only for those species which do not appear in Table 1.

3. Results

Presently at least 550 invertebrate species, representing 16 phyla, are found associated with hermit crabs (Table 1). Over 180 hermit crab species act as hosts for these associates. The best-represented groups of symbionts are the arthropods, polychaetes, and cnidarians with 126, 105, and 100 species represented, respectively (Fig. 1A). Of the associates, 114 (20.3%) appear to be obligate commensals of hermit crabs; over 10 of the obligate symbionts are found with a single hermit crab host but it is unlikely many exhibit a species-specific association with hermit crabs. Two hundred and fifteen are facultative commensals and 232 are incidental associates (38.3 and 41.4% respectively) (Fig. 1A). Most arthropods, platyhelminths, and polychaetes are free-living species while cnidarians and bryozoans are almost exclusively external epibionts (Fig. 1B). The protozoans are unique in containing mostly species that live on the hermit crab hosts. Endolithic species are most prevalent in the polychaetes but are also found among the arthropods, sponges, bryozoans, and additional phyla (Fig. 1B). The hermit crabs *Dardanus arrosor*, *Paguristes eremita*, *Pagurus bernhardus*, *Pagurus cuanensis*, and *Pagurus longicarpus* are host to the most diverse assemblages of species (Fig. 2). Some species may dominate shells (e.g., sponges, anemones, bryozoans) while others are found in multi-species assemblages (Fig. 3A–C).

3.1. Protozoa

At least 35 species of protozoans are associates of hermit crabs, either directly attaching to the exoskeleton of the hermit crabs, to the surface of the shells, or to other symbionts (Table 1). Besides two species of benthic foraminiferans, all protozoan associates of hermit crabs belong to the Phylum Ciliophora. Morado and Small (1995), Fernández-Leborans and Tato-Porto (2000a,b) and Fernández-Leborans (2001, 2003) provide comprehensive lists of epibiotic ciliophorans including those known to live on hermit crabs. The specific nature of many of these symbioses, however, remains unknown. Also unresolved is the suggestion that some protozoans are specifically located only on the body of the crab versus attachment to the inside surface of the shell.

The chonotrichous ciliate *Vasichona paguri* is attached to *Pagurus pubescens* as a facultative symbiont (Jankowski, 1972; Fernández-Leborans, 2001). *Lagenophrys eupagurus* is a facultative loricate peritrich attached to the gills of *P. longicarpus* (Kellicott, 1893; Clamp, 1989; Fernández-Leborans and Tato-Porto, 2000a). Clamp (1989) rede-

Table 1
Associates of hermit crabs

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Protozoa						
Acineta constricta	Collin, 1909	*Pagurus cuanensis*	Bell, 1845	O$^?$	C	Sprague and Couch, 1971
		Pagurus excavatus	(Herbst, 1791)			Sprague and Couch, 1971
Acineta papillifera	Keppen, 1888	*Pagurus bernhardus*	(Linnaeus, 1758)	I	C	Fernández-Leborans and Gómez del Arco, 1996
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Acineta tuberosa	Ehrenberg, 1833	*Dardanus arrosor*	(Herbst, 1796)	I	C	Fernández-Leborans, 2003
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans and Gómez del Arco, 1996
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Acinetides symbiotica	(Daday, 1907)	*Diogenes pugilator*	(Roux, 1828)	F	C	Fernández-Leborans, 2003
Actinocyathula homari	(Sand, 1899)	*Paguristes eremita*	(Linnaeus, 1767)	F	C	Fernández-Leborans, 2003
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Ascobius faurefremieti	Hadzi, 1951	*Clibanarius erythropus*	(Latreille, 1818)	I	C	Basile et al., 2002
		Paguristes eremita	(Linnaeus, 1767)			Basile et al., 2002
Chilodochona quennerstedti	Wallengren, 1859	*Pagurus prideaux*	Leach, 1815	O	C	Fernández-Leborans, 2003
Cibicides lobulatus	(Walker and Jacob, 1798)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	I	EE	Samuelsen, 1970
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
		Pagurus prideaux	Leach, 1815			Samuelsen, 1970
Conchacineta constricta	(Collin, 1909)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	C	Fernández-Leborans and Gómez del Arco, 1996
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Corynophrya anisostyla	Fernández-Leborans and Gómez del Arco, 1996	*Paguristes eremita*	(Linnaeus, 1767)	F	C	Fernández-Leborans and Tato-Porto, 2000b
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003

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Corynophrya homari	(Sand, 1899)	*Paguristes eremita*	(Linnaeus, 1767)	F	C	Fernández-Leborans and Gómez del Arco, 1996
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus cuanensis	Bell, 1845			Fernández-Leborans and Tato-Porto, 2000b
Cothurnia sp.		*Dardanus arrosor*	(Herbst, 1796)	I	C	Fernández-Leborans, 2003
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Dendrosomides grassei	Batisse, 1986	*Cestopagurus timidus*	(Roux, 1828)	O?	C	Fernández-Leborans and Tato-Porto, 2000b
Dendrosomides paguri	Collin, 1906	*Pagurus cuanensis*	Bell, 1845	O	C	Fernández-Leborans and Tato-Porto, 2000b
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans and Tato-Porto, 2000b
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans and Tato-Porto, 2000b
Ephelota cf. *gemmipara*	Hertwig, 1876	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Ephelota gemmipara	Hertwig, 1876	*Dardanus arrosor*	(Herbst, 1796)	I	C	Fernández-Leborans, 2003
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans and Gómez del Arco, 1996
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Epistylis sp.		*Coenobita brevimanus*	Dana, 1852	F	C	Fernández-Leborans and Tato-Porto, 2000a
Folliculina cf. *ampulla*		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE, C	Stachowitsch, 1980
Folliculina spirorbis	Dons, 1913	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Folliculina viridis	Wright, 1858	*Paguristes eremita*	(Linnaeus, 1767)	F	C	Fernández-Leborans and Gómez del Arco, 1996

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Protozoa						
Folliculina viridis		*Paguristes eremita*	(Linnaeus, 1767)			Fernández-Leborans and Córdoba, 1997
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans and Córdoba, 1997
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans and Córdoba, 1997
		Pagurus prideaux	Leach, 1815			Herrero and Fernández-Leborans, 1995
foraminiferan		*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Gymnodinioides sp.		*Pagurus hirsutiusculus*	Brandt, 1851	F	C	Bradbury, 1966
		Pagurus ochotensis	(Dana, 1852)			Bradbury, 1966
Gymnodinioides inkystans	Minkiewicz, 1913	*Clibanarius erythropus*	(Latreille, 1818)	F	C	Baccarani and Pessani, 1997
		Pagurus bernhardus	(Linnaeus, 1758)			Sprague and Couch, 1971
		Pagurus longicarpus	Say, 1817			Trager, 1957
		Pagurus prideaux	Leach, 1815			Sprague and Couch, 1971
Hyalophysa chattoni	Bradbury, 1966	*Clibanarius vittatus*	(Bosc, 1802)	F	C	Landers et al., 1999
		Clibanarius vittatus	(Bosc, 1802)			Grimes, 1976
		Pagurus annulipes	(Stimpson, 1859)			Bradbury and Clamp, 1973
		Pagurus hirsutiusculus	(Dana, 1852)			Bradbury, 1966
		Pagurus longicarpus	Say, 1817			Grimes, 1976
		Pagurus ochotensis	Brandt, 1851			Bradbury, 1966
Lagenophrys eupagurus	Kellicott, 1893	*Pagurus longicarpus*	Say, 1817	F	C	Clamp, 1989
Metafolliculina andrewsi	Hadzi, 1938	*Pagurus pollicaris*[?]	Say, 1817	I	C	Sprague and Couch, 1971
Paracineta limbata	Maupas, 1881	*Paguristes eremita*	(Linnaeus, 1767)	I	C	Fernández-Leborans and Gómez del Arco, 1996
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Pebrilla paguri	Giard, 1888	*Clibanarius erythropus*	(Latreille, 1818)	O	C	Sprague and Couch, 1971
		Clibanarius erythropus	(Latreille, 1818)			Fauré-Fremiet, 1936
		Clibanarius erythropus	(Latreille, 1818)			Baccarani and Pessani, 1997

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		Clibanarius erythropus	(Latreille, 1818)			Basile et al., 2002
		Pagurus bernhardus	(Linnaeus, 1758)			Fauré-Fremiet, 1936
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans and Córdoba, 1997
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans and Córdoba, 1997
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Phyllacineta jolyi	Maupas, 1881	*Paguristes eremita*	(Linnaeus, 1767)	O	C	Fernández-Leborans and Gómez del Arco, 1996
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Planorbulina mediterranensis	(d'Orbigny, 1826)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Platyfolliculina paguri	Andrews and Reinhard, 1943	*Pagurus pubescens*	Krøyer, 1838	O	C	Sprague and Couch, 1971
Pleurocoptes hydractiniae	Wallengren, 1896	*Pagurus bernhardus*	(Linnaeus, 1758)	F	HS	Fauré-Fremiet, 1961
Podocyathus paguri	Zhadan and Mikrjukov, 1996	*Pagurus pubescens*	Krøyer, 1838	O	C	Fernández-Leborans and Tato-Porto, 2000b
Polyspira delagei	Minkiewicz, 1912	*Clibanarius erythropus*	(Latreille, 1818)	F	C	Baccarani and Pessani, 1997
		Pagurus bernhardus	(Linnaeus, 1758)			Sprague and Couch, 1971
Vaginicola paguri	(André, 1910)	*Pagurus bernhardus*	(Linnaeus, 1758)	O	C	Fernández-Leborans and Tato-Porto, 2000a
Vasichona paguri	Jankowski, 1972	*Pagurus* sp.		F	C	Jankowski, 1972
Vorticella sp.		*Paguristes eremita*	(Linnaeus, 1767)	I	C	Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003
Zoothamnium sp.		*Dardanus arrosor*	(Herbst, 1796)	I	C, EE	Fernández-Leborans, 2003
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans and Gómez del Arco, 1996
		Paguristes eremita	(Linnaeus, 1767)			Fernández-Leborans, 2003
		Pagurus bernhardus	(Linnaeus, 1758)			Fernández-Leborans and Gómez del Arco, 1996
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus excavatus	(Herbst, 1791)			Fernández-Leborans, 2003
		Pagurus prideaux	Leach, 1815			Fernández-Leborans, 2003

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Porifera						
Alectona sp.		unidentified		I	En	Smyth, 1990
Amorphinopsis sp.		unidentified		I	En	Smyth, 1990
Chondrosia reniformis	Nardo, 1847	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Clathria atrasanguinea	(Bowerbank, 1866)	*Dardanus* sp.		I	EE	van Soest, 1993
		Pagurus spp.				van Soest, 1993
Clathria coralloides	(Olivi, 1792)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Cliona celata	Grant, 1826	*Dardanus arrosor*	(Herbst, 1796)	I	En	Cuadras and Pereira, 1977
Cliona ensifera[?]	Sollas	unidentified		I	En	Smyth, 1990
Cliona sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	En	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
		unidentified				Smyth, 1990
Cliona vastifica	Hancock, 1849	unidentified		I	En	Smyth, 1990
Cliona viridis	(Schmidt, 1862)	unidentified		I	En	Smyth, 1990
Demospongiae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Halichondria sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Hymedesmia coriacea	(Fristedt, 1887)	*Dardanus* sp.		I	EE	van Soest, 1993
		Pagurus spp.				van Soest, 1993
Hymeniacidon sp.		*Pagurus pubescens*	Krøyer, 1838	I	EE	Scott, 1885
Merlia tenuis	Hoshino, 1985	*Dardanus aspersus*	(Berthold, 1836)	I	EE	Hoshino, 1985
Polymastia mamillaris	Müller, 1806	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Reniera sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Rhizaxinella pyrifera	(Delle Chiaje, 1828)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Pseudospongosorites suberitoides	(Diaz et al., 1993)	*Paguristes hummi*	Wass, 1955	F	EE	Diaz et al., 1993
		Paguristes hummi	Wass, 1955			Wells, 1969
		Paguristes hummi	Wass, 1955			Sandford, 2003
		Pagurus impressus	(Benedict, 1892)			Wells, 1969

		Pagurus impressus	(Benedict, 1892)			Diaz et al., 1993
		Pagurus impressus	(Benedict, 1892)			Sandford, 1994, 1995
		Pagurus impressus	(Benedict, 1892)			Sandford and Kelly-Borges, 1997
		Pagurus impressus	(Benedict, 1892)			Sandford, 2003
		Pagurus longicarpus	Say, 1817			Sandford, 2003
		Pagurus pollicaris	Say, 1817			Wells, 1969
		Pagurus pollicaris	Say, 1817			Sandford, 2003
Suberites domuncula	(Olivi, 1792)	*Clibanarius* sp.		F	EE	Vosmaer, 1933
		Dardanus arrosor	(Herbst, 1796)			Sandford and Kelly-Borges, 1997
		Dardanus arrosor	(Herbst, 1796)			Vosmaer, 1933
		Dardanus calidus	(Risso, 1826)			Vosmaer, 1933
		Dardanus sp.				van Soest, 1993
		Elassochirus tenuimanus	(Dana, 1851)			Sandford and Kelly-Borges, 1997
		Paguristes eremita	(Linnaeus, 1767)			Vosmaer, 1933
		Paguristes eremita	(Linnaeus, 1767)			Voultsiadou-Koukoura and van Soest, 1993
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Burton, 1953
		Pagurus bernhardus	(Linnaeus, 1758)			Sandford and Kelly-Borges, 1997
		Pagurus constans	(Stimpson, 1858)			Vosmaer, 1933
		Pagurus brandti	(Benedict, 1892)			Vosmaer, 1933
		Pagurus cuanensis	Bell, 1845			Burton, 1953
		Pagurus cuanensis	Bell, 1845			Sandford and Kelly-Borges, 1997
		Pagurus cuanensis	Bell, 1845			Vosmaer, 1933
		Pagurus cuanensis	Bell, 1845			Voultsiadou-Koukoura and van Soest, 1993
		Pagurus kennerlyi	(Stimpson, 1864)			Sandford and Kelly-Borges, 1997
		Pagurus sp.				Vosmaer, 1933
		Pagurus spp.				van Soest, 1993
		unidentified				Gurjanova, 1951
Suberites ficus	(Linnaeus, 1767)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	F	EE	Balss, 1924
		Dardanus arrosor	(Herbst, 1796)			Sim, 1990
		Dardanus sp.				van Soest, 1993
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
		Pagurus cuanensis	Bell, 1845			Balss, 1924
		Pagurus kennerlyi	(Stimpson, 1864)			Sandford and Kelly-Borges, 1997

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Porifera						
Suberites ficus		*Pagurus pectinatus*	(Stimpson, 1858)			Sim, 1990
		Pagurus pectinatus	(Stimpson, 1858)			Sandford, 2003
		Pagurus pubescens	Krøyer, 1838			Balss, 1924
		Pagurus spp.				van Soest, 1993
		Pagurus stevensae	Hart, 1971			Hart, 1971
		unidentified				Voultsiadou-Koukoura and van Soest, 1993
Suberites latus	Lambe, 1892	unidentified		I	EE	De Laubenfels, 1961
Suberites pagurorum	Solé-Cava and Thorpe, 1986	*Pagurus bernhardus*	(Linnaeus, 1758)	O[?]	EE	Solé-Cava and Thorpe, 1986
Suberites puncturatus	Thiele, 1905	*Pagurus* sp.		F	EE	Desqueyroux, 1972
Suberites sp.		*Pagurus cuanensis*	Bell, 1845	F	EE	Selbie, 1921
		Pagurus cuanensis	Bell, 1845			Allen, 1967
		Pagurus pubescens	Krøyer, 1838			Reiss et al., 2003
Sycon raphanus	(Schmidt, 1862)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Tethya aurantium	(Pallas, 1766)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Thoosa bulbosa[?]	Hancock	unidentified		I	En	Smyth, 1990
Cnidaria						
Actinia equina	Linnaeus, 1758	*Paguristes eremita*	(Linnaeus, 1767)	I	EE	Balss, 1924
actinian		*Bivalvopagurus sinensis*	(De Saint-Laurent, 1972)	F[?]	EI	Lemaitre, 1993
		Munidopagurus macrocheles	(A. Milne-Edwards, 1880)	O[?]	C	Provenzano, 1971
		Paguropsis typica	Henderson, 1888	O[?]	C	Schäfer et al., 1983
		Pagurus bernhardus	(Linnaeus, 1758)	F[?]	EE	Reiss et al., 2003
		Pagurus imarpe	Haig, 1974	F[?]	EE	Haig, 1974
		Paragiopagurus bougainvillei	(Lemaitre, 1994)	F[?]	EE	Lemaitre, 1994
		Pylopagurus discoidalis	(A. Milne-Edwards, 1880)	F[?]	EE	McLaughlin and Lemaitre, 2001
		Pylopagurus macgeorgei	McLaughlin and Lemaitre, 2001	F[?]	EE	McLaughlin and Lemaitre, 2001
		Sympagurus affinis	(Henderson, 1888)	F[?]	EE	Lemaitre, 1994
		Sympagurus brevipes	(De Saint-Laurent, 1972)	F[?]	EE	Lemaitre, 1996
		Sympagurus poupini	Lemaitre, 1994	F[?]	EE	Lemaitre, 1994
		Sympagurus trispinosus	(Balss, 1911)	F[?]	EE	Lemaitre, 1994
		Sympagurus tuamotu	Lemaitre, 1994	F[?]	EE	Lemaitre, 1994

		Sympagurus wallisi	Lemaitre, 1994	F[?]	EE	Lemaitre, 1994
actinian or zoanthid		*Oncopagurus bicristatus*	(A. Milne-Edwards, 1880)	F[?]	EE	Ates, 2003
		Oncopagurus gracilis	(Henderson, 1888)	F[?]	EE	Ates, 2003
		Parapagurus alaminos	Lemaitre, 1986	F[?]	EE	Ates, 2003
		Parapagurus furici	Lemaitre, 1999	O[?]	C	Ates, 2003
		Parapagurus nudus	(A. Milne-Edwards, 1891)	F[?]	EE	Ates, 2003
		Sympagurus acinops	Lemaitre, 1989	F[?]	EE	Ates, 2003
		Sympagurus dimorphus[?]		F[?]	EE	Ates, 2003
Adamsia palliata	(Müller, 1776)	*Diogenes* sp.		O	EE	Zamponi, 1985
		Pagurus alatus	(Fabricius, 1775)			Kinzelbach, 1976
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
		Pagurus excavatus	(Herbst, 1791)			Ates, 1995
		Pagurus forbesii	Bell, 1845			Kinzelbach, 1976
		Pagurus prideaux	Leach, 1815			Ates, 1995
		Pagurus prideaux	Leach, 1815			Samuelsen, 1970
		Pagurus prideaux	Leach, 1815			Matthews, 1959
		Pagurus prideaux	Leach, 1815			Gosse, 1860
		Pagurus prideaux	Leach, 1815			Wortley, 1863
		Pagurus prideaux	Leach, 1815			Fox, 1965
		Pagurus prideaux	Leach, 1815			Ross, 1967
		Pagurus prideaux	Leach, 1815			Berner, 1953
		Pagurus prideaux	Leach, 1815			Caruso et al., 2003
Adamsia sociabilis	Verrill, 1882	*Catapagurus sharreri*	A. Milne-Edwards, 1880	O[?]	EE	Balss, 1924
		Catapagurus socialis	(Smith, 1881)			Ross, 1967
Aiptasia sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Antholoba sp.		unidentified		F	EE	Carlgren, 1930
anthozoan polyp		*Oncopagurus indicus*	(Alcock, 1905)	F[?]	EE	Lemaitre, 1996; Ates, 2003
		Oncopagurus orientalis	(De Saint Laurent, 1972)	O[?]	C	Ates, 2003
		Parapagurus richeri	Lemaitre, 1999	F[?]	EE	Ates, 2003
		Parapagurus saintlaurentae	Lemaitre, 1999	O[?]	C	Ates, 2003
Bougainvillia sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Calliactis algoaensis	Carlgren, 1938	*Dardanus arrosor*	(Herbst, 1796)	F	EE	Dales, 1957
Calliactis argentacoloratus	Pei, 1996	unidentified		F	EE	Pei, 1996
Calliactis conchiola	Parry, 1952	*Diacanthurus rubricatus*	(Henderson, 1888)	F	EE	Hand, 1975a
		Paguristes subpilosus	Henderson, 1888			Hand, 1975a
		unidentified				Pei, 1998

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Cnidaria						
Calliactis effoeta	Linnaeus, 1758	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Balss, 1924
Calliactis japonica	Carlgren, 1928	*Dardanus arrosor*	(Herbst, 1796)	F	EE	Carlgren, 1949
		Dardanus arrosor	(Herbst, 1796)			Yusa et al., 2001
Calliactis parasitica	(Couch, 1842)	*Clibanarius erythropus*	(Latreille, 1818)	F	EE	Faurot, 1932
		Dardanus arrosor	(Herbst, 1796)			Ross and Sutton, 1961
		Dardanus arrosor	(Herbst, 1796)			Cuadras and Pereira, 1977
		Dardanus arrosor	(Herbst, 1796)			Faurot, 1910
		Dardanus arrosor	(Herbst, 1796)			Brunelli, 1910
		Dardanus arrosor	(Herbst, 1796)			Brunelli, 1913
		Dardanus arrosor	(Herbst, 1796)			Faurot, 1932
		Dardanus arrosor	(Herbst, 1796)			Cotte, 1922
		Dardanus arrosor	(Herbst, 1796)			Fenizia, 1934
		Dardanus calidus	(Risso, 1826)			Ross, 1971
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Paguristes eremita	(Linnaeus, 1767)			Christidis et al., 1997
		Paguristes eremita	(Linnaeus, 1767)			Balss, 1924
		Pagurus alatus	Fabricius, 1775			Christidis et al., 1997
		Pagurus bernhardus	(Linnaeus, 1758)			Ross, 1960
		Pagurus bernhardus	(Linnaeus, 1758)			Gosse, 1860
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus excavatus	(Herbst, 1791)			Faurot, 1932
		Pagurus sp.				Zamponi, 1985
Calliactis polypores	Pei, 1996	unidentified		F	EE	Pei, 1996
Calliactis polypus	(Forskål, 1775)	*Anapagurus polynesiensis*	Nobili, 1907	F	EE	England, 1971
		Catapaguroides fragilis	(Melin, 1939)			England, 1971
		Dardanus arrosor	(Herbst, 1796)			Dales, 1957
		Dardanus deformis	(H. Milne Edwards, 1836)			Dales, 1957
		Dardanus deformis	(H. Milne Edwards, 1836)			Tudge, 1995
		Dardanus impressus	(De Haan, 1849)			Yusa et al., 2001
		Dardanus lagopodes	(Forskål, 1775)			England, 1971
		Dardanus lagopodes	(Forskål, 1775)			Yusa et al., 2001
		Dardanus pedunculatus	(Herbst, 1791)			Carlgren, 1949
		Dardanus pedunculatus	(Herbst, 1791)			England, 1971
		Dardanus tinctor	(Forskål, 1775)			Yusa et al., 2001

		Dardanus tinctor	(Forskål, 1775)			Carlgren, 1949
		Parapagurus pilosimanus	Smith, 1879			Carlgren, 1949
		unidentified				Pei, 1998
Calliactis reticulata	Stephenson, 1918	unidentified		F	EE	Pei, 1998
Calliactis sp.		*Dardanus* sp.		F	EE	Cowles, 1920a, 1920b
		Paguristes eremita	(Linnaeus, 1767)			Caruso et al., 2003
		unidentified				Pei, 1996
Calliactis tricolor	(Le Sueur, 1817)	*Clibanarius vittatus*	(Bosc, 1802)	F	EE	Pearse, 1947
		Clibanarius vittatus	(Bosc, 1802)			Sandford, 2003
		Dardanus venosus	(H. Milne Edwards, 1848)			Brooks and Rittschof, 1995
		Dardanus venosus	(H. Milne Edwards, 1848)			Cutress and Ross, 1969
		Pagurus impressus	(Benedict, 1892)			Sandford, 2003
		Pagurus longicarpus and/or *P. pollicaris*	Say, 1817			Frey, 1987
		Pagurus pollicaris	Say, 1817			Brooks and Rittschof, 1995
		Pagurus pollicaris	Say, 1817			Brooks and Mariscal, 1986b
		Pagurus pollicaris	Say, 1817			Conover, 1976
		Pagurus pollicaris	Say, 1817			McLean, 1983
		Pagurus pollicaris	Say, 1817			Sandford, 2003
		Pagurus pollicaris[?]	Say, 1817			Carlgren, 1949
		Petrochirus diogenes	(Linnaeus, 1758)			Brooks and Rittschof, 1995
		Petrochirus diogenes	(Linnaeus, 1758)			Cutress et al., 1970
		Petrochirus diogenes	(Linnaeus, 1758)			Sandford, 2003
		Petrochirus granulatus	(Olivier, 1811)			Carlgren, 1949
Calliactis variegata	Verrill, 1869	unidentified		F	EE	Carlgren, 1949
Calliactis xishaensis	Pei, 1996	unidentified		F	EE	Pei, 1996
Campanularia johnstoni	(Alder, 1856)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Clavactinia gallensis[?]	Thornely	*Diogenes avarus*	Heller, 1865	F	EE	Balss, 1924
Clavactinia multitentaculata	Millard, 1975	*Dardanus arrosor*	(Herbst, 1796)	F	EE	Millard, 1975
Clytia bakeri	Torrey, 1904	*Pagurus granosimanus*	(Stimpson, 1859)	I	EE	Walker, 1988
Dicoryne conferta	(Alder, 1856)	*Anapagurus cf. hendersoni*	Barnard, 1947	F	EE	Millard, 1975
		Pagurus bernhardus	(Linnaeus, 1758)			Kramp, 1935
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
Dicoryne conybeari	(Allman, 1864)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Reiss et al., 2003
Dicoryne valdiviae[?]	Stechow	*Parapylocheles scorpio*	(Alcock, 1894)	F	EE	Balss, 1924
Epizoanthus abyssorum	Verrill, 1885	*Parapagurus pilosimanus*	Smith, 1879	F	EE	Muirhead et al., 1986; Ates, 2003
Epizoanthus arenaceus	Delle Chiaje, 1823	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980; Ates, 2003

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Cnidaria						
Epizoanthus arenaceus		*Pagurus cuanensis*	Bell, 1845			
Epizoanthus carcinophilus	Carlgren, 1923	*Parapagurus bouvieri*	Stebbing, 1910	O	EE	Carlgren, 1938; Ates, 2003
		Parapagurus pilosimanus	Smith, 1879			Balss, 1924; Ates, 2003
Epizoanthus chuni	Carlgren, 1923	*Oncopagurus monstrosus*	(Alcock, 1894)	F?	EE	Balss, 1924; Ates, 2003
Epizoanthus egeriae	Haddon and Duerden, 1896	unidentified		F?	EE	Ates, 2003
Epizoanthus frenzeli	Pax, 1937	*Paguristes eremita*	(Linnaeus, 1767)	F?	EE	Ates, 2003
Epizoanthus incrustatus	Duben and Kuren, 1847	*Anapagurus laevis*	(Bell, 1845)	F	EE	Muirhead et al., 1986
		Catapagurus sharreri	A. Milne-Edwards, 1880			Balss, 1924
		Pagurus bernhardus	(Linnaeus, 1758)			Balss, 1924; Ates, 2003
		Pagurus excavatus	(Herbst, 1791)			Balss, 1924
		Pagurus politus	(Smith, 1882)			Balss, 1924
		Pagurus pubescens	Krøyer, 1838			Balss, 1924
		Sympagurus pictus	Smith, 1883			Balss, 1924
Epizoanthus indicus	(Lwowsky, 1913)	*Parapagurus* sp.		F?	EE	Ates, 2003
Epizoanthus michaelsarsi	Carlgren, 1923	unidentified		F?	EE	Balss, 1924; Ates, 2003
Epizoanthus mortenseni	Carlgren, 1934	probably hermit crabs		F?	EE	Ates, 2003
Epizoanthus paguricola	(Roule, 1900)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	O	EE	Ates, 2003
		Anapagurus laevis	(Bell, 1845)			Roule, 1900
		Pagurus cuanensis	Bell, 1845			Roule, 1900
Epizoanthus paguriphilus	Verrill, 1883	*Pagurus alatus*	Fabricius, 1775	O	EE	Urzelai et al., 1990
		Parapagurus pilosimanus	Smith, 1879			Urzelai et al., 1990
		Parapagurus pilosimanus	Smith, 1879			Muirhead et al., 1986
		Parapagurus pilosimanus	Smith, 1879			Balss, 1924
Epizoanthus paguropsidis	Boas, 1926	*Paguropsis typica*	Henderson, 1888	O	C	Boas, 1926; Ates, 2003
		Paguropsis typica	Henderson, 1888			Nicol, 1960
Epizoanthus parasiticus	Verrill, 1861	*Pagurus pubescens*	Krøyer, 1838	F?	EE	Ates, 2003
Epizoanthus ramosus	Carlgren, 1934	*Paguristes* sp.?		F?	EE	Ates, 2003
Epizoanthus sagaminensis?	Pax	*Paguristes palythophilus*	Ortmann, 1892	F?	EE	Balss, 1924; Ates, 2003
Epizoanthus senegambiensis	(Carter, 1882)	*Diogenes ovatus*	Miers, 1879	F?	EE	Ates, 2003
		Pagurus sp.?				Ates, 2003
Epizoanthus similis	Carlgren, 1938	*Eupagurus* sp.?		O	EE	Carlgren, 1938; Ates, 2003
		unidentified				Pei, 1998
Epizoanthus sp.		*Anapagurus pusillus*	Henderson, 1888	F?	EE	Balss, 1924; Ates, 2003
		Nematopagurus muricatus	(Henderson, 1896)	F?	EE	Balss, 1924; Ates, 2003
		Oncopagurus minutus	(Henderson, 1888)	F?	EE	Ates, 2003
		Paguristes balanophilus	Alcock, 1905	F?	EE	Balss, 1924; Ates, 2003

		Paguristes puniceus	Henderson, 1896	F[?]	EE	Balss, 1924; Ates, 2003
		Parapagurus abyssorum	(Filhol, 1885)	F[?]	C	Ates, 2003
		Parapagurus andreui	MacPherson, 1984	F[?]	C	Ates, 2003
		Parapagurus bouvieri	Stebbing, 1910	F[?]	C	Balss, 1924; Ates, 2003
		Parapagurus latimanus	Henderson, 1888	F[?]	C	Ates, 2003
		Parapagurus pilosimanus	Smith, 1879	F[?]	EE	Ates, 2003
		Sympagurus dimorphus[?]		F[?]	C	Ates, 2003
		Sympagurus papposus	Lemaitre, 1996	F[?]	C	Lemaitre, 1996; Ates, 2003
		Sympagurus villosus	Lemaitre, 1996	F[?]	C	Lemaitre, 1996; Ates, 2003
		unidentified		F[?]	EE	Ates, 2003
Epizoanthus steueri	Pax, 1937	*Paguristes eremita*	(Linnaeus, 1767)	F[?]	EE	Ates, 2003
Epizoanthus studeri	Carlgren, 1938	*Parapagurus dimorphus*	(Studer, 1883)	O	EE	Carlgren, 1938; Ates, 2003
Epizoanthus valdiviae[?]	Carlgren, 1923	*Oncopagurus monstrosus*	(Alcock, 1894)	F[?]	EE	Balss, 1924
Epizoanthus vatovai	Pax and Lochter, 1935	*Paguristes eremita*	(Linnaeus, 1767)	F[?]	EE	Ates, 2003
Eudendrium ramosum	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Gonactinia prolifera	(Sars, 1835)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	I	EE	Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Hormathia coronata	(Gosse, 1858)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Balss, 1924
Hydractinia diogenes	Millard, 1959	*Diogenes costatus*	Henderson, 1893	O	EE	Millard, 1975
*Hydractinia echinata**	(Fleming, 1828)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	F	EE	Samuelsen, 1970
		Clibanarius vittatus	(Bosc, 1802)			Mercando and Lytle, 1980
		Clibanarius vittatus	(Bosc, 1802)			Sandford, 2003
		Dardanus arrosor	(Herbst, 1796)			Cuadras and Pereira, 1977
		Paguristes hummi	Wass, 1955			Mercando and Lytle, 1980
		Pagurus acadianus	Benedict, 1901			Grant and Pontier, 1973
		Pagurus annulipes	(Stimpson, 1859)			Mercando and Lytle, 1980
		Pagurus bernhardus	(Linnaeus, 1758)			Schijfsma, 1935
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
		Pagurus bernhardus	(Linnaeus, 1758)			Balss, 1924
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Christensen, 1967
		Pagurus bernhardus	(Linnaeus, 1758)			Cunningham et al., 1991
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus carolinensis	McLaughlin, 1975			Mercando and Lytle, 1980

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Cnidaria						
Hydractinia echinata*		*Pagurus cuanensis*	Bell, 1845			Samuelsen, 1970
		Pagurus excavatus	(Herbst, 1791)			Balss, 1924
		Pagurus longicarpus	Say, 1817			Mercando and Lytle, 1980
		Pagurus longicarpus	Say, 1817			Karlson and Cariolou, 1982
		Pagurus longicarpus	Say, 1817			Conover, 1979
		Pagurus longicarpus	Say, 1817			Buckley and Ebersole, 1994
		Pagurus longicarpus	Say, 1817			McFadden, 1986
		Pagurus longicarpus	Say, 1817			Fotheringham, 1976
		Pagurus longicarpus	Say, 1817			Conover, 1976
		Pagurus longicarpus	Say, 1817			Sandford, 2003
		Pagurus pollicaris	Say, 1817			Fotheringham, 1976
		Pagurus pollicaris	Say, 1817			Mercando and Lytle, 1980
		Pagurus pollicaris	Say, 1817			Conover, 1979
		Pagurus pollicaris	Say, 1817			Brooks and Mariscal, 1986b
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
		Pagurus pollicaris	Say, 1817			McLean, 1983
		Pagurus pollicaris	Say, 1817			Sandford, 2003
		Pagurus pubescens	Krøyer, 1838			Henderson, 1886
		Petrochirus diogenes	(Linnaeus, 1758)			Mercando and Lytle, 1980
Hydractinia epiconcha	Stechow, 1907	*Dardanus arrosor*	(Herbst, 1796)	F	EE	Dales, 1957
		Pagurus gracilipes	(Yokoya, 1933)			Dales, 1957
		unidentified				Green, 1961
		unidentified				Hirohito, 1988
Hydractinia granulata	Hirohito, 1988	unidentified		F	EE	Hirohito, 1988
Hydractinia polyclina	Agassiz, 1862	*Pagurus acadianus*	Benedict, 1901	F	EE	Cunningham et al., 1991
		Pagurus acadianus	Benedict, 1901			Folino and Yund, 1998
		Pagurus longicarpus	Say, 1817			Folino and Yund, 1998
Hydractinia serrata$^?$		*Pagurus aleuticus*	(Benedict, 1892)	F	EE	Cunningham et al., 1991
Hydractinia sodalis	Stimpson, 1858	*Pagurus constans*	(Stimpson, 1858)	O$^?$	EE	Goto, 1910
		unidentified				Hirohito, 1988
Hydractinia sp.		*Pagurus longicarpus*	Say, 1817	F	EE	McDermott, 2001
Hydractinia symbiolongicarpus	Buss and Yund, 1989	*Pagurus longicarpus*	Say, 1817	F	EE	Cunningham et al., 1991
		Pagurus longicarpus	Say, 1817			Buss and Yund, 1989
		Pagurus pollicaris	Say, 1817			Cunningham et al., 1991
Hydractinia symbiopollicaris	Buss and Yund, 1989	*Pagurus pollicaris*	Say, 1817	F	EE	Buss and Yund, 1989

Hydrocorella africana	Stechow, 1921	*Clibanarius* sp.		O	EE	Millard, 1975
		Dardanus arrosor	(Herbst, 1796)			Millard, 1975
		Diogenes brevirostris	Stimpson, 1858			Millard, 1975
		Diogenes brevirostris	Stimpson, 1858			Balss, 1924
		Diogenes costatus	Henderson, 1893			Millard, 1975
		Pagurus cuanensis	Bell, 1845			Millard, 1975
Janaria mirabilis	Stechow, 1921	*Manucomplanus cervicornis*	(Benedict, 1892)	O	EE	Cairns and Barnard, 1984
		Manucomplanus varians	(Benedict, 1892)			Cairns and Barnard, 1984
		Manucomplanus varians	(Benedict, 1892)			Bouvier, 1898
Mammillifera sp.?		*Paguropsis typica*	Henderson, 1888	O	C	Ross, 1983
Neoaiptasia commensali	Parulekar, 1969	*Clibanarius padavensis*	De Man, 1888	O?	EE	Parulekar, 1969
		Diogenes custos	(Fabricius, 1798)			Parulekar, 1969
Obelia dichotoma	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Obelia geniculata	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Palythoa (?) *eupaguri*	Marion, 1882	*Eupagurus jacobi*	A. Milne-Edwards, 1880	O?	EE	Marion, 1882; Ates, 2003
Paracalliactis lacazei	Dechancé and Dufaure, 1959	*Anapagurus laevis*	(Bell, 1845)	O	EE	Dechancé and Dufaure, 1959
Paracalliactis mediterranea	Ross and Zamponi, 1982	*Dardanus arrosor*	(Herbst, 1796)	O	EE	Ross and Zamponi, 1982
		Pagurus alatus	Fabricius, 1775			Ross and Zamponi, 1982
Paracalliactis michaelsarsi	Carlgren, 1928	*Parapagurus* sp.?		O?	EE	Carlgren, 1928
Paracalliactis japonica	Carlgren, 1928	*Dardanus arrosor*	(Herbst, 1796)	O?	EE	Carlgren, 1928
		unidentified				Pei, 1998
Paracalliactis rosea	Hand, 1975	*Diacanthurus rubricatus*	(Henderson, 1888)	F	EE	Hand, 1975a
		Lophopagurus (Lophopagurus) lacertosus	(Henderson, 1888)			Hand, 1975a
		Paguristes subpilosus	Henderson, 1888			Hand, 1975a
		Parapagurus dimorphus	(Studer, 1883)			Hand, 1975a
Paracalliactis sinica	Pei, 1982	unidentified		O?	EE	Pei, 1982
Paracalliactis stephensoni	Carlgren, 1928	*Parapagurus pilosimanus*	Smith, 1879	O?	EE	Carlgren, 1928
Paracalliactis valdiviae	Carlgren, 1928	*Oncopagurus bicristatus*	(A. Milne-Edwards, 1880)	O?	EE	Carlgren, 1928
		Sympagurus andersoni	(Henderson, 1896)			Carlgren, 1928
Paranthus rapiformis?	(Le Sueur, 1817)	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976
Perigonimus repens	(Wright, 1858)	*Pagurus bernhardus*	(Linnaeus, 1758)	F?	EE	Kramp, 1935
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
Perigonimus sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	F?	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Cnidaria						
Podocoryne americana	Mayer, 1910	unidentified		F	EE	Edwards, 1972
Podocoryne areolata	(Alder, 1862)	*Anapagurus laevis*	(Bell, 1845)	F	EE	Edwards, 1972
		Pagurus bernhardus	(Linnaeus, 1758)			Edwards, 1972
Podocoryne borealis	(Mayer, 1900)	*Anapagurus laevis*	(Bell, 1845)	F	EE	Edwards, 1972
		Pagurus bernhardus	(Linnaeus, 1758)			Edwards, 1972
Podocoryne carnea	Sars, 1846	*Anapagurus laevis*	(Bell, 1845)	F	EE	Edwards, 1972
		Dardanus arrosor	(Herbst, 1796)			Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Edwards, 1972
		Pagurus bernhardus	(Linnaeus, 1758)			Balss, 1924
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus longicarpus	Say, 1817			Cunningham et al., 1991
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus longicarpus	Say, 1817			McFadden, 1986
		Pagurus longicarpus	Say, 1817			Braverman, 1960
		Pagurus pollicaris	Say, 1817			McLean, 1983
		Pagurus prideaux	Leach, 1815			Edwards, 1972
		Pagurus pubescens	Krøyer, 1838			Balss, 1924
Podocoryne exigua	(Haeckel, 1880)	*Diogenes pugilator*	(Roux, 1828)	F	EE	Cerrano et al., 1998
		Paguristes eremita	(Linnaeus, 1767)			Bavestrello, 1985
Podocoryne hayamaensis	Hirohito, 1988	unidentified		F[?]	EE	Hirohito, 1988
Podocoryne selena	Mills, 1976	*Clibanarius vittatus*	(Bosc, 1802)	F	EE	Brooks and Mariscal, 1985b
		Pagurus longicarpus	Say, 1817			Mills, 1976a
		Pagurus longicarpus	Say, 1817			Brooks and Mariscal, 1985b
		Pagurus pollicaris	Say, 1817			Mills, 1976a
		Pagurus pollicaris	Say, 1817			Brooks and Mariscal, 1985b
		Pagurus pollicaris	Say, 1817			Brooks and Mariscal, 1986b
Podocoryne sp.		*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Matthews, 1959
Polyhydra calcarea	(Carter, 1877)	unidentified		O[?]	EE	Cairns and Barnard, 1984
Sagartiogeton undatus	(Muller, 1788)	*Pagurus excavatus*	(Herbst, 1791)	O[?]	EE	Chintiroglou et al., 1992
Sagartiomorphe guttata[?]		*Dardanus venosus*	(H. Milne Edwards, 1848)	O[?]	EE	Cutress and Ross, 1969
Sagartiomorphe paguri	(Verrill, 1869)	*Dardanus deformis*	(H. Milne Edwards, 1836)	O[?]	EE, C	Tudge, 1995
		Dardanus sp.				Cutress and Ross, 1969
		Diogenes edwardsii	(De Haan, 1849)			Cutress and Ross, 1969

Sagartiomorphe sp.		*Diogenes edwardsii*	(De Haan, 1849)	O[?]	C	Ross, 1983
scyphistoma		*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Stylactaria arge	(Clarke, 1882)	unidentified		I	EE	Bouillon et al., 1997
Stylactaria carcinicola	(Hiro, 1939)	unidentified		I	EE	Hirohito, 1988
Stylactaria hooperii	(Sigerfoos, 1899)	unidentified		F	EE	Bouillon et al., 1997
		unidentified				Hirohito, 1988
Stylactaria inabai	(Hirohito, 1988)	unidentified		O[?]	EE	Hirohito, 1988
Stylactaria pruvoti	(Motz-Kossovska, 1905)	*Clibanarius erythropus*	(Latreille, 1818)	F	EE	Bavestrello et al., 2000
Stylactaria sagamiensis	(Hirohito, 1988)	unidentified		F	EE	Bouillon et al., 1997
Stylactaria cf. sagamiensis	(Hirohito, 1988)	unidentified		F	EE	Hirohito, 1988
Stylactaria spiralis	(Goto, 1910)	*Pagurus constans*	(Stimpson, 1858)	O[?]	EE	Bouillon et al., 1997
		unidentified				Hirohito, 1988
Stylobates aeneus	Dall, 1903	*Sympagurus dofleini*	(Balss, 1912)	O	EE	Dunn et al., 1980
		unidentified				Dall, 1919
Stylobates cancrisocia	(Carlgren, 1928)	*Sympagurus trispinosus*	(Balss, 1911)	O	EE	Dunn et al., 1980
Stylobates loisetteae	Fautin, 1987	*Parapagurus* sp.		O	EE	Fautin, 1987
Verrillactis paguri[?]		*Catapaguroides fragilis*	(Melin, 1939)	O	EE	England, 1971
		Dardanus lagopodes	(Forskål, 1775)			England, 1971
		Dardanus pedunculatus	(Herbst, 1791)			England, 1971
		Micropagurus polynesiensis	(Nobili, 1906)			England, 1971
		Paguristes eremita	(Linnaeus, 1767)			Balss, 1924
Urticina consors	Verrill, 1882	*Parapagurus pilosimanus*	Smith, 1879	I	EE	Balss, 1924
		Sympagurus pictus	Smith, 1883			Balss, 1924
Zanklea sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I[?]	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
zoanthid		*Iridopagurus globulus*	García-Gómez, 1983	F[?]	EE	Ates, 2003
		Sympagurus dofleini	(Balss, 1912)	O[?]	C	Ates, 2003
Platyhelminthes						
Ectocotyla hirudo	(Levinsen, 1879)	*Pagurus pubescens*	Krøyer, 1838	F	FL	Hyman, 1944
		Pagurus pubescens	Krøyer, 1838			Fleming and Burt, 1978
		Parapagurus pilosimanus	Smith, 1879			Petrov, 2000
Emprosthopharynx opisthoporus	Bock, 1925	*Petrochirus californiensis*	Bouvier, 1895	F	FL	Bock, 1925
Emprosthopharynx rasae	Prudhoe, 1968	*Calcinus latens*	(Randall, 1840)	O[?]	FL	Prudhoe, 1968
Emprosthopharynx sp.		*Dardanus venosus*	(H. Milne Edwards, 1848)	F[?]	FL	Lytwyn, 1979
		Pagurus impressus	(Benedict, 1892)			Lytwyn, 1979
		Petrochirus diogenes	(Linnaeus, 1758)			Lytwyn, 1979
Euprosthiostomum adhaerens	Bock, 1925	*Petrochirus californiensis*	Bouvier, 1895	F[?]	FL	Bock, 1925

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Platyhelminthes						
Euprosthiostomum viscosum	Palombi, 1936	*Pagurus prideaux*	Leach, 1815	F$^?$	FL	Palombi, 1936
Leptoplana tremellaris	(Müller, 1774)	*Diogenes pugilator*	(Roux, 1828)	F$^?$	FL	Palombi, 1936
Macrostomum sp.		*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Jensen and Bender, 1973
Notoplana inquilina	Hyman, 1955	unidentified		F$^?$	FL	Hyman, 1955
Stylochoplana inquilina	Hyman, 1950	unidentified		F$^?$	FL	Hyman, 1950
Stylochus ellipticus	(Girard, 1850)	*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Stylochus pulcher	Hyman, 1940	*Petrochirus diogenes*	(Linnaeus, 1758)	F$^?$	FL	Hyman, 1940
		Petrochirus diogenes	(Linnaeus, 1758)			Lytwyn, 1979
Stylochus zebra	(Verrill, 1882)	*Clibanarius vittatus*	(Bosc, 1802)	F	FL	Pearse, 1947
		Dardanus venosus	(H. Milne Edwards, 1848)			Lytwyn, 1979
		Pagurus impressus	(Benedict, 1892)			Lytwyn and McDermott, 1976
		Pagurus impressus	(Benedict, 1892)			Lytwyn, 1979
		Pagurus longicarpus	Say, 1817			Lytwyn, 1979
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus pollicaris	Say, 1817			Fotheringham, 1976
		Pagurus pollicaris	Say, 1817			Lytwyn and McDermott, 1976
		Pagurus pollicaris	Say, 1817			Verrill, 1892
		Pagurus pollicaris	Say, 1817			Pearse, 1947
		Pagurus pollicaris	Say, 1817			Wass, 1972
		Pagurus pollicaris	Say, 1817			Lytwyn, 1979
		Petrochirus diogenes	(Linnaeus, 1758)			Lytwyn and McDermott, 1976
		Petrochirus diogenes	(Linnaeus, 1758)			Lytwyn, 1979
Thysanozoon brocchii	(Risso, 1818)	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
turbellarian		*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Nemertea						
nemertean		*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
nemertean a		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
nemertean b		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
nemertean c		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Tubulanus linearis	(McIntosh, 1874)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Jensen and Bender, 1973

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Rotifera

Proales paguri	Thane-Fenchel, 1966	*Pagurus bernhardus*	(Linnaeus, 1758)	O	C	Thane-Fenchel, 1966

Nematoda

Leptosomatum sp.		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	FL	Stachowitsch, 1980
Matthesonema eremitum	Sudhaus, 1986	*Coenobita* sp.		I[?]	FL	Sudhaus, 1986
nematode		*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Polygastrophora hexabulba	(Filipjev, 1918)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	FL	Stachowitsch, 1980
Thoracostoma figuratum	(Bastian, 1865)	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Thoracostuma sp.		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	FL	Stachowitsch, 1980

Polychaeta

Arctonoe vittata	(Grube, 1855)	*Labidochirus splendescens*	(Owen, 1839)	F	FL	Hoberg et al., 1982
		Pagurus capillatus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)			Hoberg et al., 1982
Arenicola marina[?]	Linnaeus, 1758	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Jensen and Bender, 1973
Autolytus sp.		*Pagurus longicarpus*	Say, 1817	I	FL	McDermott, 2001
Boccardia berkeleyorum	Blake and Woodwick, 1971	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F	En	Williams, 2001b
		Dardanus lagopodes	(Forskål, 1775)			Williams, 2001b
		unidentified				Blake and Evans, 1973
Boccardia columbiana	(E. Berkeley, 1927)	*Pagurus granosimanus*	(Stimpson, 1859)	F	En	Woodwick, 1963
		Pagurus samuelis	(Stimpson, 1857)			Woodwick, 1963
		unidentified				Blake and Evans, 1973
Boccardia proboscidea	(Hartman, 1940)	unidentified		F	En	Blake and Evans, 1973
Boccardia tricuspa	(Hartman, 1939)	*Pagurus granosimanus*	(Stimpson, 1859)	F	En	Woodwick, 1963
		Pagurus hirsutiusculus	(Dana, 1852)			Blake and Woodwick, 1971
		Pagurus samuelis	(Stimpson, 1857)			Woodwick, 1963
		unidentified				Blake and Evans, 1973
Boccardiella hamata	(Webster, 1879)	unidentified		F	En	Blake and Evans, 1973
		unidentified				Radashevsky, 1993
Carazziella reishi	(Woodwick, 1964)	*Ciliopagurus strigatus*	(Herbst, 1804)	F	En	Williams, 2001b
Cheilonereis cyclurus	(Harrington, 1897)	*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus brachiomastus	(Thallwitz, 1891)			Buzhinskaja, 1967
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Polychaeta						
Cheilonereis cyclurus		*Pagurus ochotensis*	Brandt, 1851			Harrington, 1897
		Pagurus ochotensis	Brandt, 1851			Clark, 1956
		Pagurus ochotensis	Brandt, 1851			Hickok and Davenport, 1957
		Pagurus ochotensis	Brandt, 1851			Moore, 1908
		Pagurus ochotensis	Brandt, 1851			Berkeley and Berkeley, 1948
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Buzhinskaja, 1967
		Pagurus ochotensis	Brandt, 1851			Wu et al., 1985
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus sp.				Okuda, 1950
Cheilonereis peristomialis	Benham, 1916	*Diacanthurus rubricatus*	(Henderson, 1888)	F	FL	Hand, 1975b
		Paguristes subpilosus	Henderson, 1888			Hand, 1975b
		Parapagurus dimorphus	(Studer, 1883)			Hand, 1975b
Circeis armoricana	(St-Joseph, 1894)	*Pagurus hirsutiusculus*	(Dana, 1852)	F	EE	Rzhavsky and Britayev, 1988
		Pagurus middendorffii	Brandt, 1851			Rzhavsky and Britayev, 1988
Circeis paguri	Knight-Jones and Knight-Jones, 1977	*Pagurus bernhardus*	(Linnaeus, 1758)	O	EI, C	Al-Ogily and Knight-Jones, 1981
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Circeis spirillum	(Linnaeus, 1758)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
		Pagurus prideaux	Leach, 1815			Samuelsen, 1970
Crucigera zygophora	(Johnson, 1901)	*Elassochirus cavimanus*	(Miers, 1879)	I	EE	Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
Dipolydora alborectalis	(Radashevsky, 1993)	unidentified		F	En	Radashevsky, 1993
Dipolydora armata	(Langerhans, 1880)	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F	En	Williams, 2001b
		Calcinus latens	(Randall, 1840)			Williams, 2001b
		Calcinus minutus	Buitendijk, 1937			Williams, 2001b
		Calcinus pulcher	Forest, 1958			Williams, 2001b
		Calcinus tubularis	(Linnaeus, 1767)			Bick, 2001
		Ciliopagurus strigatus	(Herbst, 1804)			Williams, 2001b
		Clibanarius englaucus	Ball and Haig, 1972			Williams, 2001b
		Clibanarius erythropus	(Latreille, 1818)			Bick, 2001

		Dardanus lagopodes	(Forskål, 1775)		Williams, 2001b
		Paguristes runyanae	Haig and Ball, 1988		Williams, 2001b
		unidentified			Sato-Okoshi, 1999
Dipolydora bidentata	(Zachs, 1933)	*Pagurus granosimanus*	(Stimpson, 1859)	F En	Blake and Woodwick, 1971
		Pagurus samuelis	(Stimpson, 1857)		Blake and Woodwick, 1971
		unidentified			Radashevsky, 1993
Dipolydora commensalis	(Andrews, 1891)	*Clibanarius vittatus*	(Bosc, 1802)	O En	Dauer, 1991
		Elassochirus cavimanus	(Miers, 1879)		Hoberg et al., 1982
		Labidochirus splendescens	(Owen, 1839)		Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)		Hoberg et al., 1982
		Pagurus annulipes	(Stimpson, 1859)		Dauer, 1991
		Pagurus brachiomastus	(Thallwitz, 1891)		Radashevsky, 1989
		Pagurus capillatus	(Benedict, 1892)		Radashevsky, 1989
		Pagurus capillatus	(Benedict, 1892)		Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)		Hoberg et al., 1982
		Pagurus granosimanus	(Stimpson, 1859)		Hatfield, 1965
		Pagurus longicarpus	Say, 1817		Blake, 1971
		Pagurus longicarpus	Say, 1817		Andrews, 1891
		Pagurus longicarpus	Say, 1817		Hatfield, 1965
		Pagurus longicarpus	Say, 1817		Williams and McDermott, 1997
		Pagurus longicarpus	Say, 1817		Dauer, 1991
		Pagurus longicarpus	Say, 1817		Buckley and Ebersole, 1994
		Pagurus longicarpus	Say, 1817		McDermott, 2001
		Pagurus middendorffii	Brandt, 1851		Radashevsky, 1989
		Pagurus ochotensis	Brandt, 1851		Hoberg et al., 1982
		Pagurus pollicaris	Say, 1817		Fotheringham, 1976
		Pagurus pollicaris	Say, 1817		Dauer, 1991
		Pagurus pollicaris	Say, 1817		Berkeley and Berkeley, 1956
		Pagurus samuelis	(Stimpson, 1857)		Blake, 1969
		Pagurus samuelis	(Stimpson, 1857)		Woodwick, 1963
		Pagurus setosus	(Benedict, 1892)		Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)		Hoberg et al., 1982
Dipolydora concharum	(Verrill, 1879)	unidentified		F En	Radashevsky, 1993
Dipolydora elegantissima	(Blake and Woodwick, 1972)	*Pagurus granosimanus*	(Stimpson, 1859)	F En	Blake and Woodwick, 1971
Dipolydora socialis	(Schmarda, 1861)	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F En	Williams, 2001b
		Calcinus minutus	Buitendijk, 1937		Williams, 2001b
		Dardanus lagopodes	(Forskål, 1775)		Williams, 2001b

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Polychaeta						
Dipolydora socialis		*Paguristes runyanae*	Haig and Ball, 1988			Williams, 2001b
		Pagurus brachiomastus	(Thallwitz, 1891)			Radashevsky, 1993
Dipolydora tridenticulata	(Woodwick, 1964)	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F	En	Williams, 2001b
		Calcinus latens	(Randall, 1840)			Williams, 2001b
		Calcinus minutus	Buitendijk, 1937			Williams, 2001b
		Dardanus lagopodes	(Forskål, 1775)			Williams, 2001b
Dodecaceria concharum	Oersted, 1843	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F	En	Williams, unpublished data
		Dardanus arrosor	(Herbst, 1796)			Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Eulalia bilineata	(Johnston, 1840)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	FL	Jensen and Bender, 1973
Eulalia viridis	(Linnaeus, 1767)	*Pagurus cuanensis*	Bell, 1845	F	FL	Samuelsen, 1970
Eumida sp.		*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Eunice harassii	Audouin and Milne Edwards, 1833	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Eunice sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Eunice tentaculata	Quatrefages, 1865	unidentified		I	FL	Taylor, 1991
Eunicidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Eunoe depressa	Moore, 1905	*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Labidochirus splendescens	(Owen, 1839)			Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus capillatus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus rathbuni	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)			Hoberg et al., 1982
		unidentified				Moore, 1908
Eunoe nodosa	(Sars, 1861)	*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
Eunoe senta	(Moore, 1902)	*Labidochirus splendescens*	(Owen, 1839)	F	FL	Hoberg et al., 1982

		Pagurus capillatus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)			Hoberg et al., 1982
Eupolymnia nebulosa	(Montagu, 1818)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Eusyllis blomstrandi	Malmgren, 1867	*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Labidochirus splendescens	(Owen, 1839)			Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus capillatus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)			Hoberg et al., 1982
Exogone naidina	Oersted, 1845	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Jensen and Bender, 1973
Fabricia sabella	(Ehrenberg, 1837)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Filograna sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Gattyana ciliata	Moore, 1902	*Labidochirus splendescens*	(Owen, 1839)	F	FL	Hoberg et al., 1982
		Pagurus capillatus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus rathbuni	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)			Hoberg et al., 1982
Gattyana cirrosa	(Pallas, 1766)	*Pagurus bernhardus*	(Linnaeus, 1758)	I[?]	FL	Reiss et al., 2003
Gaudichaudius cimex	(Quatrefages, 1866)	*Clibanarius padavensis*	De Man, 1888	O	FL	Parulekar, 1969
		Diogenes alias	McLaughlin and Holthius, 2001			Achari, 1977
		Diogenes alias	McLaughlin and Holthius, 2001			Pettibone, 1986
		Diogenes custos	(Fabricius, 1798)			Achari, 1977
		Diogenes custos	(Fabricius, 1798)			Pettibone, 1986
		Diogenes custos	(Fabricius, 1798)			Parulekar, 1969
Grubea limbata[?]	Quatrefages	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Halosydna brevisetosa	Kinberg, 1855	*Paguristes bakeri*	Holmes, 1900	F	FL	Clark, 1956
Harmothoe coeliaca[?]	Saint-Joseph	*Pagurus bernhardus*	(Linnaeus, 1758)	F	FL	Dales, 1957
Harmothoe fraserthomsoni	McIntosh, 1897	*Pagurus bernhardus*	(Linnaeus, 1758)	I[?]	FL	Reiss et al., 2003
Harmothoe imbricata	Kinberg, 1855	*Pagurus ochotensis*	Brandt, 1851	F	FL	Pettibone, 1963
Hydroides dianthus	(Verrill, 1873)	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Pearse, 1947
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Hydroides norvegica	Gunnerus, 1768	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	I	EE	Samuelsen, 1970

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Polychaeta						
Hydroides norvegica		*Pagurus bernhardus*	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
		Pagurus prideaux	Leach, 1815			Samuelsen, 1970
Hydroides plateni	(Kinberg, 1867)	unidentified		I	EE	Creed, 2000
Hydroides pseudouncinata?		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Hydroides sp.		*Paguristes puncticeps*	Benedict, 1901	I	EE	Pearse, 1932
		Petrochirus granulatus	(Olivier, 1811)			Pearse, 1932
Iphitime cuenoti	Fauvel, 1914	*Pagurus* sp.		F	C	Fage and Legendre, 1925
		Pagurus sp.				Hartman, 1952
Iphitime paguri	Fage and Legendre, 1933	*Pagurus bernhardus*	(Linnaeus, 1758)	O	C	Fage and Legendre, 1933
		Pagurus bernhardus	(Linnaeus, 1758)			Moore and Gorzula, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Hartman, 1952
		Pagurus bernhardus	(Linnaeus, 1758)			Comely and Ansell, 1989
		Pagurus prideaux	Leach, 1815			Comely and Ansell, 1989
		Pagurus prideaux	Leach, 1815			Spooner et al., 1957
		Pagurus prideaux	Leach, 1815			Samuelsen, 1970
Janua pagenstecheri	(Quatrefages, 1865)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Lagisca extenuata	(Grube, 1840)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	FL	Brightwell, 1953
Lanassa venusta venusta	(Malmgren, 1874)	*Elassochirus cavimanus*	(Miers, 1879)	I	EE	Hoberg et al., 1982
		Pagurus capillatus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus rathbuni	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus trigonocheirus	(Stimpson, 1859)			Hoberg et al., 1982
Lepidametria commensalis	Webster, 1879	*Pagurus pollicaris*	Say, 1817	I	FL	McLean, 1983
Lepidonotus squamatus?	(Linnaeus, 1767)	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
		Discorsopagurus schmitti	(Stevens, 1925)			Caine, 1980
Lepidonotus sublevis	Verrill, 1873	*Clibanarius vittatus*	(Bosc, 1802)	F	FL	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Gardiner, 1976
		Clibanarius vittatus	(Bosc, 1802)			Dauer, 1991
		Pagurus annulipes	(Stimpson, 1859)			Dauer, 1991
		Pagurus impressus	(Benedict, 1892)			Gardiner, 1976

		Pagurus longicarpus	Say, 1817			Dauer, 1991
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus pollicaris	Say, 1817			Fotheringham, 1976
		Pagurus pollicaris	Say, 1817			Pettibone, 1963
		Pagurus pollicaris	Say, 1817			Gardiner, 1976
		Pagurus pollicaris	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Leptonereis glauca[?]		*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Neanthes acuminata	(Ehlers, 1968)	*Clibanarius vittatus*	(Bosc, 1802)	F	FL	Gardiner, 1976
Neanthes caudata	(Delle Chiaje, 1828)	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
		Dardanus arrosor	(Herbst, 1796)			Cuadras and Pereira, 1977
Neanthes fucata	(Savigny, 1818)	*Anapagurus laevis*	(Bell, 1845)	O	FL	Spooner et al., 1957
		Pagurus alatus	Fabricius, 1775			Gilpin-Brown, 1969
		Pagurus bernhardus	(Linnaeus, 1758)			Spooner et al., 1957
		Pagurus bernhardus	(Linnaeus, 1758)			Brightwell, 1951
		Pagurus bernhardus	(Linnaeus, 1758)			Goerke, 1971
		Pagurus bernhardus	(Linnaeus, 1758)			Rabaud, 1939
		Pagurus bernhardus	(Linnaeus, 1758)			Malaquin, 1890
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
		Pagurus bernhardus	(Linnaeus, 1758)			Coupin, 1894
		Pagurus bernhardus	(Linnaeus, 1758)			Comely and Ansell, 1989
		Pagurus bernhardus	(Linnaeus, 1758)			Matthews, 1959
		Pagurus bernhardus	(Linnaeus, 1758)			Clark, 1956
		Pagurus bernhardus	(Linnaeus, 1758)			Gilpin-Brown, 1969
		Pagurus bernhardus	(Linnaeus, 1758)			Chevreux, 1908
		Pagurus bernhardus	(Linnaeus, 1758)			Balss, 1924
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus cuanensis	Bell, 1845			Spooner et al., 1957
		Pagurus prideaux	Leach, 1815			Spooner et al., 1957
		Pagurus prideaux	Leach, 1815			Clark, 1956
Neanthes succinea	(Frey and Leuckart, 1847)	*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Dauer, 1991
		Pagurus annulipes	(Stimpson, 1859)			Dauer, 1991
		Pagurus longicarpus	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			Dauer, 1991
Nereidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Nereimyra punctata	(Müller, 1788)	*Pagurus cuanensis*	Bell, 1845	F	FL	Samuelsen, 1970

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Polychaeta						
Nereis pelagica	Linnaeus, 1758	*Pagurus cuanensis*	Bell, 1845	I	FL	Samuelsen, 1970
		Pagurus longicarpus	Say, 1817			Conover, 1979
		Pagurus pollicaris	Say, 1817			Conover, 1979
Paralaeospira levinseni	Caullery and Mesnil, 1897	*Pagurus villosus*	Nicolet, 1849	I	EE	Quezada and López, 1979
Pholoe inornata	Johnston, 1839	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Podarke pugettensis	Johnson, 1901	unidentified		I	FL	Berkeley and Berkeley, 1948
Polycirrus denticulatus	Saint-Joseph, 1894	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Polycirrus eximus	(Leidy, 1855)	*Pagurus longicarpus*	Say, 1817	I	FL	McDermott, 2001
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Polydora bioccipitalis	Blake and Woodwick, 1972	*Pagurus hirsutiusculus*	(Dana, 1852)	F	En	Blake and Woodwick, 1971
Polydora ciliata	(Johnston, 1838)	*Dardanus arrosor*	(Herbst, 1796)	F	En	Cuadras and Pereira, 1977
		Diogenes pugilator	(Roux, 1828)			Codreanu and Mack-Fira, 1961
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus samuelis	(Stimpson, 1857)			Woodwick, 1963
Polydora cornuta	Bosc, 1802	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Dauer, 1991
		Pagurus annulipes	(Stimpson, 1859)			Dauer, 1991
		Pagurus longicarpus	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			Dauer, 1991
Polydora limicola[?]	Annenkova, 1934	*Pagurus samuelis*	(Stimpson, 1857)	I	En	Woodwick, 1963
Polydora mabinii	Williams, 2001	*Calcinus latens*	(Randall, 1840)	F	En	Williams, 2001b
Polydora maculata	Day, 1963	unidentified		F	En	Day, 1963
Polydora neocaeca	Williams and Radashevsky, 1999	*Pagurus longicarpus*	Say, 1817	F	En	Williams and Radashevsky, 1999
Polydora pygidialis	Blake and Woodwick, 1972	*Pagurus granosimanus*	(Stimpson, 1859)	F	En	Blake and Woodwick, 1971
Polydora robi	Williams, 2000	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	O	En	Williams, 2000
		Calcinus latens	(Randall, 1840)			Williams, 2000
		Calcinus minutus	Buitendijk, 1937			Williams, 2000
		Calcinus pulcher	Forest, 1958			Williams, 2000
		Ciliopagurus strigatus	(Herbst, 1804)			Williams, 2001b
		Clibanarius cruentatus	(H. Milne Edwards, 1848)			Williams, 2000
		Clibanarius sp.				Williams, 2000
		Dardanus lagopodes	(Forskål, 1775)			Williams, 2001b
		Dardanus woodmasoni	(Alcock, 1905)			Williams, 2000
		Dardanus sp.				Williams, 2000
		Diogenes sp.				Williams, 2000

		Paguristes runyanae	Haig and Ball, 1988			Williams, 2001b
Polydora sp.		*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F	En	Williams, 2001b
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
		Pagurus granosimanus	(Stimpson, 1859)			Walker, 1988
		Pagurus prideaux	Leach, 1815			Samuelsen, 1970
		Pagurus longicarpus and/or	Say, 1817			Frey, 1987
		P. pollicaris				
		Pagurus samuelis	(Stimpson, 1857)			Walker and Carlton, 1995
		unidentified				Sato-Okoshi, 1999
		unidentified				Smyth, 1989, 1990
Polydora umangivora	Williams, 2001	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	F	En	Williams, 2001b
		Dardanus lagopodes	(Forskål, 1775)			Williams, 2001b
		Paguristes runyanae	Haig and Ball, 1988			Williams, 2001b
Polydora websteri	Hartman, 1943	*Clibanarius vittatus*	(Bosc, 1802)	F	En	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Dauer, 1991
		Pagurus annulipes	(Stimpson, 1859)			Dauer, 1991
		Pagurus longicarpus	Say, 1817			Buckley and Ebersole, 1994
		Pagurus longicarpus	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			Dauer, 1991
		unidentified				Blake, 1971
		unidentified				Sato-Okoshi, 1999
Polynoidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	F	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Pomatoceros sp.		*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE, EI	Jackson, 1913
Pomatoceros triqueter	(Linnaeus, 1767)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	F	EE	Samuelsen, 1970
		Dardanus arrosor	(Herbst, 1796)			Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Potamilla reniformis	(Müller, 1771)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	En	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Polychaeta						
Protula sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Protula tubularia	(Montagu, 1803)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Sabellaria vulgaris	(Verrill, 1873)	*Pagurus longicarpus*	Say, 1817	I	EE	McDermott, 2001
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Serpula concharum	Langerhans, 1880	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Serpula sp.		*Dardanus arrosor*	(Herbst, 1796)	I	EE	Fenizia, 1934
Serpula vermicularis	Linnaeus, 1767	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
Serpulidae		*Paguristes eremita*	(Linnaeus, 1767)	I	EE	Caruso et al., 2003
		Pagurus prideaux	Leach, 1815			Caruso et al., 2003
Sphaerodorum gracilis	Rathke, 1843	*Pagurus cuanensis*	Bell, 1845	I	FL	Samuelsen, 1970
Sphaerosyllis sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Spirorbis borealis	Daudin, 1800	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Samuelsen, 1970
Spirorbis cuneatus	Gee, 1964	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Spirorbis pagenstecheri[?]		*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Samuelsen, 1970
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Spirorbis sp.		*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Augener, 1926
		Pagurus granosimanus	(Stimpson, 1859)			Walker, 1988
		Pagurus prideaux	Leach, 1815			Augener, 1926
		Pagurus samuelis	(Stimpson, 1857)			Walker and Carlton, 1995
		Petrochirus granulatus	(Olivier, 1811)			Pearse, 1932
Spirorbis spirorbis	(Linnaeus, 1758)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Eliason, 1962
Spirorbis tridentatus	Levinsen, 1883	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	F	EE	Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Spirorbis vitreus[?]		*Pagurus cuanensis*	Bell, 1845	F	EE	Samuelsen, 1970
Syllis armillaris	(Müller, 1776)	unidentified		F	FL	Martin and Britayev, 1998
Syllis cf. armillaris	(Müller, 1776)	*Paragiopagurus boletifer*	De Saint-Laurent, 1972	F	FL	López et al., 2001
		Paguristes sp.				López et al., 2001
Syllis cornuta	(Rathke, 1843)	unidentified		F	FL	Fauvel, 1923
Syllis ferrani	Alós and San Martín, 1987	*Pagurus excavatus*	(Herbst, 1791)	F	FL	López et al., 2001

Syllis gracilis	Grube, 1840	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Syllis hyalina	Grube, 1863	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Syllis pontxioi	San Martín and López, 2000	*Clibanarius* sp.		F	FL	López et al., 2001
		Paguristes sp.				López et al., 2001
Terebella lapidaria	Linnaeus, 1767	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Tripolydora spinosa	Woodwick, 1964	*Calcinus latens*	(Randall, 1840)	I	En	Williams, 2001b
Trypanosyllis zebra	(Grube, 1860)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Vermilopsis infundibulum[?]		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Sipuncula						
Aspidosiphon mülleri[?]		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Phascolosoma annulatum	Hutton, 1879	unidentified		I	FL	Taylor, 1991
Cirripedia						
Balanus amphitrite	Darwin, 1854	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus longicarpus	Say, 1817			Conover, 1979
		Pagurus longicarpus	Say, 1817			Conover, 1976
		Pagurus pollicaris	Say, 1817			Conover, 1979
		Pagurus pollicaris	Say, 1817			Conover, 1979
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Balanus crenatus	Burgiére, 1789	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus granosimanus	(Stimpson, 1859)			Walker, 1988
Balanus eburneus	Gould, 1841	*Pagurus longicarpus*	Say, 1817	I	EE	McDermott, 2001
		Pagurus pollicaris	Say, 1817			McLean, 1983
Balanus improvisus	Darwin, 1854	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus longicarpus	Say, 1817			McDermott, 2001
Balanus laevis	Burgière, 1789	*Pagurus villosus*	Nicolet, 1849	I	EE	Quezada and López, 1979
Balanus perforatus[?]		*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Balanus sp.		*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Cirripedia						
		Pagurus longicarpus	Say, 1817			Karlson and Cariolou, 1982
		Pagurus longicarpus and/or *P. pollicaris*	Say, 1817			Frey, 1987
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
Balanus venustus	(Darwin, 1854)	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Pearse, 1947
Chirona hameri	(Ascanius, 1767)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Chthamalus fissus	Darwin, 1854	*Pagurus samuelis*	(Stimpson, 1857)	I	EE	Walker and Carlton, 1995
Chthamalus sp.		*Pagurus longicarpus* and/or *P. pollicaris*	Say, 1817	I	EE	Frey, 1987
		Pagurus pollicaris	Say, 1817			McLean, 1983
Cryptophialus zulloi[?]		unidentified		F	En	Smyth, 1989, 1990
Cryptophialus coronophorus[?]		unidentified		F	En	Smyth, 1989, 1990
Heteralepas quadrata	(Aurivillius, 1894)	unidentified		I	EE	Zullo, 1991
Koleolepas avis	(Hiro, 1931)	*Dardanus arrosor*	(Herbst, 1796)	O	HS	Yusa et al., 2001
		unidentified				Hiro, 1931
Koleolepas tinkeri	Edmondson, 1951	unidentified		O	HS	Edmondson, 1951
Koleolepas willeyi	Stebbing, 1900	unidentified		O	HS[?]	Stebbing, 1900
Lithoglyptes mitis	(Tomlinson, 1969)	unidentified		F	En	Smyth, 1989, 1990
Lithoglyptes habei	(Tomlinson, 1963)	unidentified		F	En	Tomlinson, 1969a
Lithoglyptes ivanovi	Kolbasov, 1998	unidentified		F	En	Kolbasov, 1998
Pagurolepas conchicola	Stubbings, 1940	*Dardanus aspersus*	(Berthold, 1836)	O	EI	Utinomi, 1970
		Sympagurus andersoni	(Henderson, 1896)			Stubbings, 1940
Pagurolepas conchicola atlantica	Keeley and Newman, 1974	*Tomopagurus cokeri*	(Hay, 1917)	O	EI	Keeley and Newman, 1974
Semibalanus balanoides	(Linnaeus, 1767)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Tomlinsonia asymetrica	Turquier and Carton, 1976	*Calcinus latens*	(Randall, 1840)	O	En	Turquier and Carton, 1976
Trypetesa habei	Utinomi, 1962	unidentified		O	En	Tomlinson, 1969a
		unidentified				Utinomi, 1962
Trypetesa lampas	Hancock, 1849	*Dardanus arrosor*	(Herbst, 1796)	O	En	Cuadras and Pereira, 1977
		Pagurus bernhardus	(Linnaeus, 1758)			Hagerman, 1965
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			White, 1969
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus cuanensis	Bell, 1845			White, 1969
		Pagurus longicarpus	Say, 1817			McDermott, 2001

		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
		unidentified				Tomlinson, 1969a
Trypetesa lateralis	Tomlinson, 1953	unidentified		O	En	Tomlinson, 1953
		unidentified				Tomlinson, 1955
		unidentified				Tomlinson, 1969a
Trypetesa nassarioides	Turquier, 1967	*Anapagurus hyndmanni*	(Bell, 1845)	O	En	Turquier, 1967
		Pagurus bernhardus	(Linnaeus, 1758)			Turquier, 1967
		Pagurus cuanensis	Bell, 1845			Turquier, 1967
Trypetesa spinulosa	Turquier, 1976	unidentified		O	En	Turquier, 1976
Verruca stroemia	O.F. Müller, 1776	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Copepoda						
Brianola elegans	Hamond, 1973	*Diogenes senex*	Heller, 1865	F	FL	Hamond, 1973
Brianola pori	Hamond, 1973	*Diogenes senex*	Heller, 1865	F	FL	Hamond, 1973
Brianola sydneyensis	Hamond, 1973	*Diogenes senex*	Heller, 1865	F	FL	Hamond, 1973
Calanidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Cyclopoidea a		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Cyclopoidea b		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Diosaccidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Hemicyclops geminatus	Stock, 1992	*Calcinus tibicen*	(Herbst, 1791)	O	FL	Stock, 1992
		Dardanus venosus	(H. Milne Edwards, 1848)			Stock, 1992
		Paguristes grayi	Benedict, 1901			Stock, 1992
Hemicyclops vicinalis	Humes, 1995	*Dardanus guttatus*	(Olivier, 1811)	O	FL	Humes, 1995
Laophontidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Mesnilia sp.		*Pagurus minutus*	Hess, 1865	F	HS	Williams, unpublished data
Paraidya minor	Sewell, 1940	*Dardanus guttatus*	(Olivier, 1811)	O	FL	Humes, 1981
		Dardanus lagopodes	(Forskål, 1775)			Humes, 1981
		Dardanus megistos	(Herbst, 1804)			Humes, 1981
Paraidya major	Sewell, 1940	*Dardanus guttatus*	(Olivier, 1811)	O	FL	Humes, 1981
		Dardanus lagopodes	(Forskål, 1775)			Humes, 1981
		Dardanus megistos	(Herbst, 1804)			Humes, 1981

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Copepoda						
Paraidya occulta	Humes and Ho, 1969	*Dardanus guttatus*	(Olivier, 1811)	O	FL	Humes and Ho, 1969b
		Dardanus megistos	(Herbst, 1804)			Humes and Ho, 1969b
Porcellidium brevicaudatum	Thompson and Scott, 1903	*Calcinus latens*	(Randall, 1840)	O$^?$	FL	Humes, 1972
		Calcinus latens	(Randall, 1840)			Humes, 1981
		Calcinus minutus	Buitendijk, 1937			Humes, 1972
		Calcinus minutus	Buitendijk, 1937			Humes, 1981
		Ciliopagurus strigatus	(Herbst, 1804)			Humes, 1972, 1981
		Clibanarius virescens	(Krauss, 1843)			Humes, 1972
		Dardanus deformis	(H. Milne Edwards, 1836)			Humes, 1972
		Dardanus guttatus	(Olivier, 1811)			Humes and Ho, 1969b
		Dardanus guttatus	(Olivier, 1811)			Humes, 1981
		Dardanus impressus	(De Haan, 1849)			Kim and Kim, 1996
		Dardanus lagopodes	(Forskål, 1775)			Humes and Ho, 1969b
		Dardanus lagopodes	(Forskål, 1775)			Humes, 1981
		Dardanus megistos	(Herbst, 1804)			Humes and Ho, 1969b
		Dardanus megistos	(Herbst, 1804)			Humes, 1981
		Dardanus scutellatus	(H. Milne Edwards, 1848)			Humes, 1972
		Pagurus sp.				Humes, 1972
Porcellidium paguri	Ho, 1986	*Clibanarius bimaculatus*	(De Haan, 1849)	O	FL	Ho, 1986
		Pagurus filholi	(De Man, 1887)			Ho, 1986
		Pagurus japonicus	(Stimpson, 1859)			Ho, 1986
Porcellidium similis	Kim and Kim, 1996	*Pagurus similis*	(Ortmann, 1892)	O	FL	Kim and Kim, 1996
Porcellidium sp.		*Calcinus gaimardii*	(H. Milne Edwards, 1848)	O	FL	Williams, unpublished data
Porcellidium tapui	Hicks and Webber, 1983	*Diacanthurus rubricatus*	(Henderson, 1888)	O	FL	Hicks and Webber, 1983
		Diacanthurus spinulimanus	(Miers, 1876)			Hicks and Webber, 1983
		Lophopagurus (Australeremus) cooki	(Filhol, 1883)			Hicks and Webber, 1983
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Hicks and Webber, 1983
		Lophopagurus (Lophopagurus) thompsoni	(Filhol, 1885)			Hicks and Webber, 1983
		Paguristes barbatus	(Ortmann, 1892)			Hicks and Webber, 1983
		Paguristes cf. *setosus*	(H. Milne Edwards, 1848)			Hicks and Webber, 1983
		Paguristes pilosus	(H. Milne Edwards, 1836)			Hicks and Webber, 1983
		Pagurus novizealandiae	(Dana, 1851)			Hicks and Webber, 1983
		Pagurus sp.				Hicks and Webber, 1983

		Pagurus traversi	(Filhol, 1883)			Hicks and Webber, 1983
		Pylopagurus cf. *crenatus*	(Borradaile, 1916)			Hicks and Webber, 1983
		Pylopagurus sp.				Hicks and Webber, 1983
Sunaristes dardani	Humes and Ho, 1969	*Calcinus elegans*	(H. Milne Edwards, 1836)	O	FL	Humes and Ho, 1969a
		Calcinus latens	(Randall, 1840)			Humes, 1972
		Clibanarius virescens	(Krauss, 1843)			Humes, 1972
		Dardanus deformis	(H. Milne Edwards, 1836)			Humes and Ho, 1969a
		Dardanus guttatus	(Olivier, 1811)			Humes and Ho, 1969a
		Dardanus lagopodes	(Forskål, 1775)			Humes and Ho, 1969a
		Dardanus megistos	(Herbst, 1804)			Humes and Ho, 1969a
		Dardanus scutellatus	(H. Milne Edwards, 1848)			Humes, 1971
		Dardanus setifer	(H. Milne Edwards, 1836)			Humes and Ho, 1969a
Sunaristes inaequalis	Humes and Ho, 1969	*Calcinus latens*	(Randall, 1840)	O	FL	Humes, 1972
		Clibanarius carnifex	Heller, 1861			Humes and Ho, 1969a
		Clibanarius virescens	(Krauss, 1843)			Humes, 1972
		Dardanus megistos	(Herbst, 1804)			Humes and Ho, 1969a
		Dardanus scutellatus	(H. Milne Edwards, 1848)			Humes, 1972
Sunaristes japonicus	Ho, 1986	*Clibanarius bimaculatus*	(De Haan, 1849)	O	FL	Ho, 1986
		Pagurus filholi	(De Man, 1887)			Ho, 1986
		Pagurus japonicus	(Stimpson, 1859)			Ho, 1986
		Pagurus similis	(Ortmann, 1892)			Ho, 1986
Sunaristes paguri	Hesse, 1867	*Clibanarius erythropus*	(Latreille, 1818)	O	FL	Stock, 1960
		Diogenes pugilator	(Roux, 1828)			Hamond, 1973
		Diogenes pugilator	(Roux, 1828)			Codreanu and Mack-Fira, 1961
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Chevreux, 1908
		Pagurus bernhardus	(Linnaeus, 1758)			Lang, 1948
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973
		Pagurus cuanensis	Bell, 1845			Hamond, 1973
Sunaristes sp.		*Calcinus gaimardii*	(H. Milne Edwards, 1848)	O	FL	Williams, unpublished data
		Pagurus novizealandiae	(Dana, 1851)			Hamond, 1973
Sunaristes tranteri	Hamond, 1973	*Calcinus gaimardii*	(H. Milne Edwards, 1848)	O	FL	Humes, 1981
		Calcinus latens	(Randall, 1840)			Humes, 1981
		Calcinus minutus	Buitendijk, 1937			Humes, 1981
		Calcinus sp.				Humes, 1981
		Ciliopagurus strigatus	(Herbst, 1804)			Humes, 1981
		Dardanus guttatus	(Olivier, 1811)			Humes, 1981

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Copepoda						
		Dardanus lagopodes	(Forskål, 1775)			Humes, 1981
		Diogenes senex	Heller, 1865			Hamond, 1973
Tachidiidae		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Thalestris gibba	Krøyer, 1845	*Pagurus cuanensis*	Bell, 1845	I	FL	Samuelsen, 1970
Stomatopoda						
Gonodactylus sp.		*Dardanus lagopodes*	(Forskål, 1775)	I	FL	Vannini et al., 1993
Mesacturoides fimbriatus	(Lenz, 1905)	*Dardanus lagopodes*	(Forskål, 1775)	I	FL	Vannini et al., 1993
Mysida						
Gnathomysis gerlachei	Bonnier and Pérez, 1902	*Sympagurus brevipes*	(De Saint-Laurent, 1972)	O	FL	Bonnier and Pérez, 1902
Heteromysis harpax	Hilgendorf, 1879	*Dardanus deformis*	(H. Milne Edwards, 1836)	O	FL	Vannini et al., 1993
		Dardanus deformis	(H. Milne Edwards, 1836)			Tattersall, 1962
		Dardanus gemmatus	(H. Milne Edwards, 1848)			Tattersall, 1962
		Dardanus guttatus	(Olivier, 1811)			Vannini et al., 1993
		Dardanus lagopodes	(Forskål, 1775)			Vannini et al., 1993
		Dardanus lagopodes	(Forskål, 1775)			Tattersall, 1962
		Dardanus megistos	(Herbst, 1804)			Vannini et al., 1993
		Dardanus megistos	(Herbst, 1804)			Tattersall, 1962
		Dardanus scutellatus	(H. Milne Edwards, 1848)			Vannini et al., 1993
		Dardanus sp.				Vannini et al., 1993
Heteromysis harpaxoides	Bacescu and Bruce, 1980	*Dardanus megistos*	(Herbst, 1804)	O	FL	Bacescu and Bruce, 1980
Heteromysis odontops	Walker, 1898	unidentified		O	FL	Tattersall, 1962
Heteromysis sp.		*Dardanus calidus*	(Risso, 1826)	O	FL	Wittmann and Wirtz, 1998
Heteromysis stellata	Bacescu and Bruce, 1980	*Aniculus* sp.		O	FL	Bacescu and Bruce, 1980
Amphipoda						
Abdulomelita obtusata	(Montagu, 1813)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	FL	Chevreux, 1908
		Pagurus bernhardus	(Linnaeus, 1758)			Stephensen, 1928
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Aora gracilis	(Bate, 1857)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Aora typica	Krøyer, 1845	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Chevreux, 1908
		Pagurus bernhardus	(Linnaeus, 1758)			Stephensen, 1928
Aristias neglectus	Hansen, 1887	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	HS	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			

Atylus swammerdami	(H. Milne-Edwards, 1830)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Colomastix pusilla	Grube, 1861	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	HS	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Corophium bonnelli	(Milne Edwards, 1830)	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	I	FL	Samuelsen, 1970
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
		unidentified				Vader, 1971
Corophium crassicorne	Bruzelius, 1859	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Corophium sextonae	Crawford, 1937	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Turquier, 1965
Corophium sp.		*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Dauer, 1991
		Pagurus annulipes	(Stimpson, 1859)			Dauer, 1991
		Pagurus longicarpus	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Ericthonius brasiliensis	(Dana, 1853)	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Ericthonius brevicarpus	Vader and Myers, 1996	*Dardanus arrosor*	(Herbst, 1796)	O	FL	Vader and Myers, 1996
		Strigopagurus strigimanus	(White, 1847)			Vader and Myers, 1996
Gammaropsis maculata	(Johnston, 1828)	*Pagurus bernhardus*	(Linnaeus, 1758)	F[?]	FL	Chevreux, 1908
		Pagurus bernhardus	(Linnaeus, 1758)			Stephensen, 1928
Gammaropsis nitida	(Stimpson, 1853)	*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus bernhardus	(Linnaeus, 1758)			Vader, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Stock, 1952
		Pagurus bernhardus	(Linnaeus, 1758)			Metzger, 1875
		Pagurus bernhardus	(Linnaeus, 1758)			Enequist, 1949
		Pagurus bernhardus	(Linnaeus, 1758)			Robertson, 1888
		Pagurus bernhardus	(Linnaeus, 1758)			Jones, 1948
		Pagurus bernhardus	(Linnaeus, 1758)			Hamond, 1968
		Pagurus bernhardus	(Linnaeus, 1758)			Chevreux and Fage, 1925
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
Gitanopsis paguri	Myers, 1974	*Dardanus megistos*	(Herbst, 1804)	O[?]	C	Myers, 1974

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Amphipoda						
Gnathopleustes pugettensis	(Dana, 1853)	*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
Isaea concinna[?]		unidentified		F	FL	Gurjanova, 1951
Ischyrocerus commensalis	Chevreux, 1900	unidentified		F	C	Besner, 1976
Lembos karamani[?]		*Paguristes eremita* and/or	(Linnaeus, 1767)	F	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Leucothoe euronyx[?]		*Paguristes eremita* and/or	(Linnaeus, 1767)	F	HS[?]	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Leucothoe spinicarpa	(Abildgaard, 1789)	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	HS	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Liljeborgia aequabilis	Stebbing, 1888	*Dardanus arrosor*	(Herbst, 1796)	O	FL	Vader, 1995
		Dardanus crassimanus	(H. Milne Edwards, 1836)			Inaba, 1988
		Paguristes frontalis	(H. Milne Edwards, 1836)			Vader, 1995
		Strigopagurus strigimanus	(White, 1847)			Vader, 1995
		unidentified				Moore, 1983
		unidentified				Ishimaru, 1994
Liljeborgia sp.		*Pagurus hemphilli*	(Benedict, 1892)	O[?]	FL	Taylor, 1979
Lilljeborgia dellavallei	Stebbing, 1906	*Dardanus arrosor*	(Herbst, 1796)	O	FL	Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Lysianassa plumosa	Boeck, 1871	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Megaluropus agilis	Hoek, 1889	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Melita sp.		*Elassochirus cavimanus*	(Miers, 1879)	F	FL	Hoberg et al., 1982
		Pagurus aleuticus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus confragosus	(Benedict, 1892)			Hoberg et al., 1982
		Pagurus ochotensis	Brandt, 1851			Hoberg et al., 1982
		Pagurus setosus	(Benedict, 1892)			Hoberg et al., 1982
Microprotopus maculatus	Norman, 1867	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Mucrogammarus mucronatus	(Say, 1818)	*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Orchomene humilis	(A. Costa, 1853)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Orchomenella commensalis[?]		*Pagurus bernhardus*	(Linnaeus, 1758)	F[?]	FL	Chevreux and Fage, 1925

Orchomenella nana	(Krøyer, 1846)	*Pagurus bernhardus*	(Linnaeus, 1758)	F$^?$	FL	Stephensen, 1928
		Pagurus bernhardus	(Linnaeus, 1758)			Hamond, 1968
Pagurisaea schembrii	Moore, 1983	*Paguristes pilosus*	(H. Milne Edwards, 1836)	O	FL	Moore, 1983
Podoceropsis sp.		*Pagurus arcuatus*	Squires, 1964	F	FL	Squires, 1963
Ruffojassa (Parajassa) andromedae	(Moore, 1985)	*Diacanthurus spinulimanus*	(Miers, 1876)	F	FL	Moore, 1985
		Paguristes barbatus	(Ortmann, 1892)			Moore, 1985
Ruffojassa festa	Vader and Myers, 1996	*Strigopagurus strigimanus*	(White, 1847)	F	FL	Vader and Myers, 1996
Scopelocheirus hopei	(Costa, 1851)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Reiss et al., 2003
Stenula latipes	(Chevreux and Fage, 1925)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	FL	McGrath, 1978
Stenula rubrovittata	(Sars, 1882)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	FL	Vader, 1971
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Ventojassa helenae	Vader and Myers, 1996	*Dardanus arrosor*	(Herbst, 1796)	F	FL	Vader and Myers, 1996
		Strigopagurus strigimanus	(White, 1847)			Vader and Myers, 1996
Ventojassa zebra	Vader and Myers, 1996	*Dardanus arrosor*	(Herbst, 1796)	F	FL	Vader and Myers, 1996
		Strigopagurus strigimanus	(White, 1847)			Vader and Myers, 1996
Veronajassa neptunea	Vader and Myers, 1996	*Dardanus arrosor*	(Herbst, 1796)	F	FL	Vader and Myers, 1996
Isopoda						
Cirolana sp.		*Pagurus granosimanus*	(Stimpson, 1859)	I	FL	Bouvier, 1901
Erichsonella filiformis	(Say, 1818)	*Pagurus longicarpus*	Say, 1817	I	FL	McDermott, 2001
Sphaeroma walkeri	Stebbing, 1905	*Pagurus longicarpus*	Say, 1817	I	FL	Conover, 1979
		Pagurus pollicaris	Say, 1817			Conover, 1979
Tanaidacea						
Leptochelia savignyi	(Krøyer, 1842)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Decapoda						
Aretopsis amabilis	De Man, 1910	*Dardanus guttatus*	(Olivier, 1811)	O	FL	Vannini et al., 1993
		Dardanus lagopodes	(Forskål, 1775)			Vannini et al., 1993
		Dardanus lagopodes	(Forskål, 1775)			Haig and Ball, 1988
		Dardanus lagopodes	(Forskål, 1775)			Bruce, 1969
		Dardanus megistos	(Herbst, 1804)			Vannini et al., 1993
		Dardanus megistos	(Herbst, 1804)			Bruce, 1969
Calcinus ornatus	(Roux, 1828)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Fenizia, 1934
Dromia vulgaris	H. Milne Edwards, 1837	*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
Eucyphidea		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Decapoda						
		Pagurus cuanensis	Bell, 1845			
Fabia grantia	Glassell, 1933	*Petrochirus californiensis*	Bouvier, 1895	F	HS	Glassell, 1936
Palaemonetes pugio?	(Holthuis, 1949)	*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Panopeus turgidus?		*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Pilumnus hirtellus	(Linnaeus, 1761)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	FL	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Pisidia longicornis	(Linnaeus, 1767)	*Dardanus arrosor*	(Herbst, 1796)	F	FL	Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Chevreux, 1908
		Pagurus bernhardus	(Linnaeus, 1758)			Stephensen, 1910
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
Pisidia magdalenensis	(Glassell, 1936)	*Petrochirus californiensis*	Bouvier, 1895	F	FL	Parente and Hendrickx, 2000
Porcellana cancrisocialis	(Glassell, 1936)	*Aniculus elegans*	Stimpson, 1858	F	FL	Parente and Hendrickx, 2000
		Dardanus sinistripes	(Stimpson, 1859)			Parente and Hendrickx, 2000
		Paguristes digueti	Bouvier, 1892			Parente and Hendrickx, 2000
		Petrochirus californiensis	Bouvier, 1895			Parente and Hendrickx, 2000
Porcellana paguriconviva	(Glassell, 1936)	*Aniculus elegans*	Stimpson, 1858	F	FL	Parente and Hendrickx, 2000
		Dardanus sinistripes	(Stimpson, 1859)			Parente and Hendrickx, 2000
		Paguristes digueti	(Bouvier, 1892)			Parente and Hendrickx, 2000
		Petrochirus californiensis	Bouvier, 1895			Parente and Hendrickx, 2000
Porcellana sayana	Leach, 1820	*Clibanarius vittatus*	(Bosc, 1802)	F	FL	Fotheringham, 1976
		Dardanus fucosus	Biffar and Provenzano, 1972			Werding, 1977, 1983
		Dardanus venosus	(H. Milne Edwards, 1848)			Brooks and Rittschof, 1995
		Dardanus venosus	(H. Milne Edwards, 1848)			Telford and Daxboeck, 1978
		Dardanus venosus	(H. Milne Edwards, 1848)			Gore, 1970
		Paguristes grayi	Benedict, 1901			Telford and Daxboeck, 1978
		Paguristes puncticeps	Benedict, 1901			Pearse, 1932
		Paguristes sp.				Gore, 1974
		Paguristes tortugae	Schmitt, 1933			Werding, 1977, 1983
		Pagurus pollicaris	Say, 1817			Brooks and Rittschof, 1995
		Pagurus pollicaris	Say, 1817			McLean, 1983
		Petrochirus diogenes	(Linnaeus, 1758)			Brooks and Rittschof, 1995
		Petrochirus diogenes	(Linnaeus, 1758)			Telford and Daxboeck, 1978
		Petrochirus diogenes	(Linnaeus, 1758)			Haig, 1956
		Petrochirus diogenes	(Linnaeus, 1758)			Gore, 1974

		Petrochirus diogenes	(Linnaeus, 1758)			Werding, 1977, 1983
		unidentified				Benedict, 1901
Tumidotheres maculatus	(Say, 1818)	*Pagurus pollicaris*	Say, 1817	F	HS	McDermott, unpublished data

Collembola

Coenaletes caribaeus	Bellinger, 1985	*Coenobita brevimanus*	Dana, 1852	O	FL	Bellinger, 1985
		Coenobita brevimanus	Dana, 1852			Palacios-Vargas et al., 2000
		unidentified				Mari Mutt, 1994
Coenaletes vangoethemi	(Jacquemart, 1980)	*Coenobita rugosus*	H. Milne Edwards, 1837	O	FL	Jacquemart, 1980

Pycnogonida

Anoplodactylus cf. *lentus*	(Wilson, 1879)	*Pagurus longicarpus*	Say, 1817	F	HS	McDermott, 2001

Acari

Andregamasus conchylidae	(André, 1937)	*Coenobita* sp.		O	C	André, 1937
Andregamasus steinitzii	Costa, 1965	*Coenobita* sp.		O	C	Costa, 1965
Askinasia antillarum	Fain et al., 1982	*Coenobita brevimanus*	Dana, 1852	O	C	Fain et al., 1982
Askinasia aethiopicus	Yunker, 1970	*Coenobita rugosus*	H. Milne Edwards, 1837	O	C	Yunker, 1970
Askinasia sinusarabicus	Yunker, 1970	*Coenobita scaevola*	Forskål, 1775	O	C	Yunker, 1970
Cyclothorax carcinicola	Frauenfeld, 1868	*Calcinus tibicen*	(Herbst, 1791)	O	C	Vitzthum, 1928
Ereynetes (Anereynetes) coenobitus	Hunter and Poe, 1971	*Coenobita clypeatus*	Linnaeus, 1775	O	C	Hunter and Poe, 1971
Ereynetes (Anereynetes) papuanus	Fain and Van Goethem, 1977	*Coenobita rugosus*	H. Milne Edwards, 1837	O	C	Fain and Van Goethem, 1978
Ewingia coenobitae	Pearse, 1929	*Coenobita brevimanus*	Dana, 1852	O	C	Pearse, 1932
		Coenobita brevimanus	Dana, 1852			Yunker, 1970
Hoogstraalacarus tiwensis	Yunker, 1970	*Coenobita rugosus*	H. Milne Edwards, 1837	O	C	Yunker, 1970
Laelaps pagurophilus	André, 1937	*Coenobita* sp.		O	C	André, 1937
Physalozercon paguroxenus	André, 1937	*Coenobita* sp.		O	C	André, 1937

Polyplacophora

Leptochiton asellus	(Gmelin, 1791)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973

Gastropoda

Acanthodoris pilosa	(Müller, 1789)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	FL	Jensen and Bender, 1973
Acmaea tessulata[?]		*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Acmaea virginea	(Müller, 1776)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970

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Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Gastropoda						
Anachis avara semiplicata[?]		*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Bittium varium	(Pfeiffer, 1840)	*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Bivonia cristata[?]	Biondi	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Capulus hungaricus	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Corambe obscura	(Verrill, 1870)	*Clibanarius vittatus*	(Bosc, 1802)	F	HS	Fotheringham, 1976
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Crepidula adunca	Sowerby, 1825	*Pagurus granosimanus*	(Stimpson, 1859)	F	EE, EI	Walker, 1992
		Pagurus samuelis	(Stimpson, 1857)			Walker, 1992
Crepidula atrasolea	Collin, 2000	unidentified		F	EI	Collin, 2000
Crepidula complanata	Krauss, 1848	unidentified		F	EE	Collin, 2003
Crepidula convexa	Say, 1822	*Clibanarius vittatus*	(Bosc, 1802)	F	EE	Pearse, 1947
		Pagurus longicarpus	Say, 1817			Karlson and Cariolou, 1982
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus longicarpus	Say, 1817			Frey, 1987
		Pagurus longicarpus	Say, 1817			Franz and Hendler, 1970
		Pagurus longicarpus	Say, 1817			Hendler and Franz, 1971
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Crepidula coquimbensis	Brown and Olivares, 1996	*Pagurus edwardsii*	Dana, 1852	O	EI	Brown and Olivares, 1996
		Pagurus perlatus	H. Milne Edwards, 1848			Brown and Olivares, 1996
Crepidula depressa	Say, 1822	unidentified		F	EI	Collin, 2000
Crepidula fornicata	(Linnaeus, 1758)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Thieltges et al., 2003
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus longicarpus	Say, 1817			Conover, 1979
		Pagurus longicarpus	Say, 1817			Conover, 1976
		Pagurus longicarpus	Say, 1817			Frey, 1987
		Pagurus pollicaris	Say, 1817			McLean, 1983
		Pagurus pollicaris	Say, 1817			Conover, 1979
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Crepidula grandis	(Middendorff, 1949)	unidentified		F	EE, EI	Vermeij, 1989
Crepidula incurva	(Broderip, 1834)	unidentified		F	EE	Vermeij, 1989
Crepidula maculosa	Conrad, 1846	*Pagurus pollicaris*	Say, 1817	F	EE	McLean, 1983
Crepidula cf. *nivea*	(C. B. Adams, 1852)	*Petrochirus californiensis*	Bouvier, 1895	F	EI	Glassell, 1936
Crepidula nivea	(C. B. Adams, 1852)	unidentified		F	EE, EI	Vermeij, 1989
		unidentified				Coe, 1953

Crepidula nummaria	Gould, 1846	*Pagurus samuelis*	(Stimpson, 1857)	F	EE	Walker, 1988
Crepidula perforans	(Valenciennes, 1846)	unidentified		F	EI	Vermeij, 1989
Crepidula philippiana	Gallardo, 1977	*Paguristes weddelli*	(H. Milne Edwards, 1848)	O$^?$	EI	Gallardo, 1977
Crepidula plana	Say, 1822	*Clibanarius vittatus*	(Bosc, 1802)	F	EI	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Pearse, 1947
		Clibanarius vittatus	(Bosc, 1802)			Dauer, 1991
		Isocheles wurdemanni	Stimpson, 1859			Morris et al., 1989
		Pagurus annulipes	(Stimpson, 1859)			Dauer, 1991
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus longicarpus	Say, 1817			Conover, 1979
		Pagurus longicarpus	Say, 1817			Frey, 1987
		Pagurus longicarpus	Say, 1817			Conover, 1976
		Pagurus longicarpus	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			McLean, 1983
		Pagurus pollicaris	Say, 1817			Conover, 1979
		Pagurus pollicaris	Say, 1817			Conover, 1976
		Pagurus pollicaris	Say, 1817			Dauer, 1991
		Pagurus pollicaris	Say, 1817			McGee and Targett, 1989
		Petrochirus granulatus	(Olivier, 1811)			Pearse, 1932
		unidentified				Collin, 2000
Crepidula striolata	Menke, 1851	unidentified		F	EI	Coe, 1953
Crepidula unguiformis	Lamarck, 1822	*Dardanus arrosor*	(Herbst, 1796)	F	EI	Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Crepidula walshi	(Reeve, 1859)	*Clibanarius infraspinatus*	Hilgendorf, 1869	F	EI	Yipp, 1980
		Clibanarius padavensis	De Man, 1888			Parulekar, 1969
		Dardanus crassimanus	(H. Milne Edwards, 1836)			Yipp, 1980
		Diogenes custos	(Fabricius, 1798)			Parulekar, 1969
		Diogenes sp.				Yipp, 1980
Cuthona nana	(Alder and Hancock, 1842)	*Pagurus acadianus*	Benedict, 1901	F	HS	Harris et al., 1975
		Pagurus acadianus	Benedict, 1901			Rivest, 1978
		Pagurus acadianus	Benedict, 1901			Lambert, 1991
		Pagurus acadianus	Benedict, 1901			Folino, 1993
		Pagurus acadianus	Benedict, 1901			Folino, 1997
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Cuthona sp.		*Pagurus longicarpus*	Say, 1817	F	HS	McDermott, 2001
Doris verrucosa	Linnaeus, 1758	unidentified		F	HS	Sandford, 1994
Leptonetis perplexus	Suter, 1907	unidentified		F$^?$	EI	Collin, personal communication

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Gastropoda						
Precuthona divae	Marcus, 1961	unidentified		F	HS	Marcus, 1961
Precuthona peachi	(Alder and Hancock, 1842)	*Dardanus arrosor*	(Herbst, 1796)	F	HS	Cuadras and Pereira, 1977
		Pagurus bernhardus	(Linnaeus, 1758)			Swennen, 1961
		Pagurus bernhardus	(Linnaeus, 1758)			Christensen, 1977
Sabia conica	(Schumacher, 1817)	unidentified		F	EE	Vermeij, 1989
Thais haemastoma?	(Linnaeus, 1767)	*Clibanarius vittatus*	(Bosc, 1802)	I	FL	Fotheringham, 1976
Vermetidae		*Paguristes eremita*	(Linnaeus, 1767)	I	EE	Caruso et al., 2003
Bivalvia						
Acanthocardia echinata	(Linnaeus, 1758)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Anadara ovalis	(Bruguiere, 1789)	*Pagurus longicarpus*	Say, 1817	I	EE	McDermott, 2001
		Pagurus longicarpus and/or *P. pollicaris*	Say, 1817			Frey, 1987
Anadara transversa	(Say, 1822)	*Pagurus longicarpus* and/or *P. pollicaris*	Say, 1817	I	EE	Frey, 1987
Anomia ephippium	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE, EI	Cuadras and Pereira, 1977
		Paguristes eremita and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845			Stachowitsch, 1980
		Pagurus bernhardus	(Linnaeus, 1758)			Jackson, 1913
Anomia simplex	d'Orbigny, 1842	*Pagurus pollicaris*	Say, 1817	I	EE	McDermott, unpublished data
Arca noae	(Linnaeus, 1758)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Barbatia tenera	(CB Adams, 1845)	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976
Cardium sp.		*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Chlamys varius	(Linnaeus, 1758)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Crassostrea virginica	(Gmelin, 1791)	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976
		Clibanarius vittatus	(Bosc, 1802)			Pearse, 1947
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Curvemysella paula	(A. Adams, 1856)	*Diogenes edwardsii*	(DeHaan)	O	EI	Morton and Scott, 1989
Gastrochaena dubia	(Pennant, 1777)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	En, EE	Stachowitsch, 1980
Geukensia demissa	(Dillwyn, 1817)	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Pearse, 1947
Heteromonia squamala	(Linnaeus, 1758)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Hiatella arctica	(Linnaeus, 1767)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980

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		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Modiolula phaseolina	(Philippi, 1844)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Modiolus barbatus	(Linnaeus, 1758)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Musculus subpictus	(Cantraine, 1835)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Mytilus edulis	Linnaeus, 1758	*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Pearse, 1947
		Pagurus bernhardus	(Linnaeus, 1758)			Samuelsen, 1970
		Pagurus longicarpus	Say, 1817			McDermott, 2001
		Pagurus longicarpus	Say, 1817			Andrews and Reinhard, 1943
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Mytilus sp.		*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Ostrea edulis	Linnaeus, 1758	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Ostrea puelchana	Orbigny, 1841	unidentified		I	EE	Creed, 2000
Pododesma patelliformis	(Linnaeus, 1761)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Pododesmus rudis	(Broderip, 1834)	*Pagurus longicarpus*	Say, 1817	I	EE	Conover, 1979
		Pagurus pollicaris	Say, 1817			Conover, 1979
Solenocurtus strigillatus	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Phoronida						
Phoronis ovalis	Wright, 1856	*Pagurus bernhardus*	(Linnaeus, 1758)	I	En	Reiss et al., 2003
Bryozoa						
Aetea sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Akatopora circumsaepta	(Uttley, 1951)	*Lophopagurus (Australeremus) laurente*	(McLaughlin and Gunn, 1992)	O	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Paguristes subpilosus	Henderson, 1888			Taylor et al., 1989
		Pagurus sp.				Taylor et al., 1989
Alcyonidium albescens	Winston and Key, 1999	*Pagurus longicarpus*	Say, 1817	F	EE	McDermott, 2001

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Bryozoa						
		Pagurus longicarpus	Say, 1817			Winston and Key, 1999
		Pagurus longicarpus	Say, 1817			Karlson and Cariolou, 1982
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Alcyonidium diaphanum	(Hudson, 1762)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Alcyonidium gelatinosum	(Linnaeus, 1761)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	EE	Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Alcyonidium sp.		*Pagurus villosus*	Nicolet, 1849	F	EE	Quezada and López, 1979
		Pylopagurus holmesi	Schmitt, 1921			Walton, 1954
Antropora tincta	(Hastings, 1930)	*Pagurus gordanae*	(Forest, 1956)	F	EE	Cook, 1985
		Pagurus pollicaris	Say, 1817			Maturo, 1957
Amphiblestrum flemingii	(Busk, 1854)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Arachnoidea dhondti	Franzen and Sandberg, 2001	*Parapagurus pilosimanus*	Smith, 1879	F?	C	Franzen and Sandberg, 2001
Arachnopusia unicornis	(Hutton, 1873)	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Lophopagurus (Lophopagurus) thompsoni	(Filhol, 1885)			Taylor et al., 1989
Biflustra commensale	(Kirkpatrick and Metzelaar, 1922)	*Pseudopagurus granulimanus*	(Miers, 1881)	F	EE	Kirkpatrick and Metzelaar, 1922
bryozoan		*Pylopagurus gorei*	McLaughlin and Lemaitre, 2001	F	EE	McLaughlin and Lemaitre, 2001
		Pylopagurus holmesi	Schmitt, 1921			McLaughlin and Lemaitre, 2001
Bugula avicularia	(Linnaeus, 1758)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Bugula sp.		*Pagurus longicarpus*	Say, 1817	I	EE	Frey, 1987
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Callopora aurita	(Hincks, 1877)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Callopora dumerilii	(Audonin, 1826)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Callopora lineata	(Linnaeus, 1767)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Samuelsen, 1970
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Celleporella cf. *tongima*	(Ryland and Gordon, 1977)	unidentified		I	EE	Taylor, 1991
Celleporella hyalina	(Linnaeus, 1767)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Samuelsen, 1970
		Pagurus samuelis	(Stimpson, 1857)			Morris et al., 1989
		Pagurus samuelis	(Stimpson, 1857)			Walker and Carlton, 1995

		Pagurus villosus	Nicolet, 1849			Quezada and López, 1979
Cellepora sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Celloma keruniformis[?]	Stechow, 1921	*Pagurus alcocki*	(Balss, 1911)	O[?]	EE	Stechow, 1921
Conopeum reticulum	(Linnaeus, 1767)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Conopeum sp.		*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976
		Pagurus villosus	Nicolet, 1849			Quezada and López, 1979
Conopeum tenuissimum	(Canu, 1928)	*Pagurus longicarpus*	Say, 1817	I	EE	McDermott, 2001
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Crepidacantha zelanica	Canu and Bassler, 1929	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Lophopagurus (Lophopagurus) pumilus	De Saint-Laurent and McLaughlin, 2000			Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Cribrilina punctata	(Hassall, 1841)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Disporella gordoni	Taylor et al., 1989	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Lophopagurus (Lophopagurus) thompsoni	(Filhol, 1885)			Taylor et al., 1989
		Pagurus sp.				Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Disporella hispida	(Fleming, 1828)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Electra pilosa	(Linnaeus, 1767)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Electra sp.		unidentified		I	EE	Boekschoten, 1966
Eschara sp.		*Manucomplanus ungulatus*	(Studer, 1883)	I	EE	Studer, 1889
Favosipora otagoensis	Taylor et al., 1989	*Lophopagurus (Lophopagurus) thompsoni*	(Filhol, 1885)	O	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Fenestrulina malusi	(Audouin, 1826)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Paguristes eremita and/or	(Linnaeus, 1767)			Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Bryozoa						
Foveolaria (Odontionella) cyclops	(Busk, 1854)	unidentified		I	EE	Taylor, 1991
Flustrellidra hispida	(Fabricius, 1780)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Samuelsen, 1970
Frondipora verrucosa	(Lamouroux, 1821)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Hagiosynodos latus	(Busk, 1856)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845			Stachowitsch, 1980
		unidentified				Cook, 1985
		unidentified				Taylor, 1994
Heteropora parapelliculata	Taylor et al., 1989	*Lophopagurus (Australeremus) stewarti*	(Filhol, 1883)	O	EE	Taylor et al., 1989
		Lophopagurus (Lophopagurus) thompsoni	(Filhol, 1885)			Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Heteropora sp.		*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
Hippopodinella parva	(Marcus, 1938)	*Manucomplanus ungulatus*	(Studer, 1883)	F	EE	Deichmann, 1954
		Pagurus gordanae	(Forest, 1956)			Cook, 1985
		Pagurus longicarpus	Say, 1817			Maturo, 1957
		unidentified				Cook, 1964
Hippoporidra dictyota	Ryland, 2001	*Paguristes tortugae*	Schmitt, 1933	O	EE	Ryland, 2001
Hippoporidra edax	(Busk, 1861)	*Pagurus annulipes*	(Stimpson, 1859)	F	EE	Maturo, 1957
		Pagurus cuanensis	Bell, 1845			Moore, 1937
Hippoporidra littoralis	Cook, 1985	*Pagurus gordanae*	(Forest, 1956)	F	EE	Taylor, 1994
		Pseudopagurus granulimanus "var." biafrensis	(Monod, 1927)			Cook, 1964
Hippoporidra lusitania	Taylor and Cook, 1981	*Anapagurus chiroacanthus*	(Lilljeborg, 1856)	O	EE	Bishop, 1987
		Anapagurus sp.				Bishop, 1987
		Cestopagurus timidus	(Roux, 1828)			Bishop, 1987
		Pagurus cuanensis	Bell, 1845			Moore, 1937
Hippoporidra picardi	Gautier, 1962	*Dardanus arrosor*	(Herbst, 1796)	O	EE	Cook, 1964
		Paguristes mauritanicus	Bouvier, 1906			Taylor, 1994
		Pagurus cuanensis	Bell, 1845			Cook, 1964
Hippoporidra senegambiensis	(Carter, 1882)	*Diogenes ovatus*	Miers, 1881	O	EE	Cook, 1964
		Paguristes fagei	Forest, 1952			Cook, 1964
		Pagurus alcocki	(Balss, 1911)			Andre and Lamy, 1936

		Pagurus alcocki	(Balss, 1911)		Cook, 1964
		unidentified			Cook, 1985
Hippoporida calcarea		unidentified		F	EE	Taylor et al., 1989
Hippoporidra sp.		unidentified		F	EE	Taylor and Cook, 1981
Hippothoa sp.		*Pagurus granosimanus*	(Stimpson, 1859)	I	EE	Walker, 1988
Immergentia californica	Silén, 1946	*Pagurus granosimanus*	(Stimpson, 1859)	I	EE	Walker, 1988
Keruniella valdiviae[?]	(Stechow, 1921)	*Diogenes pugilator*	(Roux, 1828)	O[?]	EE	Balss, 1924
Lichenopora radiata	(Audouin, 1826)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Lichenopora verrucaria	(O. Fabricius, 1780)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
		Pagurus cuanensis	Bell, 1845			Samuelsen, 1970
Membranipora arborescens	Robertson, 1921	*Isocheles wurdemanni*	Stimpson, 1859	I	EE	Morris et al., 1989
Membranipora membranacea	(Linnaeus, 1767)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Membranipora sp.		*Pagurus villosus*	Nicolet, 1849	I	EE	Quezada and López, 1979
Membranipora tenuis	Desor, 1848	*Pagurus longicarpus*	Say, 1817	I	EE	McDermott, 2001
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Microporella ciliata	(Pallas, 1766)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Microporella sp.		unidentified		I	EE	Taylor, 1991
Mollia patellaria	(Moll, 1803)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Odontoporella adpressa	(Busk, 1854)	*Pagurus novizealandiae*	(Dana, 1851)	F	EE	Gordon, 1972
Osthimosia monilifera	Taylor et al., 1989	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	O	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Pagurus sp.				Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Osthimosia socialis	Taylor et al., 1989	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	F	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Lophopagurus (Lophopagurus) thompsoni	(Filhol, 1885)			Taylor et al., 1989
		Pagurus sp.				Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Parkermavella curvata	(Uttley and Bullivant, 1972)	unidentified		I	EE	Taylor, 1994

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Bryozoa						
Penetrantia clionoides	Smyth, 1988	unidentified		F	En	Smyth, 1989, 1990
Penetrantia cf. *concharum*	Silén, 1946	*Pagurus samuelis*	(Stimpson, 1857)	F	En	Walker and Carlton, 1995
Plagioecia cf. *gemelligera*	(Borg, 1944)	*Pylopagurus* sp.		I	EE	Taylor et al., 1989
Reptadeonella violacea	Johnston, 1847	*Paguristes eremita* and/or	(Linnaeus, 1767)	O	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Schizobrachiella sanguinea	(Norman, 1868)	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Schizomavella trachoma	(Gordon, 1989)	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
Schizosmittina maplestonei	(MacGillivray, 1879)	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
		Lophopagurus (Australeremus) stewarti	(Filhol, 1883)			Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Schizoporella errata	(Waters, 1878)	*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus pollicaris	Say, 1817			Karlson and Shenk, 1983
Schizoporella longirostris?		*Paguristes eremita* and/or	(Linnaeus, 1767)	F	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Schizoporella unicornis	(Johnston, 1847)	*Pagurus longicarpus*	Say, 1817	F	EE	McDermott, 2001
		Pagurus pollicaris	Say, 1817			McDermott, unpublished data
Scrupocellaria scruposa	(Linnaeus, 1758)	*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Terebripora sp.		*Isocheles wurdemanni*	Stimpson, 1859	F	En	Morris et al., 1989
		unidentified				Boekschoten, 1966
Triticella pedicellata?	(Alder, 1857)	*Pagurus bernhardus*	(Linnaeus, 1758)	F	C?	Jensen and Bender, 1973
Tubulipora cf. *anderssoni*	(Borg, 1926)	*Lophopagurus (Australeremus) cooki*	(Filhol, 1883)	I	EE	Taylor et al., 1989
		Pagurus sp.				Taylor et al., 1989
		Pylopagurus sp.				Taylor et al., 1989
Tubulipora liliacea	(Pallas, 1766)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Reiss et al., 2003
Tubulipora sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
		Pagurus bernhardus	(Linnaeus, 1758)			Jensen and Bender, 1973

Echinodermata

Antedon mediterranea	(Lamarck, 1816)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	FL	Stachowitsch, 1980
Cucumaria planci	Brand, 1835	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	FL	Stachowitsch, 1980
Ophiothrix quinquemaculata[?]		*Dardanus arrosor*	(Herbst, 1796)	I	FL	Cuadras and Pereira, 1977
		Paguristes eremita and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845			Stachowitsch, 1980

Ascidiacea

Aplidium conicum	(Olivi, 1792)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Aplidium cf. *constellatum*	(Verrill, 1871)	*Pagurus pollicaris*	Say, 1817	I	EE	McDermott, unpublished data
Ascidia mentula	Müller, 1776	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Ascidiella aspersa	(Müller, 1776)	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Botryllus sp.		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Ciona intestinalis	(Linnaeus, 1758)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Paguristes eremita and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845			Stachowitsch, 1980
Didemnum maculosum	(Milne Edwards, 1841)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Didemnum sp.		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Diplosoma sp.		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Distomus variolosus	Gaertner, 1774	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
		Paguristes eremita and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845			Stachowitsch, 1980
Microcosmus claudicans	(Savigny, 1816)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Microcosmus polymorphis[?]		*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Microcosmus sulcatus	(Coquebert, 1797)	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
Microcosmus vulgaris	Heller, 1877	*Paguristes eremita* and/or *Pagurus cuanensis*	(Linnaeus, 1767) Bell, 1845	I	EE	Stachowitsch, 1980
Phallusia mammilata	(Cuvier, 1815)	*Dardanus arrosor* *Paguristes eremita* and/or	(Herbst, 1796) (Linnaeus, 1767)	I	EE	Cuadras and Pereira, 1977 Stachowitsch, 1980

Table 1 (*continued*)

Associate species	Associate authority	Host hermit crab species	Host authority	Type	Habitat	Reference
Ascidiacea						
		Pagurus cuanensis	Bell, 1845			
Polycarpa sp.		*Paguristes eremita* and/or	(Linnaeus, 1767)	I	EE	Stachowitsch, 1980
		Pagurus cuanensis	Bell, 1845			
Styela coriacea	(Alder and Hancock, 1848)	*Pagurus bernhardus*	(Linnaeus, 1758)	I	EE	Jensen and Bender, 1973
Styela partita	Stimpson, 1852	*Dardanus arrosor*	(Herbst, 1796)	I	EE	Cuadras and Pereira, 1977
unidentified tunicate		*Clibanarius vittatus*	(Bosc, 1802)	I	EE	Fotheringham, 1976
		Pagurus bernhardus	(Linnaeus, 1758)			Reiss et al., 2003
Osteichthyes						
Gobiosoma robustum	Ginsburg, 1933	*Pagurus pollicaris*	Say, 1817	I	FL	McLean, 1983

Type : Type of symbiotic relationship (I = incidental; F = facultative; O = obligate). Hab: Habitat of associate (EE = epibiotic, external; EI = epibiotic, internal; En = endolithic; FL = free-living; C = on crab; HS = hypersymbiont). Genera and species of associates are listed under higher taxa in alphabetical order.

[?] Denotes species of uncertain taxonomic status or species suspected to be incorrectly identified; ? in the Type column indicates the symbiotic relationship of the associate is not fully understood.

[*] *Hydractinia echinata* is a European species. References to *H. echinata* from the east coast of the United States probably represent *H. symbiolongicarpus* or *H. symbiopollicarus* (see Buss and Yund, 1989).
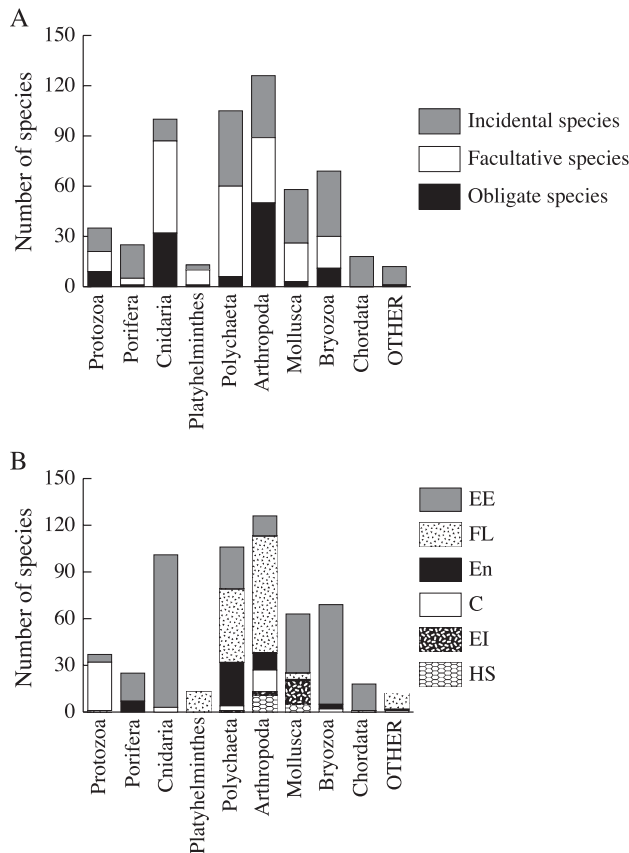
Fig. 1. (A) Number of species of hermit crab associates per major taxonomic grouping, showing the type of symbiotic relationship (obligate, facultative, or incidental). (B) Number of species of hermit crab associates per major taxonomic grouping, showing the habitat of the associates (as defined in Table 1). In calculating total species, those associates that were of questionable identity or that were not identified to the species level were not included (unless identified to genus and no additional members of the genus were represented).

scribed *L. eupagurus* from *P. longicarpus* collected in Woods Hole, MA, and further showed that the protozoan is not specific for this hermit crab, being recorded from the bodies of various penaeid and caridean shrimps and other crustaceans. An unidentified folliculinid was also found cemented to the exoskeleton of *P. longicarpus* from New Jersey (McDermott, 2001).

Folliculina viridis and *Pebrilla paguri* are found on hermit crabs from the Mediterranean (Fernández-Leborans and Cordoba, 1997; Fernández-Leborans, 2003). *P. paguri* is an obligate associate of hermit crabs attached to over 50% of the crabs in this region; it is most commonly found on the abdomen of hosts and no specimens were found on the inside of inhabited shells (Fernández-Leborans and Córdoba, 1997; Fernández-Leborans, 2003). *F. viridis* is a facultative associate of hermit crabs (63% colonized in some areas),
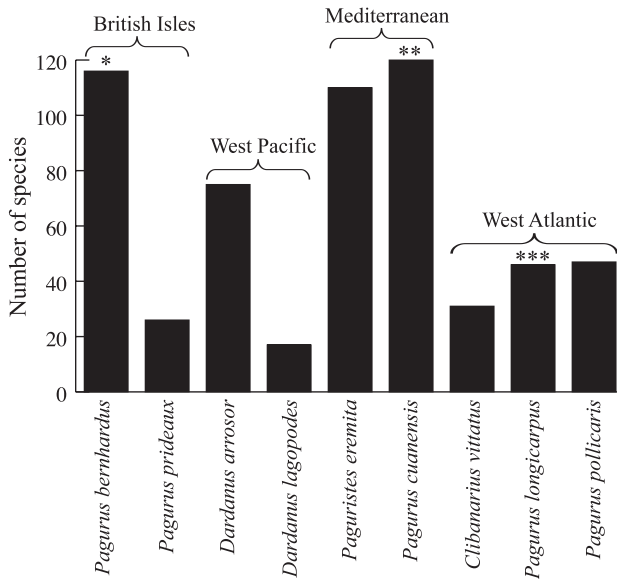
Fig. 2. Number of species associated with nine hermit crab hosts from four geographic regions. These represent the best known hermit crab assemblages (all other hermit crabs are documented with ≤ 16 associates); the total number of species represents a combination of studies but some individual investigations are largely responsible for our knowledge of certain hermit crab communities as indicated by the asterisks (*= Jensen and Bender, 1973; Reiss et al., 2003; **= Stachowitsch, 1980; ***= McDermott, 2001).

but is also found on brachyuran crabs (Fernández-Leborans and Córdoba, 1997; Fernández-Leborans, 2003). The species attaches to a wide variety of locations on hosts including the carapace, legs, and abdomen. Basile et al. (2002) found *P. paguri* co-occurring with *Ascobius faurefremieti* on *Paguristes eremita* from the Mediterranean. Other folliculinids include *Platyfolliculina paguri* from *P. pubescens* collected along the coast of Maine (Andrews and Reinhard, 1943). Eight species of suctorian ciliates have been reported from the bodies of seven species of hermit crabs and these ciliates are probably facultative symbionts (Fernández-Leborans and Tato-Porto, 2000b; Fernández-Leborans, 2003). Most suctorians found by Fernández-Leborans and Gómez del Arco (1996) and Fernández-Leborans (2003) were located on the pereopods of *P. eremita* whereas they were more common on the chelipeds of *P. bernhardus*.

Pleurocoptes hydractiniae is a hypersymbiotic species found attached to encrusting hydroids of the genus *Hydractinia* (Table 4) (Fauré-Fremiet, 1961). Additional hypersymbiotic species include protozoans attached to the setae of polydorids boring into hermit crabs shells (Table 4) (Williams and Radashevsky, 1999; Williams, 2001b). *Dipolydora armata* from the Mediterranean Sea is found with a species of *Cothurnia* sp. attached to the notopodial capillaries (Bick, 2001). Structures misidentified as spermatophores of *D. armata* by Lewis (1998) also represent *Cothurnia* sp. (Williams, 2001b). Research on *D. armata* boring into *Millepora complanata* Lamarck, 1816, from the Caribbean shows that 2–12 of these ciliates are attached to the notosetae of middle body segments of this worm (Lewis, 1998).
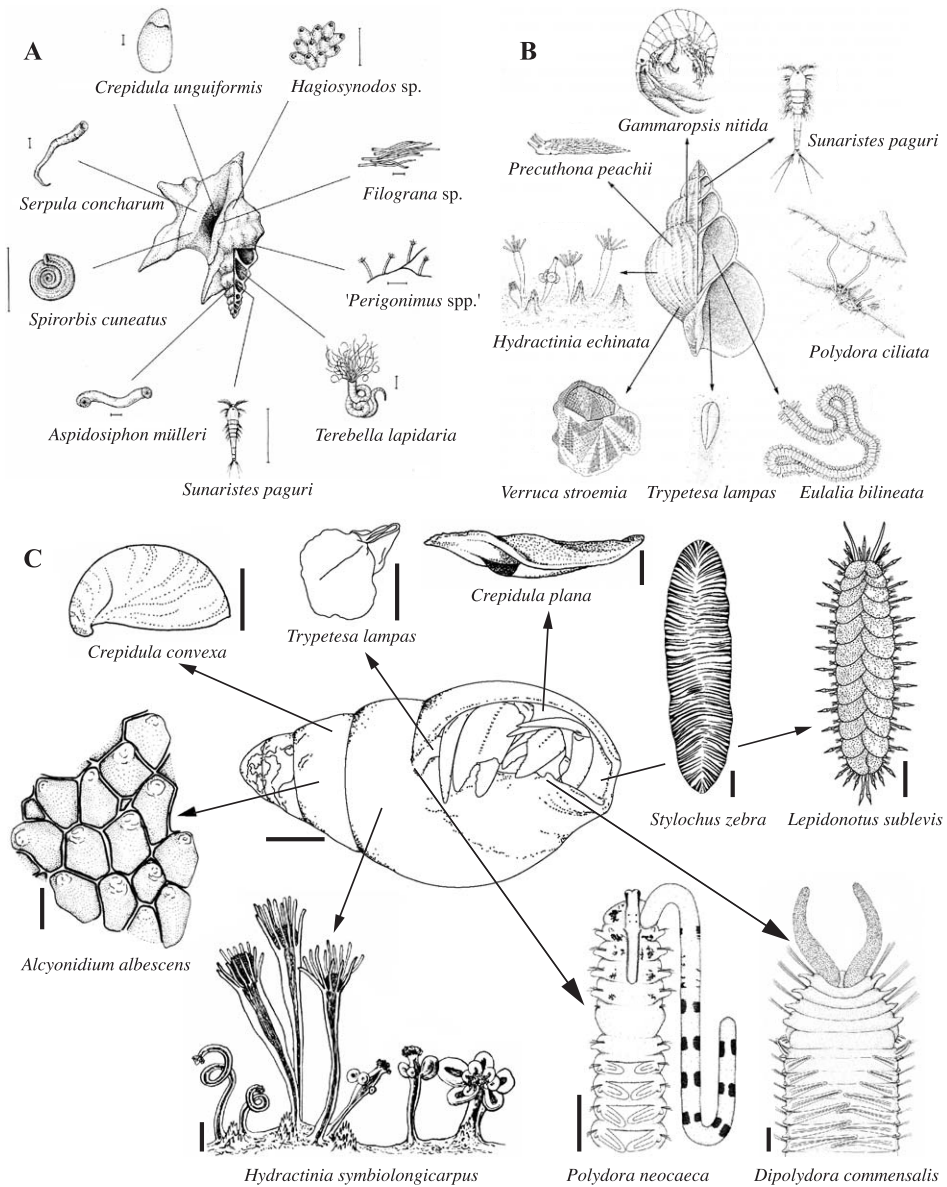
Fig. 3. Communities of hermit crab associates. (A) Symbionts associated with the gastropod shell, *Aporrhais* sp., inhabited by *Paguristes eremita* and *Pagurus cuanensis* from the North Adriatic Sea, scales = 2 mm (modified from Stachowitsch, 1980, Fig. 2). (B) Symbionts associated with shells inhabited by *Pagurus bernhardus* (modified from Jensen and Bender, 1973, Fig. 3). (C) Symbionts associated with *Pagurus longicarpus* from the east coast of the United States. Center of figure shows shell of *Nassarius obsoletus* inhabited by *P. longicarpus*. Vertical scales on left of associates = 0.5 mm, vertical scales to right of associates = 5 mm; horizontal scale for center figure = 2.5 mm [inset figures modified from Pettibone, 1963 (Fig. 3A), Blake, 1971 (Fig. 11a), Baluk and Radwański, 1991 (Fig. 8A), Weiss, 1995 (Figs. 7.01C, D; 4.06A; 6.05B), Williams and Radashevsky, 1999 (Fig. 1A)].

Bradbury (1966) described *Hyalophysa chattoni* from *Pagurus hirsutiusculus* collected along the west coast of North America; all hermit crabs collected in this region were infested by the protozoan. *H. chattoni* has also been reported from *Clibanarius vittatus* and *P. longicarpus* collected in North Carolina and Alabama (Grimes, 1976; Landers et al., 1999). Bradbury (1966) indicated that the trophonts of *H. chattonii* feed on the exuvial fluids of host hermit crabs after ecdysis (Fig. 6H).

P. longicarpus is also host for the apostome ciliate *Gymnodinioides inkystans*, which encysts on the gills (phoronts) and excysts when the crab molts. The resulting trophonts form free-living cysts in which a series of divisions produce small daughter ciliates or tomites, which are then released and drawn into the host's branchial chambers where they encyst on the gill filaments (Chatton and Lwoff, 1935; Trager, 1957). Trager (1957) found that most crabs had phoronts on the gills and 80% of the exoskeletons examined over three summers bore numerous trophonts. The species is not host specific, being found associated with other decapod crustaceans (Grimes, 1976). The apostome ciliate *Polyspira delagei* co-occurs with *G. inkystans* on *P. bernhardus* (Chatton and Lwoff, 1935; Sprague and Couch, 1971).

3.2. Phylum Porifera

Numerous sponges (∼ 25 species) are associated with hermit crabs, but members of the Suberitidae have been the most studied (Table 1). Considerable discussion of the taxonomy of *Suberites* spp. exists and extensive lists of synonymies have been produced (Vosmaer, 1933; Burton, 1953; Solé-Cava and Thorpe, 1986). In spite of taxonomic confusion, it has been shown that *Suberites domuncula* is not an obligate commensal of hermit crabs and is found associated with at least 13 hermit crab species as well as live gastropods, rocks, and the carapace of other crustaceans from the Aegean Sea, Black Sea, Mediterranean, and coast of west Africa. The association between hermit crab hosts and *Pseudospongosorites suberitoides*, *S. domuncula*, and *S. ficus* has been examined in detail (Sandford, 1994, 1995; Sandford and Brown, 1997; Sandford and Kelly-Borges, 1997). Vosmaer (1933) and Sandford (1994) suggested that the relationships are mutualistic; hermit crabs gain a home that grows with them and the sponges gain a substrate with added benefits of increased food and well-oxygenated water, as well as limited potential for burial. *P. suberitoides* is occasionally found on floating docks as well as live gastropod shells (Fig. 4A). However, almost all (>90%) of the sponges examined on Dog Island, Florida in the Gulf of Mexico were occupied by the hermit crab *Pagurus hummi*, or showed evidence of recent hermit crab occupancy (Sandford and Brown, 1997). Over a nine year period, Sandford (2003) found approximately 34% and 56% of *Paguristes impressus* and *Pagurus impressus*, respectively, inhabited shells covered by this sponge; less than 1% of *P. longicarpus*, *P. pollicaris*, and *C. vittatus* inhabited sponges. *P. suberitoides* reproduces through gemmule production, which may allow survival during periods of desiccation such as when shells abandoned by hermit crabs are washed ashore (Sandford and Brown, 1997).

Although previous researchers suggested that *P. suberitoides* eroded gastropod shells, Sandford and Brown (1997) showed that the sponge did not degrade shells, although the sponge might surround small shells that were visible only after careful dissection. Some
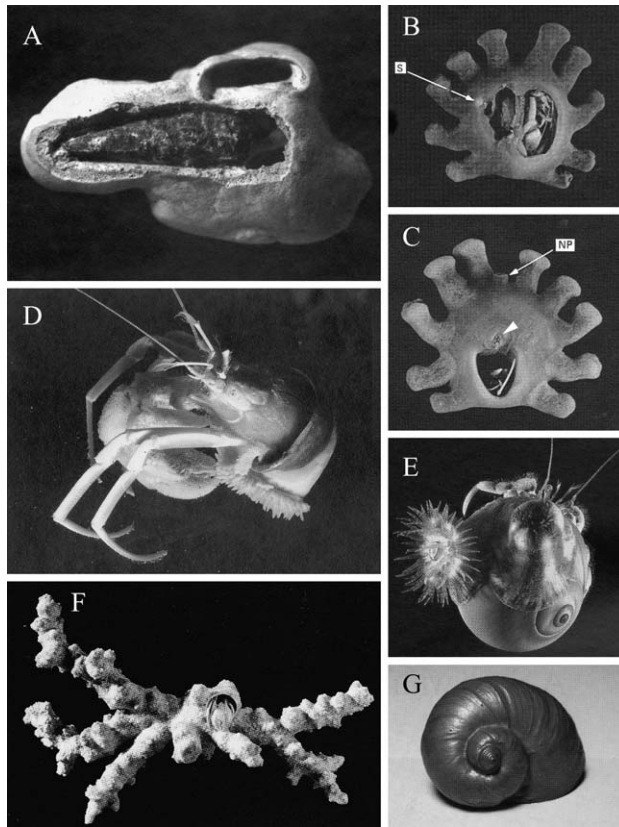
Fig. 4. Epibiotic sponges, cnidarians, and bryozoan associated with hermit crabs. (A) *Pseudospongosorites suberitoides* with cut-away showing the gastropod shell, *Pyrgospira ostrearum* (Sandford and Brown, 1997, Fig. 2). (B) *Epizoanthus paguriphilus*, dorsal view showing remaining fragment of shell (S) and cut away with hermit crab (modified from Muirhead et al., 1986, Fig. 4A). (C) *Epizoanthus paguriphilus*, ventral view showing new polyp (NP), arrowhead shows tentacles of zoanthid positioned below walking legs of host hermit crab slightly extended from aperture of the gastropod shell (modified from Muirhead et al., 1986, Fig. 4B). (D) Deep-sea hermit crab from Hawaii with *Stylobates aeneus*, note tentacles below walking legs of the host hermit crab (Fautin, 1992, p. 53). (E) *Calliactis tricolor*, two anemones attached to *Neverita duplicata* inhabited by *Pagurus longicarpus* (Ruppert and Fox, 1988, Fig. A18). (F) *Hippoporidra senegambiensis*, branched colony of the bryozoan extending from a gastropod shell with hermit crab (note chelipeds) (Vermeij, 1993, Fig. 8.2). (G) *Stylobates aeneus*, chitinous shell of anemone expanded from original gastropod shell at center (Fautin, 1992, p. 52).

have also argued that *Suberites* species had the ability to erode shells but Sandford (1994) pointed out that careful examination of sponges for shell fragments needed to be completed. Solé-Cava and Thorpe (1986) examined the genetic differences (based on isozyme patterns) among three sympatric morphotypes of *Suberites ficus* collected from the northern Irish Sea that could not be differentiated on the basis of spicules but differed in color. Only one morphotype was associated with hermit crab shells (*Suberites pagurorum*); the other two were found on the bivalve *Chlamys opercularis* (Linnaeus,

1758). Results indicated that the three morphotypes were genetically isolated and should be considered distinct species. Solé-Cava and Thorpe (1986), not able to address taxonomic confusion in the literature regarding *S. ficus*, elected to give each of these genetically determined species new names (*S. pagurorum, S. rubrus,* and *S. luridus*) although valid names may already exist. When the true identity of *S. ficus* is established, one or more of these names will be reduced to the status of junior synonyms. The status of *S. ficus* and *S. domunculus* remains problematic; some consider them to be distinct, with *S. ficus* widely distributed in the North Atlantic, North Pacific, Irish Sea, Bering Sea, Mediterranean, and North Sea, while *S. domunculus* is restricted to the Mediterranean (Solé-Cava and Thorpe, 1986; Sim, 1990).

Other sponges, some of which are commonly associated with hermit crabs, appear to be incidental associations. At least four members of the genus *Cliona* bore into the shells inhabited by hermit crabs and may negatively impact their hosts by reducing shell strength and increasing chances of predation.

3.3. Phylum Cnidaria

Of all the invertebrates associated with hermit crabs, cnidarians are probably the most studied in terms of interactions with hosts. Approximately 100 species of cnidarians live with hermit crabs (Table 1), although a number of species from deep-sea hermit crabs need further examination and may represent new species (Lemaitre, 1993, 1994; Ates, 2003). Thirty-two of the cnidarian associates are obligate commensals of hermit crabs; their symbiotic relationships are complex and in some cases mutualistic (Fig. 1A). Both solitary and colonial cnidarian external epibionts are found with hermit crabs (Fig. 1B). Among the colonial hydroids, *Hydractinia* spp. are generally considered to be facultative symbionts but show high prevalence (~ 20–50%) on shells inhabited by *P. longicarpus* and *P. pollicaris* from areas along the east coast of the United States (Mills, 1976b; Mercando and Lytle, 1980; McDermott, 2001; Damiani, 2003), and anyone wishing to find them will search for hermit crabs as a primary source because of this predilection (Figs. 3C and 5A). Sandford (2003) examined the prevalence of *Hydractinia echinata* among hermit crabs from the Gulf of Mexico over a 9-year period; 8% and 66% of *P. longicarpus* and *P. pollicaris*, respectively, inhabited shells covered by the hydroids while no *C. vittatus* or *Pagurus impressus* were associated with the hydroids. *H. echinata* was considered to be a widespread species associated with hermit crabs along the east coast of North America and in Europe. However, molecular analyses showed that *H. echinata* represented a complex of at least four species that differ only slightly morphologically (Buss and Yund, 1989) and true *H. echinata* is now considered strictly a European species where it can be found on over 80% of shells inhabited by *P. bernhardus* in some regions (Reiss et al., 2003). That each of the sibling species in the *H. echinata* complex (*H. echinata*, *H. polyclina*, *H. symbiolongicarpus*, and *H. symbiopollicaris*) is associated mainly with different species of crabs suggests some influence of the hosts on the evolution of the hydroids (see Section 4.1).

The other species of *Hydractinia* and the closely related genus *Stylactaria* that are associated with hermit crabs (Table 1) have received considerably less attention. *Hydractinia epiconcha, H. sodalis, Stylactaria inabai,* and *S. spiralis* produce hydrorhiza that extend beyond the aperture of shells inhabited by hermit crabs (Goto, 1910; Dales,
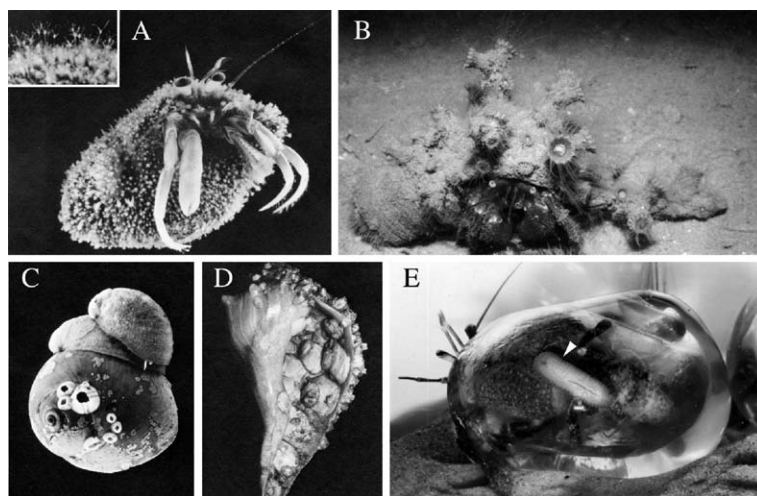
Fig. 5. Epibiotic and free-living associates of hermit crabs. (A) *Hydractinia symbiolongicarpus*, whole colony on shell occupied by *Pagurus longicarpus*, inset shows close-up of hydranths (Ruppert and Fox, 1988, Fig. 94). (B) *Epizoanthus arenaceus* and *Calliactis parasitica* (on apex of shell) associated with *Paguristes eremita* (Stachowitsch, 1980, Fig. 7). (C) *Crepidula fornicata*, *Membranipora tenuis*, and barnacles attached to the gastropod shell, *Neverita duplicata* (Ruppert and Fox, 1988, Fig 135). (D) *Crepidula plana* in the aperture of *Busycon carica* (Ruppert and Fox, 1988, Fig 135). (E) *Stylochus zebra*, ventral view of the flatworm in a clear plastic shell occupied by *Pagurus pollicaris* shown by arrowhead (modified from Lytwyn, 1979, Fig. 11).

1957; Bouillon et al., 1997). Bavestrello et al. (2000) examined asexual reproduction in *Stylactaria pruvoti* and suggested that water movement around encrusted hermit crab shells induced formation of propagules. Frank et al. (2001), who reviewed the biology of *Hydractinia* spp., explored their use as a model system for research in reproductive, developmental, and environmental studies.

Seven members of the colonial hydroid genus *Podocoryne* are associated with hermit crabs; three (*Podocoryne areolata*, *P. borealis*, and *P. carnea*) are found in western and southern European waters and elsewhere (Edwards, 1972). As in *H. echinata*, *P. carnea* represents a species complex, which has now been split into four species (*P. americana*, *P. carnea*, *P. exigua*, and *P. selena*). *Podocoryne americana* is found on the New England coast of North America where it is larger and has more tentacles than *P. carnea* (Edwards, 1972). *Podocoryne exigua* is found in the Mediterranean where Cerrano et al. (1998) examined its life cycle and showed constancy in tentacle numbers, which distinguished it from *P. carnea*. The species reached highest abundance on shells inhabited by *Diogenes pugilator* during the spring (28% of shells covered by the hydroid); during the summer the abundance decreased to 2.7% (Cerrano et al., 1998). *Podocoryne selena* co-occurs with *Hydractinia* sp. in the Gulf of Mexico where 36% and 20% of shells inhabited by *Pagurus pollicaris* and *P. longicarpus*, respectively, are covered by the hydroid (Mills, 1976b). *P. carnea* and *P. selena* are generally found in lower prevalence on hermit crab shells than *Hydractinia* spp. (Edwards, 1972; Mills, 1976b; McDermott, 2001).

The impacts of *Hydractinia* spp. and other colonial hydroids on host hermit crabs are debated. These hydroids are known to deter some predators such as octopuses and crabs (Brooks and Mariscal, 1985a) although others such as the American lobster *Homarus americanus* H. Milne Edwards, 1837, may still prey on hosts (Weissberger, 1995). The hydroids can also influence the outcome of competition between hermit crabs for shells, thereby allowing coexistence of hermit crab species in areas where shells are limited (Wright, 1973). In addition, hydroids may inhibit boring species (e.g., sponges, polydorids) from invading the shells (although some species such as *Dipolydora commensalis* are often found in shells covered with *Hydractinia* sp.) (Buckley and Ebersole, 1994). Braverman's (1960) experiments on the differentiation of spiral zooids in colonies of *P. carnea* associated with *P. longicarpus* suggest hermit crabs influence morphological differentiation in some hydractiniids. Spiral zooids differentiate on the edge of the colony around the gastropod shell aperture. Braverman (1960) clearly showed that these zooids developed only if crabs were in the shells, were reabsorbed when crabs were removed, and redifferentiated when crabs were returned to the shells. Presumably this phenomenon is affected by the continued movements of the crab within the shell aperture and crab metabolites do not appear to be involved (Braverman, 1960). The adaptive significance of the spiral zooids is not known, but it has been suggested that they function in capturing benthic organisms scraped out of the sediments during the crab's deposit feeding. It is also possible that they are used to prey on zoeae released through the aperture by brooding females (Cerrano et al., 1998; McDermott, 2001). Rees (1967) found the same general situation with *H. echinata* on shells inhabited by *P. bernhardus* and speculated that the spiral zooids might prevent undesirable organisms from entering the shell.

Experiments with *H. symbiolongicarpus* and *P. carnea* have shown that the presence of the host crab (*P. longicarpus*) affects the degree of interspecific competition between these two hydroids and also has some effect on the number of zooids in colonies and colony morphology (Van Winkle et al., 2000). More recently, Van Winkle and Blackstone (2002) showed that sexually produced colonies of *Hydractinia symbiolongicarpus* are competitively dominant to *P. carnea* but dominance on hermit crab shells is a complicated process with *P. carnea* able to overgrow *H. symbiolongicarpus* when the latter is flanked. The planula larvae of *H. symbiolongicarpus* settle on all regions of shells that are coated with bacteria; post-settlement movement and mortality determine the final distribution of colonies on shells inhabited by hermit crabs (Yund et al., 1987). In addition to competition between colonies, Brooks and Mariscal (1986b) examined interspecific competition between the sea anemone *Calliactis tricolor* and hydroids; these species rarely co-occur on hermit crab shells in nature.

Another colonial hydroid associated with hermit crabs is *Hydrocorella africana* from South Africa (Millard, 1975), a calcified hydroid that initially forms low encrusting colonies like *Hydractinia* spp. The skeleton of this hydroid becomes thicker and exhibits larger processes (Fig. 6A,B); its growth can also extend the aperture of the shell (Millard, 1975). Similar growth patterns are found in *H. sodalis* and *H. spiralis* from Japan (Goto, 1910). *Janaria mirabilis* is a calcified hydroid found along the west coast of North and South America as well as in Fiji (Cairns and Barnard, 1984) that forms distinctive branches from the gastropod shells (3–8 branches, each approximately 10–30 mm long) for which the species gets its common name "staghorns". Unlike *Hydractinia* spp., *J.*
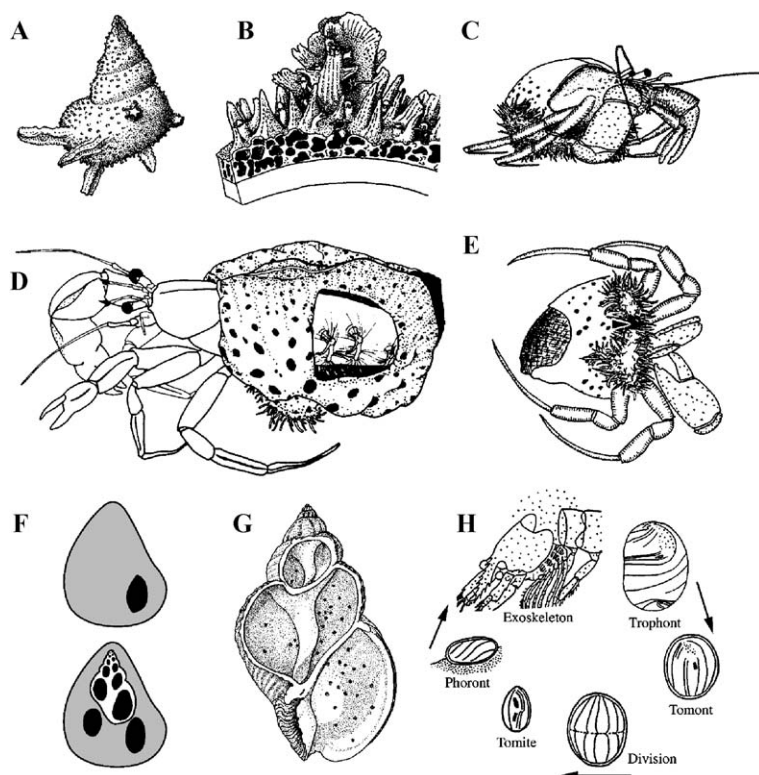
Fig. 6. Epibiotic and protozoan associates of hermit crabs. (A) *Hydrocorella africana*, whole colony on hermit crab shell (modified from Millard, 1975, Fig. 39A). (B) *Hydrocorella africana*, section of colony showing calcareous skeleton and hydranths (modified from Millard, 1975, Fig. 39B). (C) *Adamsia palliata*, lateral view of anemone associated with *Pagurus prideaux*, showing position of tentacles (modified from Ross, 1984, Fig. 2A). (D) *Adamsia palliata*, dorsal view with cut-away showing pleopods of *Pagurus prideaux* (modified from Matthews, 1959, Fig. 1). (E) *Adamsia palliata*, ventral view showing food seized by anemone (arrowhead) (modified from Ross, 1984, Fig. 2C). (F) Bryozoan growth on a gastropod shell, external view (top) and sectioned sample (bottom) (modified from Taylor 1994, Fig. 6). (G) *Circeis paguri*, tubes of the polychaete worm inside a cut-away view of the gastropod, *Buccinum* sp. (modified from Al-Ogily and Knight-Jones, 1981, Fig. 2A). (H) *Hyalophysa* sp., life-cycle diagram. Top left shows release of trophonts of the ciliate from the exoskeleton of hosts such as hermit crabs (modified from Landers et al., 1999, Fig. 1).

mirabilis encrusts the entire shell (external and internal surfaces) and does not exhibit a concentration of dactylozooids around the aperture (Cairns and Barnard, 1984).

Zoanthids associated with hermit crabs are represented by over 20 species in the genus *Epizoanthus*, including at least 13 species that attach directly to the abdomen of hosts (Ates, 2003). *Epizoanthus incrustatus*, *E. paguriphilus*, and *E. abyssorum* from the north–east Atlantic were studied by Muirhead et al. (1986). The latter two are associated with deep-water hermit crabs while the former is a shallow-water species. *E. incrustatus* colonizes hermit crab shells but is also found free-living, even forming colonies initiated on single sand grains. In *E. paguriphilus*, after settlement on a hermit crab shell, the

zoanthid begins to form polyps and an aperture cavity into which the hermit crab can grow without switching shells (Fig. 4B,C). The zoanthid will form as many as ten polyps and be molded into the form of a shell by the movements of the hermit crab abdomen (Muirhead et al., 1986; Urzelai et al., 1990). *E. abyssorum* has a maximum of four polyps, the primary one forms at the apex of the shell; ventral polyps may be positioned to ingest food particles dropped by hosts (Fig. 4C) (Muirhead et al., 1986). *Epizoanthus paguropsides* takes the place of shells for host hermit crabs (Schäfer et al., 1983). The colony covers the abdomen of *Paguropsis typica* and is held in place by modified pereopods and uropods (Balss, 1924; Schäfer et al., 1983).

Among the anemones associated with hermit crabs, most species are restricted to shallow-water hermit crabs in warmer seas and exhibit geographic distributions that largely coincide with hosts (Ross, 1967, 1983). Anemones represent the only symbionts that hermit crabs are known to feed and actively position on their shells (Fox, 1965; Ross, 1967; Kinzelbach, 1976). The "cloak anemone" *Adamsia palliata* and *Calliactis parasitica* (Fig. 5B) are found in the Atlantic from Europe to North Africa, as well as the Mediterranean (Ross, 1967; see Cornelius and Ates, 2003 for a discussion of the correct species name). It had long been suggested that *A. palliata* is an obligate commensal of *Pagurus prideaux* but Ates (1995) showed the species could be found with other hermit crabs of the same genus. *P. prideaux* is known to facilitate the detachment and reattachment of the anemone when moving shells and will feed the anemone, at least when the crabs are juveniles (Kinzelbach, 1976; Ross, 1984). The anemone is typically oriented such that the mouth is positioned below the aperture of the occupied shell and growth of this species can allow the host to avoid switching shells (Fig. 6C–E) (Ross, 1974). *A. palliata* can survive in the laboratory for years without the presence of hermit crabs, if fed sufficiently (Ates, 1995).

Caruso et al. (2003) examined the association of *A. palliata* with *P. prideaux* along a bathymetric cline in Italy. At 10–90 m, all *P. prideaux* specimens were associated with the anemone. The hermit crabs often inhabited suboptimal shells (broken or too small) and thus the anemone compensated or provided protection. However, in water deeper than 600 m, no *P. prideaux* were found with anemones. While hermit crabs lacking anemones showed no difference in shell use patterns, those with anemones preferentially inhabited globose shells (e.g., Naticidae). In the same region, *P. eremita* was found with *Calliactis* sp. in shallow water only. Individuals of *Calliactis* sp. were positioned near the apex of inhabited shells while other shell epibionts (vermetid gastropods and serpulid polychaetes) were commonly around the aperture of shells; the hermit crabs may position the anemones to balance the shells (Caruso et al., 2003), as in the association between *P. pollicaris* and *C. tricolor* (Brooks, 1989). Along the southeastern coast of the United States, *Dardanus venosus* and *D. arrosor* from waters deeper than approximately 18 m are primarilly found with *C. tricolor* (Brooks, personal communication).

Behavioral research on anemone-hermit crab associations have shown that *C. parasitica* will move from other surfaces to hermit crab shells (as well as live gastropod shells); when *P. bernhardus* was present the hermit crab was not involved in the transfer of anemones (Ross, 1967). However, *C. parasitica* is usually found associated with hermit crabs and this predilection for hermit crab shells is probably due to the abundance of potential hermit crab hosts and defense mechanisms of live gastropods that deter

settlement (Ross, 1967). In addition, *D. arrosor* assists *C. parasitica* onto occupied shells by manipulating the base of the anemones; however, typically only females assisted in such movements (Ross, 1967). Associations between *C. parasitica* and hermit crabs from the northern Aegean Sea are initiated during the first year of life for both the anemone and hosts (Christidis et al., 1997).

Cutress and Ross (1969) found the transfer of *C. tricolor* (Fig. 4E) onto shells by *D. venosus* follows a pattern similar to that observed for *C. parasitica*. Brooks and Mariscal (1986a) showed that two populations of *P. pollicaris* associated with *C. tricolor* differed in the number of transfers of anemones to their shells. Based on laboratory research, Brooks and Mariscal (1986a) found that the presence of predators such as *Octopus joubini* (Robson, 1929), induces increased numbers of anemone transfers and may explain the behavioral differences between populations. Over a nine-year period Sandford (2003) found *C. tricolor* associated with four species of hermit crabs from the Gulf of Mexico; approximately 67% of *Petrochirus diogenes* carried the anemone while 7.3% and 5.5% of shells inhabited by *Pagurus impressus* and *P. pollicaris*, respectively, had anemones. From one to eleven anemones were associated with *P. diogenes*. The anemone was rarely (0.1%) found with *C. vittatus*, probably representing cases where the anemone becomes associated with this intertidal hermit crab after shell abandonment by more appropriate hosts (Sandford, 2003).

Paracalliactis mediterranea is associated with *Pagurus alatus* (reported as *P. variabilis*) from the Mediterranean, and has been shown to preferentially associate with hermit crab shells, although *P. alatus* does not facilitate the settlement of the anemone (Ross and Zamponi, 1982). Alternatively, association with *Paracalliactis rosea* is initiated by *Sympagurus dimorphus* in New Zealand (Hand, 1975b). *Neoaiptasia commensali* is a commensal of hermit crabs from Bombay, India; the anemone may be found singly or up to four per shell (Parulekar, 1969). *Sagartiomorphe guttata* and *S. paguri* are positioned near the aperture of hermit crab shells (Cutress and Ross, 1969). Interestingly, *Sagartiomorphe* sp. is positioned by *Diogenes edwardsi* on its cheliped and the anemone covers the shell aperture when the host is withdrawn (Ross, 1975, 1983). *Sagartiogeton undatus* has been found with *Pagurus excavatus* from deep water in the northern Aegean Sea; the species forms associations with hermit crabs at a young age (Chintiroglou et al., 1992). A number of unidentified anemones have been found with hermit crabs from deep-sea regions (Fautin, 1992; Lemaitre, 1993, 1994, 1996). Lemaitre (1993) showed unidentified anemones attached to the inside of bivalve shells inhabited by specimens of the hermit crab *Bivalvopagurus sinensis*; the anemones grew beyond the shell margins and were positioned with the tentacles and mouth below sternum of hosts.

Morphology of the deep-sea anemones *Stylobates* spp., known only as hermit crab symbionts, is modified presumably as a result of their association. Gastropod shells inhabited by crabs become completely covered by the chitinous carcinoecium of these anemones (Fig. 4G) (Dunn et al., 1980). *Stylobates aeneus* occurs in Hawaii and Guam, *S. cancrisocia* off east Africa, and *S. loisetteae* off the northern coast of western Australia (Dunn et al., 1980; Fautin, 1987). *Stylobates* spp. attach to small shells inhabited by hermit crabs and then coat the shell with a chitinous parchment-like material that grows in the form of a coiled shell around the hermit crab abdomen (Fig. 4D,G) (Dunn and Liberman, 1983; Fautin, 1992). The association is inferred to be mutualistic, with anemones gaining

hard substrates in an otherwise unstable sandy or mud benthos and the hermit crabs gain homes that grow with them, thereby alleviating the need to switch shells (Fautin, 1992). Similar to the position of *A. palliata*, the oral disc of *Stylobates* sp. is found beneath the mouth of the hermit crab hosts (Fautin, 1987).

A single example of an association between sea anemones and juvenile stages of hermit crabs exists. The megalopae of *Paguropsis typica* host an unidentified nynanthean actinian that attach singly to the abdomen of larval *P. typica* from the Indo-West Pacific (Schäfer et al., 1983). Schäfer et al. (1983) indicated the dumb-bell shaped anemones might feed on food dropped by the megalopae. This association requires additional studies since the anemone has not been described and identity of the host as *P. typica* is probably not correct (McLaughlin, personal communication).

3.4. Phylum Platyhelminthes

Several species of polyclad turbellarians inhabit the lumen of shells occupied by hermit crabs (Table 1). The only species of polyclad for which the relationship with hosts has been clearly defined, however, is *Stylochus zebra* (Figs. 3C, 5E) (Lytwyn, 1976, 1979; Lytwyn and McDermott, 1976). *P. pollicaris* is its primary host but it has also been found with *P. impressus*, *P. longicarpus*, *P. diogenes*, and *D. venosus* (Lytwyn, 1976, 1979; Lytwyn and McDermott, 1976; McDermott, 2001). While *S. zebra* has been found on other substrates, abundant evidence gathered by Lytwyn (1979) and long-time observations by McDermott (unpublished data) have shown that the hermit crab shell is its main habitat.

Other polyclads associated with hermit crabs are *Emprosthopharynx opisthoporus* and *Euprosthiostomum adhaerens*, both symbionts of *Petrochirus californiensis* (Bock, 1925). Palombi (1936) described *Euprosthiostomum viscosum* as associated with *P. prideaux* from the Mediterranean Sea. Similarly, *Emprosthopharynx rasae*, was recovered from the shells inhabited by *Calcinus latens* from Hawaii (Prudhoe, 1968). Lytwyn (1979) found an unidentified species of *Emprosthopharynx* associated with *Pagurus impressus, P. diogenes*, and *D. venosus* from off North Carolina. In two cases, this worm and *S. zebra* were in the same shell with *P. impressus*. Three species of polyclads described by Hyman (1940, 1950, 1955), *Stylochus pulcher*, *Stylochoplana inquilina,* and *Notoplana inquilina*, were recorded from gastropod shells inhabited by unidentified species of hermit crabs from North Carolina, Hawaii, and Washington, respectively. *S. inquilina* was found within the umbilicus or on the surface of the gastropod shell as well as crawling over the surface of an unidentified symbiotic anemone. It is not known whether this polyclad also inhabits the shell lumen. Lytwyn (1979) found *S. pulcher* in North Carolina and identified the host as *P. diogenes*; none of the other five species of hermit crabs that he examined contained *S. pulcher*.

Lytwyn's (1979) comprehensive study on the life history of *S. zebra* was over the geographical area from Massachusetts to Florida. In Woods Hole, MA, he found that the prevalence of the polyclad reached a maximum (≈ 82%) in March, declined steadily until August, and then increased in the fall and winter. Worms cemented their egg masses to the inside of gastropod shells mainly in June and July. Hatched ''adult-like'' ciliated worms were presumably planktonic and settled out as young worms that began to appear with

crabs in August and September. The presence of *Hydractinia symbiopollicaris* may reduce the prevalence of worms with *P. pollicaris*. *S. zebra* is a predator of the eastern white slipper snail, *Crepidula plana*, that lives attached to the inside of the host's shell (Lytwyn and McDermott, 1976; Lytwyn, 1979). During the crab's brooding season, however, its embryos become additional prey for the worms. Thus, this symbiotic relationship is complex. The crab provides the worm with shelter from predation, a food source in the form of attached animals, and a continuous exchange of ambient water. While the worm presumably causes no harm to the brooding female, it surely reduces its reproductive potential due to embryo predation. Male crabs are not harmed and female crabs are affected only seasonally during brooding. Lytwyn (1979) viewed this *Stylochus–Pagurus* relationship as commensalism with a type of periodic parasitism.

Hyman (1944) originally described *Ectocotyla paguri*, a small turbellarian flatworm, from the integument of *Pagurus pubescens*, as having large embryos in the coelom but later suggested that the embryos were those of the host hermit crab (Hyman, 1964). Later, Fleming and Burt (1978) showed that *E. paguri* is a synonym of *E. hirudo*, a flatworm found previously on the surface setae of *P. pubescens* by Levinsen (1879). The structures within the body of the flatworm that Hyman (1964) identified as the host hermit crab embryos were found to be the testes of the flatworm. Such a misidentification is understandable since the gut of the flatworm serves a dual purpose in feeding and in development of the eggs after the gastrodermis breaks down. The brooding of larvae within the gut of the flatworm and release of large active hatchlings that can immediately attach to hosts is suggested to be an adaptation for the ectocommensal lifestyle of this species (Petrov, 2000). *Ectocotyla hirudo* was found by Petrov (2000) in shells of *Parapagurus pilosimanus*; the species is also found on the mouthparts, on the gills, and in the gill chamber of *Chionoectes opilio* (Fabricius, 1788) and *Hyas araneus* (Linnaeus, 1758) (Fleming and Burt, 1978). A very similar species, *Ectocotyla multitesticulata*, is also found on the same host brachyurans (Fleming and Burt, 1978) and may form associations with hermit crabs. The food and feeding habits of these species remain unknown and in spite of the previous confusion regarding reproductive structures, these flatworms may be egg predators of host crabs. *Ectocotyla* is closely related to the genus *Peraclistus*, members of which live on the egg masses of *H. araneus* and are suspected egg predators (Kuris, 1991).

3.5. Phylum Nemertea

Only one identified and three unidentified nemerteans have been found with hermit crabs and they all appear to represent incidental associations.

3.6. Phylum Rotifera

Proales paguri is a rotifer found on gills of *P. bernhardus*; up to 40 rotifers were found on the gills of a single *P. bernhardus* specimen and of the larger hermit crabs observed approximately 50% were infested (Thane-Fenchel, 1966). The rotifer feeds on epithelial cells of the host gills and while the species has been considered a parasite of hermit crabs (Bush et al., 2001), the negative impacts on hosts have not been shown. Larger hermit

crabs probably exhibit higher prevalence of the rotifer because they molt less often than young hosts and therefore provide a more stable substrate (Thane-Fenchel, 1966).

3.7. Phylum Nematoda

Hermit crab assemblages have never been examined specifically for nematodes, and thus only five presumably incidental nematode associates of hermit crabs have been documented.

3.8. Phylum Annelida, class Polychaeta

With 105 species associated with hermit crabs, the polychaete worms are the second most prevalent group in this analysis (Table 1). In addition, the polychaetes bore in shells, attach externally and internally, live freely within the lumen, and attach to hosts, thereby providing examples of nearly all of the potential forms of associations with their hosts (Fig. 1B). Most polychaetes are facultative or incidental associates but six are obligate commensals of hermit crabs (Fig. 1A).

Many epibiotic polychaetes use hermit crab shells as a substrate for settlement (e.g., *Sabellaria vulgaris*) and represent incidental associations. Most studies on these poly-chaetes are confined to the family Spirorbidae (Al-Ogily and Knight-Jones, 1981; Rzhavsky and Britayev, 1988). Six *Spirorbis* species are facultative symbionts of hermit crabs, while *Circeis paguri*, which creates tubes in the lumen of gastropod shells occupied by *P. bernhardus* (or attaches to the telson of the host), appears to be an obligate commensal (Fig. 6G) (Al-Ogily and Knight-Jones, 1981). Other epibiotic species include *Hydroides dianthus*, *Serpula concharum, S. vermicularis*, and *Terebella lapidaria*. *S. vulgaris* and *H. dianthus* were found on 3.2 % and 0.4 % of shells inhabited by *P. longicarpus* along the east coast of the United States, respectively (McDermott, 2001). *Hydroides plateni* exhibits a preference for gastropod shells occupied by hermit crabs; single shells were found with as many as 50 worms, predominately located on the dorsal side of shells collected in seagrass beds of Brazil (Creed, 2000).

Free-living polychaete worms associated with hermit crabs are largely confined to the families Iphitimidae, Nereidae, Polynoidae, and Syllidae (Clark, 1956; Gilpin-Brown, 1969; Goerke, 1971; Achari, 1977; Pettibone, 1986; Comely and Ansell, 1989). The commensal relationships between polynoids and invertebrate taxa are diverse and have been reviewed (e.g., Clark, 1956; Martin and Britayev, 1998). Several polynoids that are found inside the shells of hermit crabs take up a considerable amount of internal volume and possibly act as egg predators (no evidence for this behavior has been reported but see section 4.3.3 on egg predation). *Lepidonotus sublevis* is a common scaleworm associate of *Pagurus* spp. from the east coast of the United States, usually found singly in shells; approximately 25% of shells inhabited by *P. longicarpus* contain this worm that can reach lengths of ~ 3.5 cm (McDermott, 2001). A species of *Lepidonotus* (originally identified as *L. squamatus* but probably *L. sublevis*) has been found with *Discorsopagurus schmitti*, a hermit crab that inhabits the tubes of *Sabellaria cementarium* Moore, 1906, and *Serpula vermicularis* Linnaeus, 1767, from Japan and Washington (Caine, 1980). *Gaudichaudius cimex* is another scaleworm species found in shells occupied by *Diogenes dubius* (reported

as *D. custos*) and *D. alias* (reported as *D. diogenes*) along the east and west coasts of India; typically 2 to 3 specimens feed on particles from the meals of host hermit crabs (Achari, 1977). The scaleworms were found in hermit crab shells with actinians attached as well as on bivalve shells carried by *Dorippe* sp. (Achari, 1977). *Eunoe depressa* from the Alaskan Shelf was found in 46–99% of hermit crab shells examined while *Arctonoe vittata* was found in ∼ 6 % of shells from the Norton Sound of Alaska (Hoberg et al., 1982). *Lagisca extenuata* is found in approximately 30% of shells inhabited by *P. bernhardus* from Plymouth, England (Brightwell, 1953).

Other free-living worms in the lumen of shells include *Neanthes fucata*, which is an obligate symbiont of hermit crabs. The species steals food from hosts (kleptoparasitism) and ingests the eggs of *P. prideaux* and *P. bernhardus* in the laboratory (Brightwell, 1953; Matthews, 1959). Gilpin-Brown (1969) showed young worms extended their anterior ends from burrows on the benthos until coming into contact with hermit crab shells into which they then entered. Shell entry behavior was also examined by Cram and Evans (1980). Searching behavior appears to be induced by mechanical stimuli from shells being dragged on the sediment rather than chemical cues from the host. Adult worms were observed to enter shells from the dorsal side via the upper lip and quickly moved to the apical whorls (Brightwell, 1951) where mucous tubes were produced (Cram and Evans, 1980). Typically, the worms are positioned with the anterior end over the abdomen of hermit crabs (Fig. 8A); when feeding, the worm will extend over the hermit crab and feed on particles between the third maxillipeds of the host (Brightwell, 1951). The worm will also feed on hermit crab eggs soon after extrusion from the gonopores of hosts, prior to their fixation on pleopod setae (Matthews, 1959). Host hermit crabs do not attack worms once they are in the shells. Special mucous secreting glands within the parapodia may enhance the ability of *N. fucata* to move over the surface of shells [these glands are lacking in free-living nereids (Martin and Britayev, 1998)]. Active searching for hosts and specialized structures indicate a symbiotic (commensal or transient parasite) relationship, not the incidental one suggested by some (see review by Clark, 1956). As many as 50–90% of hermit crabs from different localities may harbor *N. fucata*, usually with one worm per shell (Jackson, 1913; Clark, 1956; Reiss et al., 2003). Such high prevalence of worms motivated fisherman of Britain to collect hermit crabs to secure worms for bait (Jackson, 1913). Male and female worms mature in two and three years, respectively (Goerke, 1971).

Harrington (1897) described the nereid *Cheilonereis cyclurus* in association with *Pagurus ochotensis*; approximately 20% of hermit crab shells from the northeastern Gulf of Alaska contain this worm, which has now been found with seven species of hermit crabs (Hoberg et al., 1982). Harrington (1897) suggested that the nature of the symbiosis was mutualistic, with worms gaining food and protection from hosts, while hosts could possibly benefit by the worm removing parasites such as bopyrids and rhizocephalans before they have had a chance to parasitize hermit crabs. Harrington also provided data on morphological modification of the worms, such as that found in *N. fucata*. Modifications in *C. cyclurus* include muscular degeneration in the posterior segments protected by the shell (although branchiae are fully developed) and striped pigmentation on the anterior segments that may mimic the legs of host hermit crabs (Harrington, 1897). Harrington found only adult female worms associated with hermit crabs suggesting that males might

be free-living. Hand (1975b) observed *Cheilonereis peristomialis* extending from shells of *Parapagurus dimorphus* at the same time as the host crabs stimulated *Paracalliactis rosea* to move onto shells. The worms would move among the tentacles of the anemones without harm and feed on food particles suspended by the hermit crab host. Additional nereids associated with hermit crabs include *Neanthes caudata*, *N. succinea*, *Nereis acuminata*, and *N. pelagica* but little is known of their association with hosts.

López et al. (2001) found three species of *Syllis* facultatively associated with hermit crabs in the Indian and Pacific Oceans, *Syllis pontxioi* and *S. ferrani* in the shell lumen and *S.* cf. *armillaris* in the apical whorl and under the base of actinian polyps attached to the shell. *Eusyllis blomstrandi* produced parchment tubes in the apical whorls of shells (López et al., 2001) and was found in 3.4% of shells inhabited by hermit crabs from the northeastern Gulf of Alaska (Hoberg et al., 1982). López et al. (2001) indicated that the feeding biology of the syllids remained unknown; the worms might feed on host food or eggs of the host as well as materials brought in by respiratory currents.

In their original description, Fage and Legendre (1933) indicated that *Iphitime paguri* is found on the gills of host hermit crabs, and suggested it is a parasite of host crabs. However, others (Moore and Gorzula, 1973; Comely and Ansell, 1989) have noted it only in the apical whorls of shells inhabited by host hermit crabs. Thus, it appears that *I. paguri* is usually in the apical whorls of hermit shells, while other species such as *I. cuenoti* are gill symbionts of various brachyuran species. More recent research has indicated that the worms are commensals, feeding on materials captured by hosts or brought in through respiratory currents (Martin and Britayev, 1998). Approximately 3–7% of *P. bernhardus* are found with *I. paguri* (Fage and Legendre, 1925; Comely and Ansell, 1989).

Shell-boring polychaetes belonging to the families Cirratulidae, Sabellidae, and Spionidae negatively impact host hermit crabs by reducing shell strength and thereby increasing risk of predation. *Polydora* and related genera (termed polydorids) within the family Spionidae are the most prevalent borers in hermit crab shells. Twenty-one polydorids are considered facultative associates of hermit crabs; three are obligate commensals of hermit crabs (*Dipolydora commensalis*, *Polydora bioccipitalis* and *P. robi*). Some species, such as the widely distributed *D. armata* that is found on the west coast of North and South America, the Caribbean Sea, New Zealand, Australia, Japan, Philippines, Indonesia, and Europe, can reach high densities (hundreds of individuals, up to 35–40 worms per square centimeter) within borings in the calcareous algal coverings of hermit crab shells (Bick, 2001; Williams, 2001b; Radashevsky and Nogueira, 2003). In the Mediterranean Sea the species is found in up to 70% of shells inhabited by hermit crabs (Bick, 2001), while in the Philippines the species is found in up to 24% of shells occupied by eight species of hermit crabs (Williams, 2001b). Asexual reproduction (via architomy) allows for rapid use of the substrate and high densities.

The biology of the obligate polydorids *D. commensalis* and *P. robi* has been the subject of considerable research (Andrews, 1891; Hatfield, 1965; Radashevsky, 1989; Dauer, 1991; Williams and McDermott, 1997; Williams, 2000, 2001a, 2002). While other polydorids create U-shaped burrows with silty tube extensions distributed relatively randomly over hermit crab shells (see Blake and Evans, 1973), *D. commensalis* and *P. robi* create unique burrows that follow the columella of shells inhabited by hermit crabs. The burrow of *D. commensalis* is initiated on the columella near the outer lip and winds

around toward the apex where the worm can have access to the lumen (Fig. 7B, D). The burrow of *P. robi* is initiated on the columella along the lumen of the shell and leads to an opening to the exterior of the shell at the apex (Fig. 7A) (Williams, 2000, 2001a). *D.*
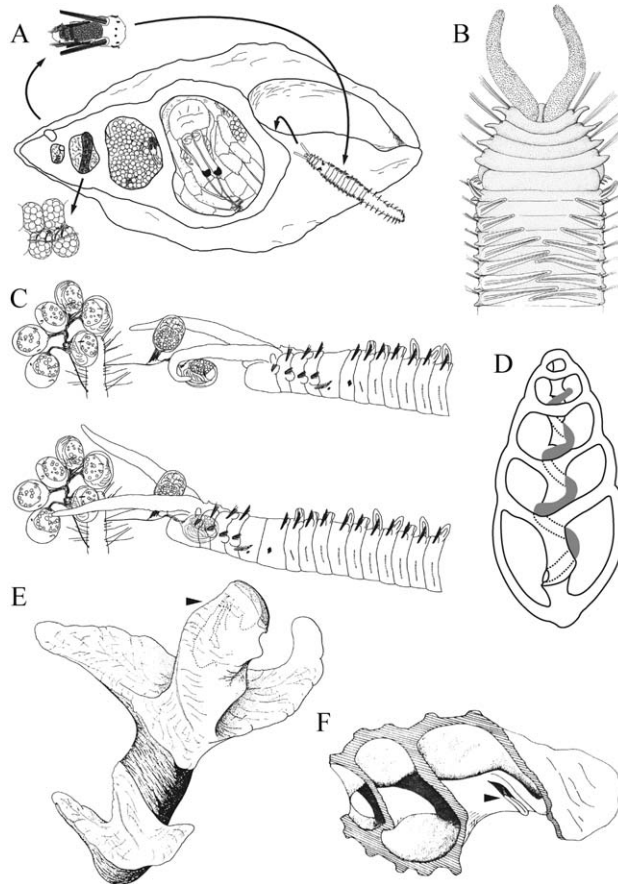
Fig. 7. Boring organisms associated with hermit crabs. (A) *Polydora robi*, life-cycle diagram of the worm. Adult worm is shown in apex of cut away *Drupella cornus* shell among the eggs of host hermit crab, *Calcinus gaimardii*. Egg capsules of worm shown on lower left, three segment larvae of worm shown in upper left and 20 segment juvenile shown on the columella of shell (Williams, 2001a,b, Fig. 6). (B) *Dipolydora commensalis*, anterior end of adult worm showing palps (feeding appendages) (Blake, 1971, Fig. 11a). (C) *Polydora robi*, embryo predation. Top figure shows palps of adult worm contacting embryos of *Calcinus latens*, bottom figure shows ingestion of an embryo (attachment stalk between embryo and pleopod setae is unbroken) (Williams, 2002, Fig. 5). (D) *Dipolydora commensalis*, burrow morphology in *Nassarius obsoletus* (modified from Williams, 1995, Fig. 1). (E) *Tomlinsonia asymetrica*, an adult boring barnacle specimen removed from a gastropod shell; the twisted shape of the barnacle conforms to its position in the columella, arrowhead shows anterior end of barnacle with cirri inside (modified from Turquier and Carton, 1976, Fig. 1A). (F) *Trypetesa nassarioides*, cut-away view of *Nassarius incrassatus* shell with arrowhead showing opening of the boring barnacle on the columella (modified from Turquier, 1967, Fig. 3).

commensalis is found in approximately 35–50% of a variety of gastropod shells inhabited by *P. longicarpus* along the east coast of the United States (Dauer, 1991; McDermott, 2001). *P. robi* is found in up to 35% of shells inhabited by hermit crabs from the Philippines (Williams, 2002). Both species reduce shell strength and are egg predators of host hermit crabs although the impacts of *D. commensalis* on host hermit crab reproductive success has not been evaluated (Williams, 2002).

D. commensalis and *P. robi* feed with a pair of palps that contain a ventral ciliated food groove. The worms are able to suspension and deposit feed; food particles collected from the water or embryos removed from pleopod setae are captured and then transferred to the mouth for ingestion through a combination of muscular and ciliary action (Fig. 7C) (Williams and McDermott, 1997; Williams, 2002). Both species produce egg capsule strings that are attached to the inside of the female burrow. *D. commensalis* produces approximately 2400 eggs (Hatfield, 1965; Blake, 1969); *P. robi* has been documented to produce over 8000 eggs (Williams, 2001a). Larvae develop in these capsules until the 5 and 3-segment stages, respectively, at which time planktotrophic larvae are released. After a period of development in the water, the juvenile worms will settle on gastropod shells inhabited by hermit crabs (Fig. 7A). Cues responsible for settlement on hermit crabs shells have not been studied in these species but chemical cues detected by sensory nuchal organs are suspected to be involved, as described in other commensal polydorids (Hsieh, 1994).

In spite of the prevalence of polydorids in commercially important molluscs (e.g., mussels, oysters and scallops), the boring mechanism is not completely understood (Sato-Okoshi, 1999). The boring process appears to be accomplished by a combination of mechanical abrasion of the shell with the fifth setiger spines of the worm and enzymatic digestion of the shell by secretions of the worm (Dorsett, 1961; Haigler, 1969; Zottoli and Carriker, 1974; Sato-Okoshi and Okoshi, 1993). *P. robi* and additional polydorids possess glands in the fifth segment as juveniles that may be used in burrow formation soon after settlement on shells occupied by hermit crabs (Williams, 2001a).

Boring cirratulids and sabellids have been examined in association with both gastropod and bivalve molluscs (Blake, 1969; Oakes and Fields, 1996; Martin and Britayev, 1998). *Dodecaceria concharum* is a common cirratulid borer of molluscs, including shells occupied by hermit crabs; numerous shells of *Calcinus gaimardii* contained *Dodecaceria* sp. from sites in the Philippines (Williams, unpublished data). *Dodecaceria* sp. reproduces asexually through architomy and can thus reach high densities in such substrates. Boring sabellids include *Pomatoceros triqueter* and *Potamilla reniformis*; these are filter-feeding worms that extend their tentacular crowns from borings within the gastropod shells and feed on suspended particles.

3.9. Phylum Sipuncula

Two species of sipunculan worms have been found with hermit crabs, including *Phascolosoma annulatum* a species found behind pagurids inhabiting bryozoan tubes collected in New Zealand (Taylor, 1991). While these are incidental associates, certain sipunculans occupy empty gastropod shells and thus may compete with hermit crabs for shells in some regions (Morris et al., 1991; Vermeij, 1993).

3.10. Phylum Arthropoda

Arthropods are the most prevalent hermit crab associates; 50 of the 126 associates are obligate commensals (Table 1; Fig. 1A). Members of the phylum Arthropoda fill all of the potential forms of associations with hosts (Fig. 1B) and are the only species found with terrestrial hermit crabs. Amphipods, barnacles, copepods, and decapods are the most abundant groups with 40, 28, 19, and 13 species represented, respectively.

3.10.1. Infraclass Cirripedia, superorder Acrothoracica

The acrothoracican barnacles bore into a variety of calcareous substrates including mollusc shells and corals (Tomlinson, 1969a,b; White, 1969; McDermott, 2001). The family Trypetesidae contains six extant species among two genera (*Trypetesa* and *Tomlinsonia*), which are obligate commensals of hermit crabs from the western Atlantic, California, the French coast of the English Channel, Japan, Madagascar, and the Philippines (Hancock, 1849; Tomlinson, 1953; Utinomi, 1962; Turquier, 1967, 1976; Turquier and Carton, 1976). Hancock (1849) described the first acrothoracican, *Trypetesa lampas* (originally as *Alcippe lampas*), from dead gastropod shells collected in the waters of Great Britain. Hermit crabs were not mentioned, but it is evident that these shells were at one time occupied by hermit crabs. *T. lampas* bores into nine species of gastropod shells occupied by three species of European hermit crabs (Table 1) (Turquier, 1967; White, 1969; Reiss et al., 2003). The barnacle was also discovered along the east coast of the United States (and the Gulf of Mexico) in association with *P. longicarpus* and *P. pollicaris* (Tomlinson, 1969a; Spivey, 1979; McDermott, 2001) as well as in the Philippines (Rosell, 1982). In the eastern Pacific, *Trypetesa lateralis* is found along the coast of California in four species of gastropod shells occupied by four species of *Pagurus* (Table 1) (Tomlinson, 1953). *Trypetesa nassarioides* was described by Turquier (1967) from the Atlantic coast of France where it bores into shells used primarily by *Anapagurus hyndmanni* (Fig. 7F). Utinomi (1962) described *Trypetesa habei* from shells occupied by unidentified hermit crabs collected in Japan. Further morphological information on this barnacle was provided by Tomlinson (1969a). One other trypetesid associated with hermit crabs is *Tomlinsonia asymetrica*, which is found with *C. latens* from Madagascar (Turquier and Carton, 1976). Both *Trypetesa* and *Tomlinsonia* exhibit simplification of the feeding structures, presumably correlated with their mode of microphagous feeding (Turquier and Carton, 1976).

To establish the barnacle–crab relationship, the invasive cyprid larvae must metamorphose on the gastropod shell and begin the boring process. The barnacle cyprid's predilection for hermit crab inhabited shells may be due to some influence of the crab, the shell itself, or both. White (1969) showed that *Buccinum undatum* Linnaeus, 1758 shells harboring *P. bernhardus* had a significantly higher prevalence of *T. lampas* than several other gastropod species. There was a significant positive correlation between the length of *B. undatum* and prevalence of the barnacle, but this was not the case with *Neptunea antiqua* (Linnaeus, 1758) shells. The numbers of barnacles per *B. undatum* shell was positively correlated with shell length. All of White's findings suggest that both size and species of shell and the presence of a hermit crab are in some way involved in cyprid metamorphosis; he concluded that the attractive forces remain to be determined. In the

western Atlantic there was a significantly greater prevalence of *T. lampas* in shells of *Nassarius obsoletus* than *N. trivittatus* occupied by *P. longicarpus* (two of the most common shell species used by this crab; 95% of all 15 species of shells recorded) (McDermott, 2001). *N. obsoletus* was the larger and more abundant of the two species and had a larger maximum number (4 versus 1) of barnacles per shell. McDermott (2001) suggested that shell size, some difference in the calcareous composition, and/or the greater abundance of *N. obsoletus* shells (76% versus 19% of all shells) might be involved in the apparent difference in prevalence. Turquier's (1970) experimental approach showed that cyprid larvae of *T. lampas* and *T. nassarioides* settled almost exclusively on shells inhabited by hermit crabs and that there were significant differences in the discrimination of crab and gastropod shell types. Lambers and Boekschoten (1986) completed morphological analyses of bore hole morphology of *T. lampas* in hermit crabs shells from the Wadden Sea. They found the barnacles were concentrated around the columella and most of the barnacles were small (mean length 0.44 mm). The lack of large barnacles was suggested to be due to the frequent changes of shells by hermit crabs, leading to the death of barnacles (Lambers and Boekschoten, 1986). However, this is not likely because in most hermit crab populations empty shells are very limited and those that are abandoned are quickly occupied (e.g., Kellogg, 1976). Growth and development of *T. lampas* is also influenced by environmental factors (Lambers and Boekschoten, 1986).

Trypetesa uses the chitinous teeth of the mantle for rasping a bore hole within the shell substrate, and there is evidence from *T. nassarioides* that carbonic anhydrase from the mantle may aid the boring process by loosening the shell's protein matrix (Turquier, 1968). These teeth are replaced at molting (Tomlinson, 1969a,b). The female barnacle produces its bore holes on the lumen side of the shell. These bore holes are expanded as the barnacle grows but the aperture remains as a relatively small slit (Fig. 7F). *T. lateralis*, however, may continue boring through to the outside of the shell, thus allowing water to circulate in and out of the lumen around the barnacle (Tomlinson, 1969a). Such an accessory exit was also documented in *Trypetesa polonica* from the Korytnica Basin of Central Poland (Baluk and Radwański, 1991). These authors suggested that the accessory exit aids in passive flow of water, especially important to the survival of the barnacles if shells are abandoned by hermit crabs and perhaps during feeding; as indicated above, however, abandoned shells are quickly occupied in most hermit crab populations. *T. habei* and *T. spinulosa* typically produce borings in the columella but are also found in the sutures of shells. *Trypetesa nassaroides* and *T. asymetrica* are found only in the columella and the bodies of these barnacles are coiled to conform to the spiral of the shell (Fig. 7E) (Baluk and Radwański, 1991). These species reach large sizes (taking up a large portion of the columella) and *T. asymetrica* exhibits extensions from the body that penetrate into areas of the shell away from the columella (Fig. 7E) (Turquier and Carton, 1976).

Little is known of the food or feeding in trypetesids, but the reduced cirri may allow ingestion of particles suspended by the respiratory currents of the hermit crab or particles dropped during the masticatory activities of the crab. Based on observations of ingestion and digestion of ink particles in *T. lateralis*, Tomlinson (1969a) suggested that trypetesids could not engage in macrophagous feeding. However, particles need not be very minute as evidenced by an acrothoracican from the Philippines that feeds on the embryos brooded by host hermit crabs (Williams, 1999). Baluk and Radwański (1991) suggested that

trypetesids may feed on food particles discarded by hermit crabs or the feces of hermit crabs. Dwarf males are involved in reproduction and have no gut or cirri. In *T. lampas* there is a free-living naupliar stage whereas in *T. lateralis* the nauplii metamorphose into cyprid larvae, which are then released (Tomlinson, 1953, 1955, 1969a). Lack of potentially widespread larvae may be responsible for the patchy distribution of *T. lateralis* along the coast of California noted by Tomlinson (1960). *T. lampas* in British waters seems to be uniformly distributed (White, 1969).

Lithoglyptes habei, although reported from a shell occupied by one unidentified hermit crab collected in New South Wales, Australia, is a borer of dead mollusc shells and corals (Tomlinson, 1969a). In this regard it resembles two other members of the genus that are facultative associates of hermit crabs.

3.10.2. Infraclass Cirripedia, superorder Thoracica

There are many thoracican barnacles known to populate the outside of gastropod shells inhabited by hermit crabs (e. g., Jensen and Bender, 1973; McLean, 1983; McDermott, 2001) but only two appear to be truly commensal. Zullo (1991) reported that *Heteralepas quadrata* was associated with the shell of an unidentified hermit crab from Santa Fe Island in the Galápagos archipelago, attached to the columella of the gastropod *Malea* sp. This pedunculate, plateless barnacle, however, is considered by Hickman and Zimmerman (2000) to be primarily an epibiont of the red spiny lobster *Panulirus penicillatus* (Oliver, 1791) and the slipper lobster *Scyllarides astori* Holthuis, 1960.

Three members of the symbiotic, pedunculate barnacle genus *Koleolepas* attach to gastropod shells, positioned under sea anemones (Table 1). *Koleolepas willeyi* was described from a single specimen attached inside a hole near the apex of a gastropod shell covered with anemones collected in the Loyalty Islands of New Caledonia (Stebbing, 1900). *Koleolepas tinkeri* was described from shells (*Tonna* sp.) collected in Oahu, HI, with *Calliactis armillatas* attached (Edmondson, 1951). Unfortunately, the hermit crabs were not identified and limited data on their relationship with host crabs exist. *Koleolepas avis* attaches to the outside of gastropod shells that harbor the hermit crab *D. arrosor* in Japan (Hiro, 1931, 1933; Yusa and Yamato, 1999; Yusa et al., 2001). The barnacles were found with one or more specimens of the symbiotic anemone *Calliactis japonica*, up to 97% of the time (Yusa et al., 2001). The barnacle was not found on shells with *Dardanus tinctor* (originally as *D. varipes*), *D. impressus*, or *D. lagopodes,* all of which were associated with the anemone *Calliactis polypus*. The barnacles were attached to shells around and underneath the anemones' pedal discs and averaged $\approx$ 3 per shell. Their number was positively correlated with the total diameters of the anemones on the shell (Yusa et al., 2001), but was not correlated with their total weight or number; the barnacles fed on the tentacles of the anemone. Thus, there is a hypersymbiotic complex involving barnacle and anemone commensals of hermit crabs (Table 4). If *C. japonica* is found to provide the hermit crab some protection from predators, mutualism may be involved.

Another thoracican associated with hermit crabs is *Pagurolepas conchiola* described as a new species by Stubbings (1940) from shells inhabited by *Sympagurus andersoni* (originally as *Parapagurus andersoni* var. *brevimanus*), collected near Zanzibar at 732 m during the John Murray Expedition of 1933–1934. This barnacle (only two observed) was deep within the spire attached to the lumen walls of unidentified gastropod shells. Utinomi

(1970) identified a single barnacle, *P. conchiola,* attached to a shell with *Dardanus aspersus* (originally as *D. diogenes*) found at 64 m in Japan. The subspecies *P. conchicola atlantica*, inhabiting shells with *Tomopagurus cokeri* from 220 to 256 m off southern Florida, was described by Keeley and Newman (1974). Stubbings (1940) speculated that *P. conchicola* might feed on the crabs' feces, but the barnacle's food and feeding habits remain unknown (Keeley and Newman, 1974).

3.10.3. Subclass Copepoda

Approximately 20 species of copepods are associated with hermit crabs, 14 of them apparently obligate commensals in the lumen of inhabited shells (Table 1). Among the harpacticoid copepods, members of the genera *Hemicyclops, Paraidya,* and *Sunaristes* exhibit an elongate form more typical of planktonic species and are usually found in the apical whorls of the shells (Fig. 8B). In contrast, members of the harpacticoid genus
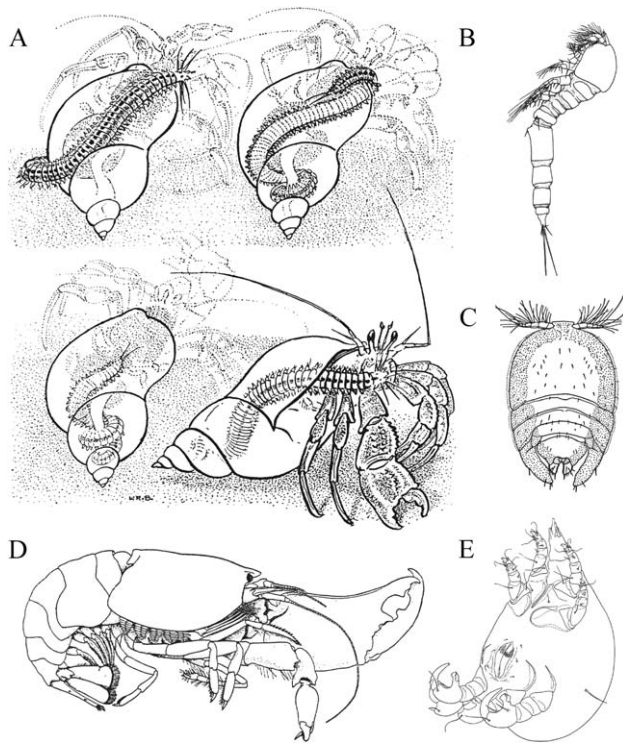
Fig. 8. Free-living species and mites associated with hermit crabs. (A) *Neanthes fucata*, sequence showing the movement of the worm into a glass shell occupied by *Pagurus bernhardus*. Picture in bottom right shows worm in position to steal food from the mouthparts of the host hermit crab (modified from Brightwell, 1951, Fig. 3). (B) *Sunaristes japonicus*, lateral view of adult female copepod (modified from Ho, 1986, Fig. 3). (C) *Porcellidium paguri*, dorsal view of adult female copepod (modified from Ho, 1986, Fig. 25). (D) *Aretopsis amabilis*, lateral view of adult male shrimp with large claw (modified from Bruce, 1969, Fig. 1). (E) *Ewingia coenobitae*, ventrolateral view of female (note large claws on third and fourth legs for attachment to host gills) (modified from Yunker, 1970, Fig. 1).

Porcellidium are dorso-ventrally flattened and are found crawling on the inside surface of shells (Fig. 8C).

Most members of the Porcellidiidae are found on the surface of seaweeds, although some are associates of invertebrates (e.g., echinoids and oysters), including four species that are obligate commensals of hermit crabs. *Porcellidium brevicaudatum* was originally described from washings of invertebrates but has now been documented from 12 species of hermit crabs in Korea, Madagascar, Mauritius, New Caledonia, New Guinea, and Sri Lanka (Humes and Ho, 1969b; Humes, 1972; Kim and Kim, 1996). *Porcellidium paguri* (Fig. 8C), *P. similis,* and *P. tapui* were described from hermit crabs collected in Japan, Korea, and New Zealand, respectively (Hicks and Webber, 1983; Kim and Kim, 1996). An unidentified species of *Porcellidium* is known from hermit crabs in the Philippines (Williams, unpublished data). Thus, members of the genus *Porcellidium* associated with hermit crabs are restricted to the Indo-West Pacific. These species produce small broods of eggs (2–6 per brood; each egg ~ 100–130 μm in diameter) not enclosed by an egg sac, and copepodids are found with adults in hermit crab shells. Humes (1972) found as many as 253 females, 241 males, and 129 copepodids of *P. brevicaudatum* in one shell occupied by *Dardanus megistos*.

The genera *Parasunaristes* and *Sunaristes* contain five described species that are obligate commensals of hermit crabs. Fiers (1982) split the genus *Sunaristes* into *Parasunaristes* and *Sunaristes*, and the former now contains *P. dardani*, an associate of hermit crabs from Madagascar, Mauritius, Eniwetok Atoll, and New Caledonia (Humes and Ho, 1969a; Humes, 1971, 1972). Three *Sunaristes* species are known from the Indo-West Pacific, *S. inaequalis* (Madagascar, Mollucas, Red Sea and Australia), *S. japonicus* (Japan) (Fig. 8B), and *S. tranteri* (Red Sea, Madagascar, and New Caledonia); *S. paguri* is known from European hermit crabs. Hamond (1973) found a potentially undescribed species of *Sunaristes* in association with *Pagurus novizealandiae* from New Zealand, but Ho (1986) indicated that it might represent *S. inaequalis*. Codreanu and Mack-Fira (1961) found a total of 55 specimens of *S. paguri* from washings of 246 shells occupied by *D. pugilator* from the Mediterranean (~ 22% prevalence). Females of *Sunaristes* species produce two egg sacs containing many eggs (each ~ 57 μm in diameter) and shells are often found with large numbers of developing copepodid larvae (Ho, 1988). Dispersal is probably via nauplius larvae (Ho, 1988). Specimens of *Sunaristes* have been found within hermit crab shells collected from the Philippines, Singapore, and Hong Kong (Williams, unpublished data).

While Sewell (1940) described *Paraidya major* and *P. minor* from sea weed-washings, Humes (1981) suggested they may have been dislodged from hermit crab shells and the genus appears to contain three obligate commensal species found with hermit crabs from Madagascar and Moluccas. Females produce approximately four large oval eggs (each 175 μm long in *P. minor*, 279 μm in *P. major*, and 213 μm in *P. occulta*). As in *Porcellidium* and *Sunaristes* species, copepodid larvae of *Paraidya* are associated with adults in hermit crab shells; for example, Humes (1981) found 28 females, 22 males, and 17 copepodids from one *Dardanus lagopodes* host on Ceram Island, Indonesia. *Paraidya occulta* and *P. brevicaudatum* co-occurred in 13 collections of hermit crabs and in three instances *P. occulta*, *P. brevicaudatum* and *S. dardani* occurred in the same hermit crab shells. Similarly in the Philippines, *Porcellidium* sp. and *Sunaristes* sp. occur in the same shells occupied by *Calcinus gaimardii* (Williams, unpublished data).

The genus *Brianola* contains three species associated with hermit crabs from Australia. Hamond (1973) suggested that these might be facultative associates of hermit crabs since many of the other species within this genus are free-living. Among 1000 specimens of *Diogenes senex* examined, Hamond (1973) found 20 female, 30 male, and 33 copepodid larvae of *B. pori*, 9 female, 9 male, and 105 copepodid larvae of *B. sydneyensis*, and 13 female and 12 male of *B. elegans* from Australia. All of these species and *Sunaristes tranteri* were found in the same population of hermit crabs from the coast of Sydney. Fiers (1982) recorded *B. elegans* free-living in Papua New Guinea and indicated that it was a facultative symbiont. Reproduction in members of the genus *Brianola* is similar to that of *Sunaristes* in which two eggs sacs are produced, each with many small eggs.

The copepod order Poecilostomatoida is represented by two members of the genus *Hemicyclops* associated with hermit crabs. *Hemicyclops geminatus* is found with three species of hermit crabs from Curaçao where up to five copepods are found per shell (Stock, 1992). *Hemicyclops vicinalis* was described by Humes (1995) from *Dardanus guttatus* collected in Madagascar; only two females and one male were collected from a single hermit crab. For this reason the symbiotic relationship is not clear until more collections are made. Additional copepod associates of hermit crabs appear to be incidental associations. However, *Asterocheres suberitis* is often found associated with *Suberites domuncula* attached to shells inhabited by hermit crabs. Thus it represents an example of hypersymbiosis (Table 4). Although not an obligate commensal of *S. domuncula*, *A. suberitis* feeds on sponges (Mariani and Uriz, 2001). Unfortunately such data on the feeding biology of obligate copepod commensals of hermit crabs (e.g., *Sunaristes* and *Porcellidium*) is lacking; it is likely that they feed on material brought in by the branchial currents of the crab hosts and/or their feces. Another copepod hypersymbiont, *Mesnilia* sp., is found in the burrows of *Dipolydora* cf. *socialis* from hermit crabs collected in Hong Kong (Williams, unpublished data). Presently there are only two described *Mesnilia* species [*Mesnilia cluthae* (Scott, 1896) and *Mesnilia martinensis* Canu, 1898, both from the British Isles] from the burrows of *Dipolydora* species (Gotto, 1993).

3.10.4. Order Mysida

Some members of the Mysida (opossum shrimp) are symbionts within the lumen of hermit crab shells. *Heteromysis harpax* is the most familiar hermit crab associate in this predominantly symbiotic genus; six *Dardanus* species act as hosts for *H. harpax*. Relatively little was known of this mysid's relationships with its hosts (Tattersall, 1962) until the detailed studies of Vannini et al. (1993, 1994). The latter employed specially fabricated glass shells for viewing the intimate interactions of the mysids and hermit crabs.

H. harpax lives inside occupied gastropod shells, typically within the apical shell whorls but also swimming or crawling to other parts of the lumen (Vannini et al., 1994). It feeds on the feces of the host (Tattersall, 1962), as well as suspended particles and plankton (Vannini et al., 1994). In a communication to Tattersall (1962), Bruce reported that *H. harpax* from Zanzibar was found in about 75% of the *Dardanus* specimens examined. Vannini et al. (1993) examined several species of *Dardanus* along the coasts of Somalia and Kenya where 46% and 66% of the crab shells were infested with mysids, respectively. No differences in infestation rates were apparent among the various species of *Dardanus*, nor between the sexes and sizes of the crabs. The mysids were usually found

as adult pairs, or with many smaller individuals ($\approx$ 13% of the infestations), possibly representing one or more broods; a maximum of 77 mysids occurred with one of the crabs. The average brood number was 7.7 (16 maximum), and there was a significant positive correlation between brood size and mysid length. Specimens of both sexes reach 7.8 mm in total length ($\approx$ 5.0 mm carapace length) and therefore occupy a considerable portion of the lumen.

Both males and females of *H. harpax* have massive, subchelate third thoracic endopods (thoracopods). Bacescu and Bruce (1980) refer to these thoracopods as being amphipod-like. Since these large appendages are found only in the species of this genus, which inhabit hermit crab shells, they may be adapted for holding on to the abdomen of the crab (Tattersall, 1962; Vannini et al., 1993). Vannini et al. (1994) showed that the mysids follow their hermit crab host as it moves into a new shell. Thus, all evidence indicates that *H. harpax* is an obligate symbiont of *Dardanus* species from Mozambique northward to Tanzania, Kenya, Somalia, and the Red Sea (Tattersall, 1962; Vannini et al., 1993). The alpheid decapod *Aretopsis amabilis* also used gastropod shells that harbored *Dardanus* species, but *A. amabilis* was never found in the same shells with *H. harpax* (Vannini et al., 1993). Unlike the mysid it occurs only in pairs. In Somalia 58% of the shells harbored one or the other symbiont (46% with mysids and 12% with alpheids). In Kenya where alpheids did not occur, 66% of the hermit shells were infested with *H. harpax.*

Three other species of *Heteromysis* live with hermit crabs. *H. harpaxoides*, a symbiont of *D. megistos* in Australia, was described as a new species by Bacescu and Bruce (1980). It is morphologically very similar to *H. harpax. Heteromysis stellata*, another new Australian species described by Bacescu and Bruce (1980), was recovered from hermit crabs belonging to the genus *Aniculus. Heteromysis odontops* was recorded in unidentified "*Pagurus* shells" by Tattersall (1951) from the coasts of Washington, California and the west coast of Panama. There is no further information on the host relationships for these species. *Heteromysis australica* Bacescu and Bruce, 1980 and *H. abrucei* Bacescu, 1979 have apparently not been linked with hermit crabs.

3.10.5. Order Amphipoda

There are many references in the literature to amphipods living in the lumen of shells with hermit crabs, but most represent incidental associations; possibly obligate relationships exist only with amphipods of the families Liljeborgiidae and Isaeidae. Those occurring incidentally are well-known associates of a variety of invertebrates, e.g., burrows of polychaetes, synaptid holothurians, and mud shrimps (Vader, 1995). *Liljeborgia aequabilis* appears to be an obligate symbiont of hermit crab shells from Australia (Vader, 1995; Vader and Myers, 1996). This amphipod is often found in pairs, and sometimes with a few cohorts of juveniles. Approximately 40–70% of *Dardanus arrosor*, *Paguristes frontalis*, and *Strigopagurus strigimanus* were infested in Australia (Vader, 1995). Unlike many other amphipods recorded as hermit crab associates, *L. aequabilis* is usually found in the apical whorls of gastropod shells. This is true also for *L. dellavallei* in the Mediterranean Sea (Cuadras and Pereira, 1977) and *Liljeborgia* sp. from New Zealand (Vader, 1995). Taylor (1979) recorded the occurrence of a single specimen of *Liljeborgia* sp. living in a shell with *Pagurus hemphilli* from California. Vader (1995) suggested that *L. aequabilis*, although in close contact with the hermit crab

in the shell lumen, is not a symbiont of the crab itself because of the absence of subchelate pereopods or specialized dactyls. In the association between *Pagurisaea schembrii* and *Paguristes pilosus*, the amphipods not only occupy the apical shell whorls but also are located in the dense setae on the legs and cephalothorax of the crab (Moore, 1983). Moore found 50 or more amphipods per crab, and he suggested that they feed on detritus adhering to the setae. It is likely that *P. schembrii* and similar amphipods living in the apical shell whorls would at times be in intimate contact with the crab and might be expected to reside on the body of the crab. Myers (1974) reported that individuals of *Gitanopsis paguri* were in the branchial chambers and attached to the body of *Dardanus megistos* from Kenya, but were not free in the shell lumen. This amphipod then is seemingly only a crab symbiont. Myers referred to this relationship as commensalism, but we suggest that further study is needed to decide whether this amphipod exists free in the lumen as does *P. schembrii*.

Vader and Myers (1996) recorded five new species of amphipods (Ischyroceridae) associated with hermit crabs in Australia; *Ericthonius brevicarpus* from *D. arrosor* and *Strigopagurus strigimanus*, *Ruffojassa festa* from *S. strigimanus*, *Ventojassa helenae* and *V. zebra* from *D. arrosor* and *S. strigimanus*, and *Veronajassa neptunea* from *D. arrosor*. None of these amphipods appeared to live in the top whorls of the host shells, nor did any information suggest their relationships were anything more than facultative. *Ruffojassa andromedae* is known to produce mucous tubes around the aperture of shells inhabited by hermit crabs from New Zealand (Moore, 1985).

Hoberg et al. (1982) examined 8594 gastropod shells that harbored nine species of hermit crabs from otter trawls at five locations in waters of Alaska (including sponge material that may have overgrown the gastropod shells). Amphipods were found only among the 389 crabs collected at the northeastern Gulf of Alaska location. The hermit crabs with amphipods were *Pagurus aleuticus*, *P. confragosus*, *P. ochotensis*, *P. setosus*, and *Elassochirus cavimanus*. Species of *Melita* (Melitidae) were the most common amphipods; *Gnathopleustes pugettensis* and *Gammaropsis* (= *Podoceropsis*) *nitida* were also collected. A total of only 33 amphipods was recovered from the 389 crabs, all of which Hoberg et al. (1982) called commensals. No evidence was presented, however, which would suggest that they should be so classified. Reiss et al. (2003) found *Gammaropsis nitida* in 64–87% of shells occupied by *P. bernhardus* from the North Sea.

3.10.6. Order Decapoda, infraorder Caridea (with notes on orders Stomatopoda and Mysida)

The only caridean shrimp known to associate with hermit crabs is *Aretopsis amabilis* (Fig. 8D), which has been found with species of *Dardanus* from the northeast coast of Africa, the Red Sea, Seychelles and Japan (Table 1) (Bruce, 1969; Vannini et al., 1993). In the waters of Somalia, shrimp used some of the same hermit crab shells that harbored the mysid *Heteromysis harpax*, but were never found with the mysids (Vannini et al., 1993), presumably due to some behavioral mechanism. Shrimp occurred in pairs in 12% of the shells, and were usually located in the apical whorls of the shells. Vannini et al. (1993) also found stomatopods (*Mesacturoides fimbriatus* and *Gonodactylus* sp.) in two shells with *Dardanus lagopodes*, and suggested that these free-living predators would have evicted or eaten either of the two symbionts. These symbioses are amenable to experimental studies

dealing with factors involved in establishment of relationships, competition between the symbionts, and predator avoidance.

3.10.7. Order Decapoda, infraorder Anomura

Four species of porcellanid crabs inhabit shells with hermit crabs (Table 1). Glassell (1936) described three of these from the eastern Pacific Ocean as new species. He suggested that *Pisidia magdalenensis* was probably free-living. Parente and Hendrickx (2000) found this crab associated with *Petrochirus californiensis* in Mexican waters but confirmed that the crab was also found free-living. Gore and Abele (1976) found *P. magdalenensis* free-living along the Pacific coast of Panama. *Porcellana cancrisocialis* and *P. paguriconviva* are found with *P. californiensis* as well as other hermit crab species.

Glassell (1936) described an interesting symbiotic web involving *P. californiensis*, which is usually found in the shell of *Murex nigritus* Philippi, 1845. An unidentified polynoid polychaete was often in the lumen of shells occupied by a pair of *Porcellana paguriconviva* and occasionally the white slipper snail *Crepidula* cf. *nivea* was attached. Some of the slipper snails harbor the pinnotherid brachyuran *Fabia granti* (Table 4). Unfortunately little else is known of these relationships. Ranging from North Carolina to Brazil, *Porcellana sayana* is associated with eight species of hermit crabs (Table 1) but it also has been found free-living (Haig, 1956; Gore, 1970, 1974; Felder, 1973; Fothering-ham, 1976; Telford and Daxboeck, 1978; Williams, 1984; Brooks and Rittschof, 1995). This porcellanid is also a symbiont attached to the foot or in the mantle cavity of the queen conch *Strombus gigas* Linnaeus, 1758. Approximately 80% of conchs observed in the spring of 1976 in Barbados harbored *P. sayana*; typically there was one crab per conch, but no more than two (Telford and Daxboeck, 1978). The sympatric milk conch, *Strombus costatus* Gmelin, 1791 was never infested. In Barbados only hermit crabs in queen conch shells were infested (usually with more than one porcellanid per crab; to a maximum of eleven) (Telford and Daxboeck, 1978). In North Carolina where there were no queen conchs, *Dardanus venosus, Pagurus pollicaris* and *Petrochirus diogenes* were often found in the shells of *Neverita duplicata* (Say, 1822) and *Fasciolaria lilium hunteri* (G. Perry, 1811). Telford and Daxboeck (1978) observed that when *P. diogenes* moved into empty shells in the laboratory, the porcellanids followed. They suggested that the association of *P. sayana* with live conchs was of secondary importance to symbioses with hermit crabs because of the greater number of symbionts per host and that the color pattern of the porcellanids tended to mimic that of the hermit crabs, particularly *P. diogenes*.

Brooks and Rittschof (1995) conducted laboratory experiments to assess the chemical sensitivity to host effluents and host selection of *P. sayana* collected in North Carolina. Aside from the host hermit crabs themselves, they were particularly interested in the effects on *P. sayana* of co-occurring symbionts (e.g., the symbiotic sea anemone *C. tricolor*, on which the porcellanid would often locate rather than the shell surface itself). *P. sayana* was attracted to the effluent of *C. tricolor* significantly more often than to effluents from the host crab *D. venosus*, the free-living anemone *Aiptasia pallida* (Verrill, 1864), or tissue from the gastropod *Neverita duplicata*. Furthermore, the attraction of *P. sayana* to *C. tricolor* was significantly greater than to shells that harbored the hermit crab or to *A. pallida*. *P. sayana* was seldom seen in close contact with the latter and is apparently sensitive to the adverse effects of its nematocysts. Thus, *P. sayana* is strongly attracted to the symbiotic anemone. It

would have been informative had Brooks and Rittschof (1995) used the other host hermit crabs in their tests since Telford and Daxboeck (1978) made no mention of *C. tricolor* being involved in the porcellanid–hermit crab relationship in Barbados.

P. sayana harbors the bopyrid parasite *Aporobopyrus curtatus* (Richardson, 1904) in its branchial chamber (Markham, 1975) (Table 4). This parasite is found also in three other species of porcellanids [*Petrolisthes armatus* Gibbes, 1850, *P. galathinus* (Bosc, 1802), and *P. haigae* Chace, 1962].

Interestingly there is one report of a hermit crab hosting another hermit crab. Fenizia (1934) found *Calcinus tubularis* (originally as *C. ornatus*) in empty serpulid tubes attached to the shells of *Pagurus striatus* (with *Adamsia rondelettii* also attached); *C. tubularis* fed on food suspended by the host hermit crab.

3.10.8. Order Collembola

Collembola (springtails and allies) are mostly known from soil habitats but two species are obligate symbionts of tropical land hermit crabs of the genus *Coenobita* (Table 1). *Coenaletes vangoethemi* is found in the shells of *Coenobita rugosus* from New Guinea (Jacquemart, 1980) while *C. caribaeus* is known from *Coenobita* spp. in the Dominican Republic, St. Croix, and Mexico (Bellinger, 1985; Mari Mutt, 1994; Palacios-Vargas et al., 2000).

3.10.9. Class Pycnogonida

A single pycnogonid species, *Anoplodactylus* cf. *lentus*, has been found with *P. longicarpus*, on which it is found among the polyps of *H. symbiolongicarpus* (McDermott, 2001). Other pycnogonids such as *Phoxichilidium femoratum* (Rathke, 1799) found with hydroids are suspected hypersymbionts of hermit crabs (Table 4).

3.10.10. Order Acari

Twelve mite species are associated with hermit crabs; most are restricted to land hermit crabs and, as in the case of collembolid associates, all are obligate symbionts (Table 1). Mites of the genera *Ewingia* and *Hoogstraalacarus* use modified third and fourth legs to attach between the gill lamellae of hosts (Fig. 8E). Members of the genus *Askinasia* attach to the setae of the vas deferens on the fifth legs of hosts (Pearse, 1932; Fain et al., 1982). Pearse (1932) found up to 172 mites of the species *Ewingia coenobitae* on *Coenobita clypeatus* from the Dry Tortugas. Two *Askinasia* species are found on land hermit crabs from Kenya and *Hoogstraalacarus tiwiensis* is found on land hermit crabs from Egypt (Yunker, 1970). André (1937) described *Andregamasus conchylidae*, *Laelaps pagurophilus*, and *Physalozercon paguroxenus* from *Coenobita* sp. collected in Vanuatu (New Hebrides). *Andregamasus steinitzii* was described associated with *Coenobita scaevola* collected from Dahlak Kebir Island in the Red Sea (Costa, 1965). Mites of the genera *Andregamasus, Laelaps*, and *Physalozercon* do not exhibit the stout claws for clutching onto hosts crabs as in the genera *Askinasia, Ewingia* and *Hoogstraalacarus*; members of the former three genera appear to roam over the abdomen of host hermit crabs (Costa, 1965).

Hunter and Poe (1971) described the mite *Ereynetes (Anereynetes) coenobitus* associated with *Coenobita clypeatus* from Puerto Rico. However, the mites were discovered after maintaining the hermit crabs within terrariums at the University of Missouri for over a year.

Mites crawled over the surface of host crabs and on the surface of occupied shells; approximately 30 mites were found on the largest crab. Feeding was not observed directly but the mites were occasionally found in regions of the gill filaments, perhaps ingesting fluid (Hunter and Poe, 1971). The closely related species *Ereynetes* (*Anereynetes*) *papuanus* has been found with *C. rugosus* from New Guinea (Fain and Van Goethem, 1978).

3.11. Phylum Mollusca, class Gastropoda

Most living gastropods found with hermit crabs form incidental associations. However, *Crepidula convexa*, *C. fornicata* and especially *C. plana* show some predilection for hermit crab shells, the former two species on the outside and the latter in the lumen (Fig. 5C, D) (Franz and Hendler, 1970; Frey, 1987; Collin, 2000; McDermott, 2001). Franz and Hendler (1970) found that *C. convexa* attached to shells inhabited by *P. longicarpus* had a significantly higher height/width ratio than *C. convexa* attached to clam shells. Both *C. convexa* and *C. plana* represent species complexes (Collin, 2000, 2002). *C. convexa* has been divided into two species, with *C. convexa* occurring along the east coast of North America while *C. ustulatulina* Collin, 2002 is found in the Gulf of Mexico and southeastern Florida (Collin, 2002). Due to its recent recognition as a new species, *Crepidula ustulatulina* has not been reported from hermit crabs but it is probable the species has been identified previously as *C. convexa* from hermit crabs. *C. plana* has been divided into *C. atrasolea, C. depressa* (Gulf of Mexico and southeastern coast of the United States) and *C. plana* (New England to Georgia) (Collin, 2000). *C. plana* has been introduced to California from the Atlantic (Morris et al., 1980). Shenk and Karlson (1986) found colonization of hermit crab shells by *C. convexa*, *C. fornicata*, and *C. plana* was inhibited by colonial hydroids (*Hydractinia* sp.). In addition, postcolonization processes such as interspecific competition altered the distribution of *C. plana* and *C. fornicata* (more abundant on shells inhabited by *P. pollicaris*) but not *C. convexa* (more abundant on shells inhabited by *P. longicarpus*) (Shenk and Karlson, 1986).

Other *Crepidula* inhabit the inner surfaces of hermit crab shells (Table 1); all have a concave morphology that conforms to the shape of the shells and lack pigmentation or spiny periostracal projections (Hoagland, 1977; Yipp, 1980; Vermeij, 1989; Brown and Olivares, 1996; Fatima, 2003). Yipp (1980) examined the feeding biology of *Crepidula walshi* from hermit crabs in Hong Kong. The gastropods attach inside hermit crab shells and become positioned dorsal to the carapace of hosts. Here the gastropods benefit from an increased food supply, decreased predation, and a stable environment. *C. walshi* and other *Crepidula* species that attach inside hermit crab shells do not form stacks of individuals but rather one basal female and two attached males are found in shells (Yipp, 1980; Fatima, 2003). *Crepidula philippiana* is found inside of shells occupied by *Paguristes weddelli* from Chile and exhibits direct development after nurse egg consumption (Gallardo, 1977). Juveniles of *C. philippiana* may colonize new shells when hermit crabs are clustered, as suggested for mobile males of *C. coquimbensis* (Brown and Olivares, 1996).

While some species of *Crepidula* are largely restricted to the interior of hermit crab shells, *C. grandis* attaches to the exterior and interior of hermit crab shells as well as other substrata (Vermeij, 1989). Vermeij found up to 23% and 25% of hermit crab shells from Japan with *C. grandis* on the exterior or interior, respectively. *Crepidula adunca* is found

on the exterior of hermit crab shells as on the living gastropod, *Tegula funebralis* (A. Adams, 1855) (Putnam, 1964; Walker, 1992). In addition to members of the genus *Crepidula*, *Sabia conica* is a facultative associate found on the exterior of hermit crab shells from the Indo-Pacific (Vermeij, 1989) and *Leptonetis perplexus* is found attached inside of hermit crab shells from New Zealand (Collin, personal communication).

Several nudibranchs exhibit a distinct association with epibionts such as sponges, hydroids, or bryozoans on hermit crab shells (e. g., *Doris verrucosa* on sponges, *Cuthona nana* and *Precuthona peachi* on hydroids and *Corambe obscura* on bryozoans). These predatory nudibranchs, as well as most of their prey species, are probably facultative associates of hermit crabs. It seems likely, however, that some of these nudibranchs have developed relationships with their prey species (hydroids, bryozoans) living on hermit crab shells that is more intimate than just predation (Table 4). That is, the presence of the prey may induce the metamorphosis of their veliger larvae (e.g., Harris et al., 1975; Christensen, 1977).

3.11.1. Class bivalvia

Bivalves attached to hermit crab shells are mostly incidental species. Most attach to the outside of shells with juvenile byssus threads (e. g., *Anadara ovalis*, *Chlamys varius*), persistent threads (e.g., *Modiolus barbatus*, *Mytilus edulis*), a calcareous byssus (e.g., *Anomia simplex*, *Pododesmus patelliformis*), or cementation of the whole left valve (e.g., *Crassostrea virginica*, *Ostrea edulis*). Species such as *Gastrochaena dubia* and *Hiatella arctica* may bore into the shells.

In contrast to those recorded above, *Curvemysella paula* appears to be an obligate symbiont of hermit crabs. Morton and Scott (1989) found *C. paula* inside gastropod shells inhabited by *D. edwardsii* from Hong Kong; the bivalve has also been recorded from Japan and Australia (Tanaka, 1991). Due to its attachment inside the shells inhabited by hermit crabs, the species exhibits a characteristic concave ventral margin (Savazzi, 2001).

3.12. Phylum phoronida

One phoronid worm *Phoronis ovalis* has been found to bore into shells occupied by *P. bernhardus* from the North Sea (Reiss et al., 2003).

3.13. Phylum bryozoa, order Cyclostomata

Taylor et al. (1989) listed 13 species of bryozoans associated with six species of hermit crabs off the Otago Peninsula of New Zealand. Six of these symbionts, associated with six species of hermit crabs, belong to the Cyclostomata (*Favosipora otagoensis, Disporella gordoni, Heteropora parapelliculata, Heteropora* sp., *Plagioecia* cf. *gemelligera, Tubulipora* cf. *anderssoni*). Five of the six crabs are in the family Paguridae and the other in the Diogenidae (Table 1). These bryozoans show no apparent specificity for shells occupied by particular species of hermit crabs (Taylor et al., 1989). All of these species tend to completely encrust the gastropod shells (Fig. 6F), often extending out beyond the aperture as elongated tubes of varying lengths and curvatures.

Two of the cyclostomes, *F. otagoensis* and *H. parapelliculata*, were found only on shells with hermit crabs, and thus were considered possible obligate species. As Taylor et al. (1989, p. 1082) pointed out, "this may reflect more an incomplete knowledge of the New Zealand bryozoan fauna than obligatory symbiosis." Tubes produced by the cyclostome bryozoans (some quite massive, often 100 times the hermit crab weight) are inhabited by an array of organisms similar to those that associate with the typical gastropod shells of hermit crabs. Taylor (1991) noted that the deposit-feeding sipunculan *P. annulatum* might live simultaneously with a hermit crab inside the tube constructed by *D. gordoni*. Similarly, the tube produced by *H. parapelliculata* is occupied by the carnivorous polychaete *Eunice tentaculata*. Just inside the apertures of these bryozoan tubes may be serpulid polychaetes, folliculinids, and other species of bryozoans. The outer surfaces may harbor sponges, barnacles, serpulids, bivalves, tanaidaceans, cheilostomes, or spionid worms (Taylor, 1991). The nature of these symbioses has yet to be determined.

3.13.1. Order Cheilostomata

Of six hermit crab species from New Zealand, Taylor et al. (1989) recorded seven bryozoans from the Cheilostomata (*Akatopora circumsaepta, Arachnopusia unicornis, Crepidacantha zelanica, Osthimosia monilifera, O. socialis, Schizomavella trachoma, Schizosmittina maplestonei*). Both *O. monilifera* and *A. circumsaepta* have been found only on hermit crab shells and are considered obligate associates, with the aforementioned caveat (Taylor et al., 1989). *Akatopora circumsaepta* was the only one among the 13 bryozoan species from the Otago region to have been found previously with hermit crabs (Taylor et al., 1989).

As compared to most of hermit crabs, those living in shells encrusted with bryozoan tubes rarely engage in shell fights or shell exchanges because the host shell lumen continues to enlarge as a result of the bryozoan growth beyond the aperture (Taylor et al., 1989). Thus, when a heavy bryozoan colony is found on a shell, a mutualistic situation may exist. Crabs benefit by being exposed less to predation by minimizing shell exchanges. The added shell weight, however, may decrease locomotive rate or demand greater energy expenditure to maintain normal movement (Taylor, 1994). Species of hermit crabs that have morphological and physiological adaptations for filter feeding would be less affected by locomotive inhibition (Schembri, 1982). Probably any encrusting bryozoan colony benefits from its attachment to a hermit crab shell because burial is avoided. The feeding currents generated by some hermit crabs may bring additional particulate food to the colony.

Gordon (1972) showed that *Hippopodinella adpressa* from Goat Island Bay, New Zealand was found mainly on gastropod shells (97% of 200 shells), 50% of which contained the hermit crab *P. novizealandiae*. Living gastropods were not encrusted, but colonies were found infrequently (3%) on other surfaces. Gordon (1972) suggested that the aggregating behavior of the hermit crabs in shallow water might help to facilitate cross-fertilization among the *H. adpressa* colonies. Other advantages include prevention of desiccation and sedimentation of the colonies. Although such advantages for the bryozoan exist, Gordon (1972) suggested that competent larvae of *H. adpressa* are attracted to calcareous substrates rather than to hermit crabs themselves. This can be substantiated only by appropriate experiments on larval selection. Experiments by Cook (1968, 1985)

showed that larvae of *Hippoporidra senegambiensis* were more attracted to *Turritella* sp. shells inhabited by hermit crabs than to live gastropods or other hard surfaces. Taylor (1994) considered *H. senegambiensis* (Fig. 4F) and *H. picardi* to be obligate commensals of hermit crabs from West Africa. A third West African species, *H. littoralis*, is associated with hermit crabs as well as live gastropods and rocks (Taylor, 1994).

Hippoporidra lusitania, from the British Isles, seems to be an exclusive associate of the hermit crabs *Anapagurus chiroacanthus*, *Cestopagurus timidus,* and *Pagurus cuanensis* (Taylor and Cook, 1981; Bishop, 1987). *Hippoporidra edax* ranges from North Carolina to the Gulf of Mexico where it is an obligate commensal of hermit crabs (Taylor, 1994). Ryland (2001) described *H. dictyota* from hermit crab shells collected in North Carolina. The bryozoan forms thick, encrusting colonies with tubular extensions (mammillae) that contain male zooids. Ryland (2001) indicated the mammillae concentrate exhalant currents of the bryozoan and thus aid in feeding and discharge of sperm. A closely related genus contains *Biflustra commensale,* an associate of the hermit crab *Petrochirus granulimanus* from West Africa (Kirkpatrick and Metzelaar, 1922). *B. commensale* is also found with live gastropods and is thus a facultative symbiont of hermit crabs (Taylor, 1994). Colonies of *Hippoporidra* and related genera that form such extensions are commonly referred to as 'longhorn shells' (Fig. 4F) (Deichmann, 1954; Smith, 1966; Morris et al., 1991).

3.13.2. Order Ctenostomata

Alcyonidium albescens is a facultative associate of shells inhabited by *P. longicarpus* and *P. pollicaris* (Karlson and Cariolou, 1982; Karlson and Shenk, 1983; Buss and Yund, 1988; McDermott, 2001). The outer surfaces of 12% of 2905 shells and 27% of 5041 shells with *P. longicarpus* examined from the waters of Connecticut and New Jersey, respectively, were colonized with this encrusting, gelatinous bryozoan (Buss and Yund, 1988; McDermott, 2001). As compared to other encrusting bryozoans, this species tends to have a predilection for shells with hermit crabs. Lines of demarcation separating colonies have been observed on shells (McDermott, unpublished data). Buss and Yund (1988) found that *A. albescens* outcompeted the hydroid *Hydractinia* for space on shells with *P. longicarpus*. Furthermore, the presence of *A. albescens* attracted the predatory nudibranch *Corambe obscura*, which also layed its egg strings on the bryozoan colony (McDermott, 2001). A total of 78 of 2838 shells with hermit crabs (2.7%) were found with this nudibranch (Table 4). *C. obscura* was nearly always found on bryozoan-covered shells (75 of 78 shells with the nudibranch were covered by *A. albescens*) (McDermott, 2001). The nudibranch is a facultative predator of *A. albescens* since it also feeds on *A. verrilli* and cheilostomes (e.g., *Conopeum tenuissimum* and *Membranipora tenuis* which may or may not be attached to hermit crab shells; Cory, 1967; Franz, 1967; Perron and Turner, 1977). *Alcyonidium gelatinosum* was recorded in Scandinavian waters and the North Sea from shells inhabited by the *P. bernhardus* (Jensen and Bender, 1973; Reiss et al., 2003) [bryozoan originally identified as *A. polyoum* (see Winston and Key, 1999; Ryland and Porter, 2003)].

One ctenostome bryozoan *Arachnoidea dhondti* is found attached to the exoskeleton of host hermit crabs, the species forms colonies on the legs of *P. pilosimanus* collected off the coast of North America at 500 m (Franzen and Sandberg, 2001).

3.14. Phylum Echinodermata

Three species of echinoderms (a brittlestar, a featherstar, and a sea cucumber) are incidental associates of hermit crabs (Table 1).

3.15. Phylum Chordata, class Ascidiacea

Among the urochordates, only sea squirts have been recorded on hermit crab shells. Some of the 17 species (both solitary and colonial) associated with six hermit crab species cover the shells extensively, but all are incidental relationships (Table 1). Stachowitsch (1980) found 11 species of tunicates on the shells of *P. eremita* and *P. cuanensis*. Most ascidians were colonial, and their main impact seemed to be that they rapidly overgrew available shell space as well as smothering other sessile species. It is surprising that among the >5000 *P. longicarpus* shells examined in New Jersey, no tunicates were detected (McDermott, 2001).

3.15.1. Class Osteichthyes

The code goby, *Gobiosoma robustum*, may rarely inhabit shells with hermit crabs (McLean, 1983). In the field the goby entered empty shells and was sometimes displaced by *P. pollicaris*. It appears *G. robustum* and hermit crabs compete for empty shells and McLean (1983) observed one goby driving off a hermit crab trying to enter a shell in which developing embryos of the fish were cemented.

4. Discussion

4.1. Evolutionary considerations

Debate over the evolutionary history of the Anomura and particularly the origin of hermit and king crabs exists. While morphological evidence indicates that the hermit crabs arose from a fully calcified lithodid ancestor (McLaughlin and Lemaitre, 1997, 2000), molecular and ontogenetic studies indicate that the lithodids arose from a hermit crab ancestor (Cunningham et al., 1992; Harvey, 1998; Morrison et al., 2002). Regardless of hermit and king crab relationships, it is hypothesized that utilization of shells and other domiciles by paguroids initially developed for concealment and then protection of the abdomen of these crustaceans (McLaughlin, 1983). Posterior pereopods and uropods were modified for positioning of the paguroid in its shell, the abdomen became decalcified, and pleopods became positioned on one side for maximal utilization of gastropod lumen space during reproduction (McLaughlin, 1983).

Hermit crab exoskeletons are poorly represented in the fossil record but date from at least the lower Cretaceous (Hyden and Forest, 1980; Bishop, 1983; Fraaije, 2003); a few citations of hermit crabs from the early Jurassic (Glaessner, 1969) are based on chelae of questionable affinity (McLaughlin, personal communication). However, the presence of empty gastropod shells and associated organisms has been used, in combination with other evidence such as shell wear, to infer the occupation of shells

by hermit crabs (Frey, 1987; Darrell and Taylor, 1989; Walker, 1992; Taylor and Wilson, 2003). These records indicate hermit crabs provided a new niche for epibiotic and endolithic organisms in marine ecosystems during the middle Jurassic (Walker, 1992). The following is a discussion of what is known of the shared evolutionary history of hermit crabs and their associates.

Little work has addressed the evolutionary history between hermit crabs and protozoan symbionts. Clamp (1989) suggested *Lagenophrys eupagurus* was originally a symbiont of palaemonid shrimp (its most common host). The present distribution and host use of *L. eupagurus* is thought to be a result of ancestral populations coming into contact with a wide variety of crustacean hosts including hermit crabs through their original association with widely distributed shrimp species. Clamp also indicated that the association of *L. eupagurus* with hermit crabs was supported by enhanced feeding of the protozoan due to the activities of host crabs. Detrital particles, diatoms, and dinoflagellates are probably carried via the respiratory currents of the host to the protozoans attached to the gills. Such enhanced feeding by symbiotic ciliates has been suggested in other species such as *Cothurnia* sp. associated with boring polychaetes in hermit crab shells (Williams, 2001b).

Although a sponge (*Thalmospongia* sp.) was found encrusting gastropod shells inhabited by hermit crabs from the Cretaceous of France (Douvillé, 1906), the fossil record of poriferans associated with hermit crabs is limited. However, molecular analyses have been used to distinguish closely related species in the *S. ficus* sibling-species group. Using estimates from Nei's genetic distance based on isozyme data, Solé-Cava and Thorpe (1986) indicated that the two species of *Suberites* associated with bivalve shells and *S. pagurorum* associated with *P. bernhardus* exhibited a divergence time of ~ 7–8 MYA. Sandford and Kelly-Borges (1997) indicated that convergent evolution was exhibited between sponge associates of hermit crabs (i.e., *P. suberitoides* and *Suberites* species) based on similarities in morphological features. As discussed for the groups below (e.g., Cnidaria, Bryozoa), hermit crab shells provided a hard surface for settlement of sponges; the association between sponges and hermit crabs was then reinforced by benefits of increased food availability and reduced chances of permanent burial.

Waggoner and Langer (1993) described the cnidarian *Mesodendrium oktibbehaensis,* a hydroid tentatively placed in the family Campulariidae that was potentially the oldest known association between hydroids and hermit crabs (the crabs were collected from the Upper Cretaceous of Mississippi); the symbiosis was inferred from the position of the hydroid on the shell and presence of a cheilostome bryozoan. Hydractinians are associated with hermit crabs from the Cretaceous of Antarctica (Olivero and Aguirre-Urreta, 1994) and *Hydractinia* spp. are associated with *Pagurus* spp. from the Western Atlantic in the Miocene (Cunningham et al., 1991; Walker, 1992). Based on molecular evidence, Cunningham et al. (1991) showed that *Hydractinia* spp. exhibited a shared evolutionary history with *Pagurus* spp. hosts. Specifically, ancestral populations of *P. bernhardus* (with *H. echinata*) from Europe became divided during the Northern Hemispheric Glaciation (~ 2.5–3.1 MYA) and gave rise to *Pagurus acadianus* along the northeastern Atlantic where *H. polyclina* is now found. In addition, populations of *P. longicarpus* in the Gulf of Mexico and Florida were divided by the closure of the Suwanee Straits (3.8–4.2 MYA) and shells occupied by these hermit crabs were covered by an undescribed *Hydractinia* sp. and *H. symbiolongicarpus*, respectively. Current research suggests that the Gulf of Mexico

and eastern Atlantic populations of *P. longicarpus* may represent separate species (Young et al., 2002).

It has been theorized that hydractiniids (such as *Polyhydra* spp.) evolved the ability to produce a calcified skeleton from a *Hydractinia*-like ancestor in the early Tertiary (Cairns and Barnard, 1984). From this first calcified form arose additional species within the genera *Kerunia*, *Hydrocorella*, and *Janaria* associated with hermit crabs (Cairns and Barnard, 1984). *Kerunia cornuta* is known from the Eocene of Egypt (Douvillé, 1906; Ziko, 2003); the species forms branches on gastropod shells inhabited by hermit crabs similar to those produced by *Janaria mirabilis*.

Ross (1974, 1983) explored evolutionary considerations for the association between anemones and hermit crabs, believing that the associations evolved independently multiple times. He suggested that anemones first utilized live gastropods and then became associated with shells inhabited by hermit crabs, as evidenced by the fact that some anemones will transfer to gastropod shells unaided. Also, some anemones such as *Calliactis conchiola* are found both on live gastropod shells and shells occupied by hermit crabs (Hand, 1975a,b). Associations with hermit crabs were reinforced by the protection from predators afforded to hosts by the anemones. Eventually certain hermit species evolved specialized behaviors to actively aid in the process of anemone colonization of shells (Ross, 1974, 1983). Other anthozoan associates include *Septastrea marylandica*, the only known scleractinian symbiont of hermit crabs (Darrell and Taylor, 1989). The extinct coral formed encrusting colonies on gastropod shells presumably inhabited by hermit crabs from the Pliocene of Florida.

Ectosymbiotic flatworms associated with hermit crabs and other invertebrates exhibit some adaptations to their symbiotic mode of life but show less specialization than endoparasitic members of the Platyhelminthes (Jennings, 1988). Jennings (1974) suggested that the association between flatworms and invertebrates initially evolved due to the host providing a substrate for the flatworm symbiont. Such associations were then reinforced by enhancement of feeding (through feeding on particles dropped by hermits, hermit crab embryos, and other associates of hermit crabs). The association between turbellarians and hermit crabs evolved multiple times.

A similar evolutionary history is thought to have occurred between certain polychaete associates of hermit crabs. Evidence from the fossil record shows that the ichnofossil *Helicotaphrichnus commensalis* Kern, Grimmer and Lister 1974 [which produces burrows identical to that produced by *Dipolydora commensalis*—an obligate commensal of hermit crabs (Fig. 7D)] is represented in the Miocene Korytnica Basin of central Poland (Kern, 1979). The fossil evidence and behavioral modification in feeding (including predation on hermit crabs embryos) indicates a long shared evolutionary history between hermit crabs and certain polydorids such as *D. commensalis* and *Polydora robi* (Williams, 2002). Presumably the association first evolved because the hermit crabs shells provided a suitable substrate for boring. This also appears to be the case in free-living polychaetes (e.g., *Nereis fucata*) as well as epibiotic species (e.g., *Circeis paguri*) associated with hermit crabs. The special mucus-secreting glands within the parapodia of *N. fucata* suggest a shared evolutionary history with hermit crabs. These associations were reinforced by enhanced food resources (e.g., egg predation by polydorids, kleptoparasitism by *N. fucata*).

Ho (1988) completed a cladistic analysis based on morphological features of the copepod genus *Sunaristes* to investigate the vicariant events that led to the present distribution of these copepod associates of hermit crabs. *Sunaristes* species are believed to have a short dispersal period (based on naupliar development of ∼ 6 days in closely related species) and larval stages of host hermit crabs may disperse in the plankton for 3 months (Ho, 1988). Based on these differences, Ho (1988) inferred that *Sunaristes* originated in Eurasia after the formation of the North Atlantic Ocean; the absence of *Sunaristes* from the New World is explained by the inability of larvae of *Sunaristes* species to migrate large distances. Presumably in the late Paleocene (60–59 MYA), ancestors of *Sunaristes* formed an association with hermit crabs along the Eurasian coast of the Tethys Sea and eventually *S. paguri* evolved after expansion into the Mediterranean; *S. paguri* was the most basal species in the cladistic analysis. Expansion into areas of the Indo-West Pacific and Japan eventually gave rise to *S. inaequilis*, *S. japonicus*, and *S. tranteri* in a complex process. As indicated by Ho (1988) and others, hermit crabs from many regions (particularly the Indo-West Pacific) have not been examined for harpacticoid copepods, and thus the proposed evolutionary history of *Sunaristes* species will probably need to be re-examined.

Hicks and Webber (1983) found a considerable degree of intraspecific variation within the copepod *Porcellidium tapui*. Although free-living *Porcellidium* species presumably exhibit high gene flow, Hicks and Webber (1983) indicated that *P. tapui* and other species associated with hermit crabs are isolated from other such populations. This isolation could limit gene flow and lead to genetic drift, thereby explaining the observed variation in *Porcellidium* species associated with hermit crabs. Phenotypic variation could also be attributed to the association with different hermit crab and shell species (Hicks and Webber, 1983).

Boring barnacles of the order Acrothoracica found in gastropod shells inhabited by hermit crabs date from the Miocene (Seilacher, 1969; Rodriguez and Gutschick, 1977; Baluk and Radwański, 1991). Although members of the genera *Lithoglyptes* and *Weltneria* have formed facultative associations with hermit crabs and live gastropods, the trypetesid barnacles (*Trypetesa* sp. and *Tomlinsonia* sp.) are obligate commensals of hermit crabs. Seilacher (1969) indicated that hermit crabs opened a new niche for boring barnacles and thus led to a number of evolutionary changes among trypetesids. It appears that the prevalence of hermit crabs in intertidal communities during the Mesozoic provided a refuge to shell boring acrothoracicans and this association was reinforced by the activity of hermit crabs, which allowed for enhanced feeding of the barnacles (Baluk and Radwański, 1991). Most acrothoracican barnacles exhibit reduction in appendages and this trend is particularly evident in trypetesid barnacles that exhibit uniramous cirri and lack thoracic and caudal appendages as well as an anus (Seilacher, 1969; Tomlinson, 1969a; Turquier, 1976; Turquier and Carton, 1976). Modifications in the bore hole morphology include a more regular orientation along the columella, increased lateral development of the barnacles under the surface of the shell (i.e., a trend toward increased broadness versus depth within the shells), decrease in the thickness of the shell roof overlying the barnacle (due to the protective nature of the shell and position on the columella), and a secondary opening to the bore holes through which water flows (Seilacher, 1969; Baluk and Radwański, 1991). Although some trypetesids such as *T. lateralis* are found in various

areas around the shell, *T. nassaroides* and *T. asymetrica* are confined to the columella (Fig. 7F). Thus their bodies exhibit further adaptations to a life associated with shells inhabited by hermit crabs including a characteristic spiral morphology (Fig. 7E), reflecting their expansion through the columella of the shell.

Gastropods of the genus *Crepidula* originated in the Cretaceous (Hoagland, 1977). Hoagland (1977) indicated that members of this genus exhibit unique changes from the calyptraeid ancestor, including flattening of the shell and decrease in shell coiling such that the columella becomes a simple partition. Species of *Crepidula* adapted for life in dead shells (including shells inhabited by hermit crabs) are unpigmented and more planar in form (Hoagland, 1977; Yipp, 1980). In spite of the lack of morphological differentiation, molecular analyses have shown that three species of such flat white-shelled *Crepidula* are associated with hermit crabs from the east coast of the United States, and it is possible that additional cryptic species exist in the Atlantic (Collin, 2000).

Mollusc shells in general, and particularly the gastropod shells carried by hermit crabs, are attractive substrates for attachment by bryozoans. The advantages furnished to bryozoans by hermit crabs have no doubt been important evolutionary factors in the establishment of bryozoan–hermit crab relationships (Gordon, 1972; Taylor, 1994; Key et al., 1996). These associations date to the middle Jurassic as revealed by paleontological studies of pagurized shells (Palmer and Hancock, 1973; Walker, 1992; Taylor, 1994), and have been recorded from the intertidal to upper slopes of the ocean, ranging from the tropics to cold temperate environments. The fossil record shows that such associations had multiple origins. Symbiotic species among bryozoan families are in the minority except for the Hippoporidridae whose evolutionary history suggests a very close association with hermit crabs (Taylor, 1994; Taylor and Schindler, 2004). *Hippoporidra portelli* from the late Eocene of Florida represents the oldest known *Hippoporidra* encrusting hermit crab shells (Taylor and Schindler, 2004). Coevolutionary features, however, are not evident. For example, the helicospiral tube growth produced by the hippoporidrids is not unique to bryozoan–hermit crab relationships and can be accounted for by the plasticity of normal bryozoan growth influenced by movements of the asymmetrical hermit crab (Taylor, 1994). Aside from members of the *Hippoporidra*, most bryozoan symbionts do not have obligatory relations with hermit crabs. In fact, Taylor (1994, p. 165) concludes that ''it is inevitable that the number of obligatory bryozoans will diminish with increased sampling.'' Nevertheless, Taylor indicates that there is a greater dependency of the bryozoans on hermit crabs than vice versa, based on the benefits gained from hermit crab hosts (see Table 2).

One of the positive ancillary outcomes of studying bryozoan-pagurized fossil gastropod shells (and other types of pagurization) is insight into the geological history of hermit crabs gained in spite of the fact that hermit crabs themselves are rarely fossilized (Morris et al., 1991; Walker, 1992). For example, *Biflustra commensale* from the Pliocene Imperial Formation of southeastern California is a widely distributed facultative symbiont of hermit crabs that ranges back to the Miocene (Kirkpatrick and Metzelaar, 1922; Kidwell and Gyllenhaal, 1998). *B. commensale* produces large encrustations over shells inhabited by hermit crabs, as evidenced by the growth of the bryozoan colony as a tube extending from the aperture in a helicospiral fashion.

Table 2

Costs and benefits derived by hermit crabs and their associates through their interactions (based partly on Taylor, 1994)

	Benefits	Costs
Hermit Crabs	Increase shell strength	Reduce shell strength
	Increase domicile space	Decrease lumen size
	Domicile growth with hermit	Increase shell weight
	Protection from predators (e.g., nematocysts, camouflage)	Egg/embryo predation or
	Feed on associates or food collected by associates	increased predation on adults[a]
	Reduce shell competition	Food stolen by associates
	Protection from parasites or settlement of negative associates[b]	
Associates	Increase food resources (feces, dropped food particles, areas	Food stolen by hermit crab
	of high flow, eggs/embryos)	Damage due to hermit activity
	Substrate for colonization	(shell dragging)
	Protection from burial	
	Protection from predators	
	Oxygen rich waters	
	Increased potential for cross-fertilization	

[a] Increased predator attacks because hermit crabs are more visible or susceptible to predators.

[b] Inhibit potentially detrimental associates from settling on shells (e.g., *Hydractinia* sp. can inhibit *Crepidula* sp.).

Colonies of *B. commensale* compete for space on hermit crabs shells and exhibit standoffs, producing mineralized walls and projections that are often colonized by other hermit crab symbionts such as barnacles and polychaetes (Kirkpatrick and Metzelaar, 1922).

4.2. Cost/benefit analysis between hermit crabs and their associates

The discussion below indicates benefits as well as costs gained by both hermit crabs and their associates. Table 2 provides a summary of these interactions.

4.3. Hermit crabs—negative effects from associates

4.3.1. Stinging hydroids

Some hermit crabs such as *Pagurus annulipes* reject shells covered by *Hydractinia* sp.; this aversion is supported by field research in which such shells are rarely (<1%) occupied by *Pagurus annulipes* and *P. brevidactylus* (Mercando and Lytle, 1980). Similarly, *Clibanarius vittatus*, which is rarely found in shells covered by hydractiniid hydroids (Fotheringham, 1976; Mercando and Lytle, 1980), rejects them in the laboratory (Wright, 1973). *C. vittatus* also provides an unsuitable habitat for hydroids (and settlement of planula larvae) since the hermit crab often is exposed during low tide (Mills, 1976b). In contrast, *P. bernhardus*, *P. longicarpus,* and *P. pollicaris* may prefer shells with *Hydractinia* sp. or *Podocoryne* sp. and approximately 20–50% of shells in the field inhabited by these hermit crabs are covered with hydractiniid hydroids (Jensen, 1970; Wright, 1973; Conover, 1976; Fotheringham, 1976; Mills, 1976a,b; McDermott, 2001; Damiani, 2003). Brooks and Mariscal (1985b) found that *C. vittatus, P. longicarpus,* and

P. pollicaris chose bare shells in the laboratory except in one experiment in which a population of *P. pollicaris* from a region where *Octopus* sp. was more abundant initially selected shells with hydroids. Apparently, hermit crabs are sensitive to stinging hydroids but competition for shells and pressure exerted by predators (see discussion on protection from predators below) as well as abiotic factors influence the distribution of hermit crabs among bare and encrusted shells. Some hermit crabs may be less sensitive to the stinging nematocysts and/or may feed on hydractiniid hydroids in order to gain immunity (Wright, 1973). While seasonal factors (including abundance of host hermit crab populations in relation to encrusted shells) influence the degree of association between hydractiniid hydroids and hermit crabs, shell selection behavior appears to determine the species specificity of the hydractiniid hydroid-hermit crab symbioses (Mercando and Lytle, 1980).

4.3.2. Kleptoparasitism

The polychaete *N. fucata* steals food from *P. bernhardus* (Brightwell, 1951) and the scaleworm *Gaudichaudius cimex* may similarly take food from *Diogenes* spp. (Achari, 1977).

4.3.3. Egg predation

Ten species of hermit crab associates are known to prey on host's broods (Williams, 2002). Not all egg predators live on the crabs themselves (Table 3); some live on the outside of the gastropod shell, in the lumen, or bore into the shell and make contact with the lumen. This is in contrast to the better known nemertean embryo predators of decapods other than hermit crabs (e.g., *Carcinonemertes* spp.) which live on the crustacean hosts and their broods (see Kuris, 1993).

Lytwyn (1976, 1979) found that the flatworm *S. zebra* feeds on the eggs attached to the pleopods of *P. pollicaris*. This polyclad is normally found on the inner surface of occupied shells but during egg predation the flatworm will move onto the egg mass and remain there for as long as 10 h while feeding on at least 80 eggs (Lytwyn, 1979). The prevalence of *S. zebra* reached over 80% among *P. pollicaris* collected in Woods Hole, Massachusetts, during March indicating they may have substantial impacts on hermit crab reproduction. Observations of egg predation in the laboratory have been confirmed in the field by collection of *S. zebra* with maroon guts (the color of host hermit crab eggs). Williams (2002) reported similar evidence for unidentified flatworms associated with hermit crabs from the Philippines. Bock (1925) did not rule out the possibility that the flatworm *E. adhaerens* ingested the eggs of *P. californiensis*.

Among polychaete egg predators, two boring worms from the Philippines *P. robi* and *P. umangivora* ingest the eggs of hermit crabs. Field investigations showed that *P. robi* and *P. umangivora* preyed upon the eggs of seven and three species of diogenid hermit crabs, respectively (Williams, 2002). The worms extend from their burrow openings and remove eggs attached to pleopodal setae through the use of two peristomial palps (Fig. 7C). In laboratory trials, *P. robi* was able to ingest a maximum of 70 embryos over a 6 h period. For hermit crab species that produce small broods (e.g., *Paguristes runyanae* with generally fewer than 200 eggs), the worms can have large impacts on reproduction (Williams, 2002).

Table 3

Invertebrate species known and suspected to feed on eggs, embryos, or larvae of host hermit crabs (based partly on Williams, 2002)

Egg/embryo predator species	Host hermit crab	Authors[a]
Cnidaria		
Adamsia palliata	*Pagurus bernhardus*	Matthews, 1959
	Pagurus prideaux	
Podocoryna carnea	*Pagurus bernhardus*	Matthews, 1959
Podocoryna exigua	*Diogenes pugilator*[b]	Cerrano et al., 1998
Hydractinia echinata	*Pagurus bernhardus*	Bunting, 1894; Christensen, 1967
Platyhelminthes: Turbellaria[c]		
Ectocotyla hirudo	*Pagurus pubescens*	
Emprosthopharynx rasae	*Calcinus latens*	
Euprosthiostomum viscosum	*Pagurus prideaux*	
Euprosthiostomum adhaerens	*Petrochirus californiensis*	
Stylochus pulcher	*Petrochirus diogenes*	
Stylochus zebra	*Pagurus pollicaris*	Lytwyn, 1979
Annelida: Polychaeta		
Neanthes fucata	*Pagurus bernhardus*	Matthews, 1959; Goerke, 1971
	Pagurus prideaux	
Polydora bioccipitalis	*Pagurus hirsutiusculus*	
Dipolydora commensalis	*Pagurus longicarpus*	Williams, unpublished data
Eusyllis blomstrandi	*Pagurus* spp.	
Lepidonotus sublevis	*Pagurus* spp.	
Polydora umangivora	*Calcinus gaimardii*	Williams, 2001a, 2002
	Dardanus lagopodes	
	Paguristes runyanae	
Polydora robi	*Calcinus gaimardii*	Williams, 2000, 2001a, 2002
	Calcinus latens	
	Calcinus minutus	
	Calcinus pulcher	
	Clibanarius cruentatus	
	Clibanarius englaucus	
	Dardanus lagopodes	
Syllis pontxioi	*Paguristes* sp.	
	Clibanarius sp.	
Arthropoda: Crustacea		
Liljeborgia spp.	various hermit crabs	
Pagurisaea schembrii	*Paguristes pilosus*	
Pagurolepas spp.	*Tomopagurus cokeri*	
Ruffojassa spp.	various hermit crabs	
Tomlinsonia asymetrica	*Calcinus latens*	
Trypetesa sp.	*Calcinus gaimardii*	Williams, 1999
	Calcinus latens	
Ventojassa spp.	various hermit crabs	
Veronajassa neptunea	*Dardanus arrosor*	

[a] References provided for documented egg predators; all others are suspected egg predators.

[b] Recently released larvae of the host hermit crab were ingested.

[c] In addition to the flatworms listed, there is evidence of an unidentified species which preys on the embryos of hermit crabs from the Philippines; see text.

Another polychaete egg predator is *N. fucata*, which can ingest the eggs of *P. bernhardus* as they are extruded (before attachment to pleopodal setae) (Matthews, 1959). *N. fucata* also ingests the eggs of *P. prideaux* (Goerke, 1971). The numbers of eggs ingested by this species is unknown but based on its size, the worm could have significant impacts on the reproduction of these hermit crabs. Overstreet (1983) indicated that gravid hermit crabs change shells more often than those without broods and may reduce predation by seeking shells without worms. However, no data were provided and experiments to address the impacts of *N. fucata* and other egg predators on shell choice by gravid females remain to be completed. Other researchers have found that gravid hermit crabs changed shells less often than non-gravid females but were more likely to change from suboptimal shells (smaller) to optimal shells than male crabs (Neil and Elwood, 1985).

Hydractinia colonies actively feed on hermit crabs embryos and a considerable amount of their diet may consist of this food supply when available (unpublished observations by G. Thorson and associates, cited in Rees, 1967). Matthews (1959) observed that *P. carnea* could ingest eggs of *P. prideaux* lost prior to their cementation on pleopodal setae and eggs were occasionally ingested by the anemone *Adamsia pallinata*. Although the hydroids (*Hydractinia* sp. and *Podocoryne* sp.) can feed on embryos when ovigerous hermit crabs extend from the shells, the largest impact on hermit crab reproduction is suspected to occur when larvae are released (Brunenmeister, 1980). Limited research has addressed the impact of predation on hermit crab larvae, although this was documented for *H. echinata* (Bunting, 1894) and *P. carnea* (Cerrano et al., 1998). In addition, Cerrano et al. (1998) found that the hydroid *P. exigua* fed on the larvae of *D. pugilator*. McDermott (2001) suggested that the long, specialized zooids of hydractiniid hydroids such as *P. carnea* produced along the shell aperture might be adapted for collecting small benthos stirred up by the crab or the crabs' zoeae.

Damiani (2003) found reduced clutch sizes of *P. longicarpus* isolated in tanks when inhabiting shells colonized by *H. symbiolongicarpus*. In addition, ovigerous female hermit crabs exhibited higher loss of embryos when inhabiting hydroid-encrusted shells. In contrast, field-collected hermit crabs inhabiting hydroid-encrusted shells showed no reduction in clutch size as compared to hermit crabs in bare shells (Damiani, 2003). Damiani suggested that shell switching in the field could account for the discrepancy between field and laboratory data. Regardless, Damiani (2003) indicated that the negative impacts on hermit crab reproduction was not from direct predation on eggs or larvae by the hydroids but perhaps from reducing feeding or aeration activities of host hermit crabs.

In addition to the documented egg predators, at least 15 invertebrates are potential or suspected egg predators of hermit crabs (Table 3). In support of this suspicion, Fotheringham (1976) documented 10 invertebrates associated with hermit crabs that were able to ingest isolated eggs; however, no data on egg predation in nature were recorded.

Suspected egg predators include *Eusyllis blomstrandi*, a polychaete that creates parchment tubes in apical whorls of hermit crab shells and in this way has access to eggs similar to that seen in *P. robi* (López et al., 2001). The scaleworm *Lepidonotus sublevis* is also a suspected egg predator found free-living in the lumen of shells in the same region as the abdomen of hermit crabs. Since ~ 25% of shells in certain regions along the east coast of the United States may harbor this large worm, it may have considerable impacts on

hermit crab populations. Fotheringham (1976) showed *L. sublevis* ingested eggs and larvae removed from the pleopods of *P. longicarpus* and fed to worms isolated in the laboratory.

Barnacles of the genus *Pagurolepas* are found in areas from the columella to the lumen of shells inhabited by hermit crabs (Keeley and Newman, 1974). In this region of the shells, the barnacles would have access to the eggs of host hermit crabs and might have the ability to remove them from pleopods. Although members of the genus *Trypetesa* have reduced feeding appendages and were thought to be microphagous feeders (Tomlinson, 1969a), Williams (1999) found the embryos of host hermit crabs from the Philippines in the guts of *Trypetesa* sp.

Among amphipods, Taylor (1979, pg. 187) indicated "Egg parasitism cannot be ruled out" for *Liljeborgia* sp. found with *Pagurus hemphilli* although his research was based on a single specimen. Vader and Myers (1996) suggested that some amphipods might impact hermit crabs in a manner similar to amphipods associated with lithodid crabs. For example, the amphipod *Ischyrocerus* sp. is an egg predator of the Alaskan king crab, *Paralithodes camtschaticus* (Tilesius, 1815) (Kuris et al., 1991).

4.3.4. Reduction in shell adequacy (strength, size, weight)

Buckley and Ebersole (1994) found shells harboring *Polydora* spp. were weaker and therefore exposed the host hermit crabs (*P. longicarpus*) to increased predation by shell-crushing predators (e.g., brachyuran crabs). Walker (1988) has similarly shown the negative effects of spionid boring behavior on hermit crab shells. Bryozoans (e.g., *Immergentia californica* and *Terebripora* sp.) are also known to bore into hermit crab shells (Boekschoten, 1966). Pechenik et al. (2001) showed *P. longicarpus* preferentially chose gastropod shells (*Littorina littorea*) lacking holes produced by predatory gastropods [e.g., moon snail *Euspira heros* (Say, 1822)]. As in burrows created by polydorids, the holes reduced the shell strength and increased successful predation on hermit crabs by decapods such as the green crab, *Carcinus maenas* (Linnaeus, 1758). Thus, some hermit crabs may be able to detect the presence of holes (at least the size produced by *E. heros*, 3.6 mm) and are able to choose homes based on shell condition. It should be noted that some predators such as fish that ingest the whole shell and digest the hermit crab inside (McDermott, 1964), may not be deterred by the strength of shells, so boring species would not influence predation success on hosts.

Shell weight and size influence clutch size in many hermit crab species and some hermit crab associates such as *Crepidula* spp. reduce internal volume of shells (Conover, 1976; Fotheringham, 1976). The barnacle *Balanus amphitrite* also adds weight to the shells and causes their rejection by *P. longicarpus* and *P. pollicaris* (Conover, 1976). Epibionts such as barnacles and slipper shells can also negatively impact hermit crabs by changing the center of gravity of shells (Conover, 1976). When predators are not present, *D. arrosor* abandons association with the anemone *C. parasitica*, presumably to reduce energy costs associated with carrying a shell with large anemones attached (Ross and Boletzky, 1979). Sandford (1995, 2003) found that *Pagurus impressus* showed no preference for shells covered by *P. suberitoides* and would switch to shells free of the sponge; 95% of the hermit crabs that switched out of shells overgrown by the sponge subsequently chose clean shells (Sandford, 2003). This sponge adds approximately 1–2 g of dry weight to shells (Sandford, 1994). The

lack of available shells and presence of competitors for shells (e.g., *P. pollicaris*) could explain the high prevalence of *P. impressus* in sponge domiciles from the Gulf of Mexico (Sandford, 1995, 2003). The sponge also makes hermit crabs more susceptible to being washed ashore by waves (Sandford, 2003).

Other encrusting forms such as bryozoans add significant weight to hermit crab shells (see Fig. 4F). However, few studies (e.g., Taylor, 1991) have quantified the weights of these symbionts or their energetic costs to hosts. The colonial tunicate *Apilidium* sp. added over 223 g of weight to a shell inhabited by *P. pollicaris* (representing ∼ 19 times the weight of the host hermit crab) (McDermott, personal observation).

L. sublevis occupies free lumen space and interferes with shell entry behavior and shell choice of hermit crabs (Mercando and Donaghy, 1984). Male hermit crabs are ∼ 25 times more likely to harbor these worms then females (Mercando, 1983); this could be due to the larger size of males or perhaps females abandon shells with the worms more often than males. Lively (1989) showed that the hermit crab, *Clibanarius digueti* Bouvier, 1898 preferentially chose shells that had empty lumens over those that were experimentally plugged in the apical whorls (thereby reducing lumen space available to the hermit crabs). Similar obstructions of the apical whorls are caused by associates such as *P. robi* that produces mucous tubes (Fig. 7A) and may influence shell choice.

4.4. Hermit crabs—positive effects from associates

4.4.1. Increase shell strength, shell size, or shell replacement

Stylobates spp. and certain *Epizoanthus* spp. (Fig. 5B) are associated with hermit crabs in deep-water areas (Muirhead et al., 1986; Fautin, 1987). As a result of the increased dissolution of calcium carbonate shells at depth, Fautin (1987) indicated that these cnidarians might play an important role in allowing exploitation of deep-sea regions by hermit crabs. Dunn et al. (1980) suggested that the anemone *S. aeneus* might impede the dissolution of gastropod shells inhabited by hermit crabs. The anemone eventually secretes its own paper-like shell (carcinoecium) inhabited by the host crab and the original shell is reduced or missing (Fig. 4G) (Fautin, 1992). Other anemones are known to provide protection to the soft abdomen of host hermit crabs, taking the place of gastropod shells (Ross, 1967, 1974; Provenzano, 1971). The anemones grow with the host hermit crabs, relieving the hermit crabs from the need to seek new gastropod shells (Ross, 1967, 1974, 1983; Dunn et al., 1980). Jensen (1970) and Harris et al. (1975) suggested that the hydroid *H. echinata* might provide increased space by growth over the outer lip of inhabited gastropod shells. *H. sodalis* and *H. spiralis* are other examples of hydractinian hydroids that grow with host hermit crabs (*Pagurus constans*) and obviate the need for shell switching. In fact, the name *P. constans* was chosen to acknowledge the ability of hermit crab to remain in a single shell (Stimpson, 1858, 1907). Hydractinian "staghorns" as well as bryozoan "longhorns" may be associated in this manner with hermit crabs (Smith, 1966).

A number of sponges provide homes to hermit crabs, completely overgrowing or replacing gastropod shells. *S. domuncula* and *P. suberitoides* are two well-known examples (Van Soest, 1993; Sandford, 1994, 2003). Although the hermit crab-sponge associations were thought to be mutualistic, with the sponges providing a shelter that grows with the hermit crabs, Sandford (1995, 2003) found that *Pagurus impressus* does

not prefer sponge shelters. The hermit crabs are believed to provide food and well-oxygenated water to the sponge associates (Vosmaer, 1933). The hermit crabs appear to derive advantages from avoiding shell switching and thereby reducing susceptibility to predation, at least while juveniles (Sandford, 2003). Kirkpatrick and Metzelaar (1922) indicated that the bryozoan *B. commensale* exhibited tube-like prolongations of shell apertures thereby allowing longer occupation by the host hermit crab, *Pseudopagurus granulimanus*. Taylor and Cook (1981) found similar overgrowth of shell apertures by bryozoans. Taylor (1994) suggested that the symbiotic nature of the association between bryozoans and hermit crabs was complex, involving a temporal switch from mutualism to parasitism as the bryozoan colonies grew so large and heavy they inhibited hermit crab movement (Figs. 4F and 6F).

Cnidarians, sponges, and bryozoans may also inhibit other symbionts from settling on shells and thus can benefit host crabs by decreasing their association with symbionts that reduce shell adequacy (e.g., boring organisms or epibionts). For example, *Crepidula* species are negatively associated with hermit crab shells covered by *Hydractinia* sp., indicating the hydroid may benefit hermit crabs by inhibiting this snail from settling and causing increased energetic costs to hosts (Karlson and Cariolou, 1982; Shenk and Karlson, 1986). Brunenmeister (1980) suggested symbionts that inhibit settlement of boring species benefit hermit crabs by decreasing the need for finding new homes when shells become inadequate. However, Buckley and Ebersole (1994) did not find a negative association between *Hydractinia* sp. and polydorids.

4.4.2. Reduce shell competition

Wright (1973) and Mercando and Lytle (1980) showed that hydractiniid associates of hermit crabs could reduce the interspecific competition of hermit crabs for gastropod shells, a limiting resource in most hermit crab communities.

4.4.3. Food

Cerrano et al. (1998) showed that the hermit crab *D. pugilator* fed on particles collected by the polyps of the hydroid *P. carnea* that surrounded the aperture of the shell. Wright (1973) found that *Pagurus* sp. feeds on hydractiniid hydroids but Mills (1976b) found this occurred only when crabs were starved for several days. Balasch and Mengual (1974) showed that *D. arrosor* would feed on the anemone *C. parasitica* when the hermit crabs lacked food or were in high population densities. Similarly, *Dardanus pedunculatus* will prey on *C. polypus* attached to their own shells or those of conspecifics (Imafuku et al., 2000). Brightwell (1951) noted that *Pagurus berhardus* would remove food from the gastric cavity of *Calliactis* sp. attached to shells. Aside from these instances, it seems that hermit crabs derive relatively little nutritional benefit from their associates.

4.4.4. Protection from predators or parasites

Although sponges appear to protect hermit crabs from predators by production of noxious chemicals or camouflage (Sandford, 2003), the clearest examples of protection from predators are found in the cnidarian associates of hermit crabs. Among hermit crab-hydroid symbioses, Rees (1967) discussed the possible role of the spiral dactylozooids was that of inhibiting predators from entering the shell. In spite of this characterization, the

exact function of these structures remains unknown (see Mills, 1976b). Grant and Pontier (1973) showed that predation on *P. acadianus* by the rock crab, *Cancer irroratus* Say, 1817, was reduced by occupancy of shells encrusted by *H. echinata*. Other hermit crab predators, including the stone crab *Menippe mercenaria* (Say, 1818) and the octopus, *Octopus joubini* were deterred from preying on *P. pollicaris* inhabiting shells encrusted by *Hydractinia* sp., while the calico crab, *Hepatus epheliticus* (Linnaeus, 1763) was not inhibited from preying on these hermit crabs (Brooks and Mariscal, 1985a). In contrast to studies indicating protection from predators, Weissberger (1995) showed that *H. symbiolongicarpus* provided no protection for *P. longicarpus* from predation by *Homarus americanus* and the hermit crabs did not choose hydroid-covered shells over bare ones. Jensen (1970) showed *P. bernhardus* preferred shells covered by *H. echinata*, but suggested that the hydroid did not deter predators or provide camouflage. In laboratory and field experiments with tethered hermit crabs, Buckley and Ebersole (1994) showed that the blue crab, *Callinectes sapidus* Rathbun, 1896, preyed on *P. longicarpus* in shells with *Hydractinia* sp. and shells lacking the hydroid in approximately equal proportions. However, those hermit crabs in shells with hydroids survived fewer attacks than those without the hydroids. Buckley and Ebersole (1994) suggested that the decrease in survival was due to reduced strength of hydroid covered shells (such shells are often older and harbor boring symbionts such as polydorid worms). Thus it is likely that protection from predators by hydroids depended on the species of predator in question (e.g., cephalopods, branchyurans, fishes, birds) and additional biological factors.

Among hermit crab-anemone symbioses, Ross and Boletzky (1979) and Balasch and Mengual (1974) showed that *D. arrosor* would actively seek out and place *C. parasitica* on their shells while in the presence of cephalopod predators. Ross (1971) found that both *D. arrosor* and *D. callidus* were protected from predation by the octopus *Octopus vulgaris* Cuvier, 1797, when inhabiting shells with *C. parasitica.* The geographic distribution of *C. parasitica* in warm temperate and tropical regions closely matches that of *O. vulgaris*, a predator of *Dardanus* spp. (Ross, 1971). The cloak anemone, *A. palliata*, did not stop *Octopus vulgaris* from ingesting *P. prideaux* associated with this anemone but the octopus was initially deterred in its attacks and in one case retreated after the first encounter; those hermit crabs without an association with *A. palliata* were immediately ingested (Ross, 1984). *Sympagurus dimorphus* initiated association with *P. rosea* but the impacts on predation are unknown (Hand, 1975b). Poulton (1922) showed that *P. bernhardus* associated with *C. parasitica* and *P. cuanensis* associated with the sponge *S. domuncula* were protected from predation by fish. The presence of young hermits lacking association with *C. parasitica* in the gut contents of fish supports the conclusion that the anemones provide protection from predators. Elmhirst (1910) discussed similar avoidance by fish of "strawberry crabs" (*P. prideaux* in shells with *A. palliata* attached). Such results should be interpreted carefully because larger hermit crabs may have refuge from predation regardless of association with anemones.

Some researchers have suggested that hermit crabs may benefit from their associates by their action of feeding on parasite larvae (e.g., bopyrid isopods, rhizocephalan barnacles) before the parasites have a chance to infect hermit crab hosts (Harrington, 1897; Reiss et al., 2003). However, no tests or data to support this hypothesis have been recorded.

4.5. Associates—positive effects from hermit crabs

4.5.1. Food

Bruce (1969) suggested *H. harpax* may feed on the feces of host hermit crabs and this was apparently confirmed by Tattersall (1962) although Vannini et al. (1993) found no evidence for feeding on feces. Stubbings (1940) speculated that the barnacle *Pagurolepas conchiola* might feed on the feces of its host, *Sympagurus andersoni* (based on the position of the barnacle within shells), but the feeding habits of the barnacle remain unknown (Keeley and Newman, 1974). Lytwyn (1979) indicated that feces were not a possible food source for the polyclad flatworm *S. zebra* but suggested that lumen symbionts, such as the often abundant slipper limpet, *C. plana*, might be. The latter was consumed readily in laboratory trials (Lytwyn and McDermott, 1976; Lytwyn, 1979).

Fox (1965), Ross (1967, 1984) and Ates (1995) described the feeding of *A. palliata* by host hermit crabs. Cerrano et al. (1998) showed that *Podocoryne exigua* carried by *D. pugilator* fed on particles at the sediment surface. *H. echinata* and *P. carnea* may ingest food dropped by host hermit crabs during feeding (Wright, 1973). Dauer (1991) and Williams and McDermott (1997) have shown that *D. commensalis* ingests food particles dropped by the host hermit crabs or food particles attached to the host hermit crab legs. Nereid worms associated with hermit crabs (e.g., *C. peristomialis* and *N. fucata*) feed on food particles being handled or dropped by hosts (Brightwell, 1951; Hand, 1975b).

Hermit crabs also expose epibionts to new areas of food resources through their movements (e.g., Stachowitsch, 1980; Cerrano et al., 1998). As indicated by Jennings (1974, p. 141) and others, the hermit crab's respiratory currents bring in "a supply of easily ingested food". Yipp (1980) indicated that the filter-feeding gastropod *Crepidula walshi* enjoyed increased food supply through its position inside hermit crab shells. Taylor (1991) indicated that the feeding currents of host hermit crabs were much greater than those of tube-building bryozoans and those currents might enhance the feeding of bryozoans, as evidenced by the increased colony growth around shell apertures. This situation appears to be analogous to that found in *Hydractinia* spp. which exhibit long tentacles for feeding arranged around the apertures of inhabited shells.

4.5.2. Substrate

Hendler and Franz (1971) have shown that juveniles of the direct developing *Crepidula convexa* attached to the shells of *P. longicarpus* may attach to other hermit crab shells or colonize surrounding hard substrates (e.g., stones, bivalve shells, etc.). *C. convexa* inhabiting other hard substrates differ in morphology, behavior, and maturation rate from those on hermit crab shells (Franz and Hendler, 1970; Hendler and Franz, 1971). Karlson and Cariolou (1982) found that *C. convexa* rapidly colonized shells inhabited by hermit crabs introduced into the Delaware Bay where sediment rich environments dominate (41% and 87% of shells were colonized after 1 d and 2 wk, respectively). *C. convexa* will also settle on shells inhabited by *P. pollicaris* (Shenk and Karlson, 1986). Karlson and Sullivan (1989) showed that the gastropods were mobile and tended to move from shells occupied by *P. pollicaris* in high densities to more favorable associations with *P. longicarpus*. Although sponges

such as *P. suberitoides* benefit from the mobile substrate offered by hermit crab shells, Sandford and Kelly-Borges (1997) found sponges abandoned by host crabs could settle in deep water and continue to grow.

4.5.3. Protection from burial

Wright (1973) indicated the hydroids *H. echinata* and *P. carnea* benefited from their association with hermit crabs by not being buried. Conover (1975) showed that burial of gastropod shells is prevented by hermit crabs, thus providing critical benefits to epibiotic associates. Creed (2000) found that the tube-building polychaete *Hydroides plateni* was more abundant on the dorsal side of hermit crab shells where the worms were not exposed to sediment. However, the oyster *Ostrea puelchana* showed no preference for dorsal or ventral sides of hermit crab shells, indicating the species is more resistant to burial or because the oyster can direct its shell growth upwards (Creed, 2000). Some hermit crabs burrow periodically in sediments during ebbing daytime tides (Rebach, 1974; Kuhlmann, 1992; McDermott, personal observation) but permanent burial of discarded shells is reduced because shells are limited in many hermit crab populations. During burrowing by hermit crabs, the activities of epibiotic organisms are unknown. Investigations on the activity of *Hydractinia* spp., polydorids, and other associates during such periods would be an informative area of research.

4.5.4. Protection from predators

In addition to gaining protection from burial, it has been suggested that hermit crabs provide protection from predators by their locomotion (e.g., Hoberg et al., 1982; Conover, 1975). Brooks and Gwaltney (1993) showed that *Calliactis* sp. and hydroids (*Hydractinia* sp. or *Podocoryne* sp.) were protected from predation by sea stars, and the anemone was also protected from fireworms, *Hermodice carunculata* (Pallas, 1776).

4.5.5. Exposure to favorable environmental conditions

Various authors (e.g., Balss, 1924; Vosmaer, 1933; Morris et al., 1989) have suggested that epibionts gain access to favorable environmental conditions (oxygen, salinity, temperature) by association with hermit crabs. Epibionts of intertidal *P. longicarpus* in the northern latitudes of the western Atlantic are protected from freezing by migration of crabs to subtidal locations during the winter (Rebach, 1974; McDermott, 1999). Water carried in the shells of terrestrial hermit crabs can be used by collembolid and mite associates (Greenaway, 2003).

4.5.6. Reproduction

Movement and clustering behavior of hermit crab hosts (e.g., Gordon, 1972; Turra and Leite, 2000) may enhance the reproductive success of associates through increased potential for cross-fertilization. Taylor (1994) and Ryland (2001) suggested that this might occur among bryozoan associates of hermit crabs. The male zooids on mammillae may allow sperm released from their tips to be transferred to colonies brought together by hermit crab movements (Ryland, 2001; Taylor, personal communication). Hendler and Franz (1971) showed that mobile males of the slipper shell *C. convexa* move to new hosts when crabs are clustered, and thus they may fertilize more than one female. Similarly,

Table 4
Hypersymbionts associated with hermit crabs

Primary symbiont	Hypersymbiont	Hermit crab	References
Protozoa			
Platyfolliculina paguri	*Pottsia infusorium*[a]	*Pagurus pubescens*	Sprague and Couch, 1971
Porifera			
Pseudospongosorites suberitoides	*Doris verrucosa*	*Pagurus impressus*	Sandford, 1994
Suberites domuncula	*Aristias neglectus*[a]	*Paguristes eremita* *Pagurus cuanensis*	Stachowitsch, 1980
	Asterocheres simulans[a]	unidentified[b]	Ivanenko, 1997
	Colomastix pusilla[a]	*Paguristes eremita* *Pagurus cuanensis*	Stachowitsch, 1980
	Leucothoe spinicarpa[a]	*Paguristes eremita* *Pagurus cuanensis*	Stachowitsch, 1980
Suberites sp.	*Asterocheres suberites*[a]	unidentified[b]	Mariani and Uriz, 2001
Cnidaria			
Calliactis armillatus	*Koleolepas tinkeri*	unidentified	Edmondson, 1951
Calliactis japonica	*Koleolepas avis*	*Dardanus arrosor*	Yusa et al., 2001
Hydractinia cf. *echinata*	*Cuthona nana*	*Pagurus acadianus* *Pagurus arcuatus*	Harris et al., 1975 Lambert, 1991 Folino, 1993, 1997
Hydractinia cf. *echinata*	*Phoxichilidium femoratum*	*Pagurus acadianus*[b] *Pagurus arcuatus*	Harris et al., 1975
Hydractinia echinata	*Precuthona peachi*	*Pagurus bernhardus*	Christensen, 1977
Hydractinia echinata	*Pleurocoptes hydractiniae*[a]	*Pagurus bernhardus*	Fauré-Fremiet, 1961
Hydractinia sp.	*Precuthona divae*	unidentified	Marcus, 1961
Hydractinia symbiolongicarpus	*Anoplodactylus* cf. *lentus*	*Pagurus longicarpus*	McDermott, 2001
Hydractinia symbiolongicarpus	*Cuthona* sp.	*Pagurus longicarpus*	McDermott, 2001
Platyhelminthes			
Stylochus zebra[c]	*Crepidula plana*	*Pagurus pollicaris*	Lytwyn, 1976, 1979 Lytwyn and McDermott, 1976
Annelida			
Dipolydora armata	*Cothurnia* sp.[a]	*Calcinus tubularis*	Bick, 2001
Dipolydora cf. *socialis*	*Mesnilia* sp.[a]	*Pagurus minutus*	Williams, unpublished data
Dipolydora cf. *socialis*	peritrichous ciliophora[a]	*Calcinus* spp.	Williams, unpublished data
Dipolydora tridenticulata	peritrichous ciliophora[a]	*Calcinus* spp.	Williams, 2001b
Polydora neocaeca	peritrichous ciliophora[a]	*Pagurus longicarpus*	Williams and Radashevsky, 1999

Table 4 (*continued*)

Primary symbiont	Hypersymbiont	Hermit crab	References
Mollusca			
Crepidula cf. *nivea*	*Fabia granti*[d]	*Petrochirus californiensis*	Glassell, 1936
Anomia simplex	*Tumidotheres maculatus*[d]	*Pagurus pollicaris*	McDermott, unpublished data
Arthropoda			
Porcellana sayana	*Aporobopyrus curtatus*[d]	*Dardanus venosus* *Petrochirus diogenes*	Gore, 1970 Markham, 1975, 1988
Bryozoa			
Alcyonidium albescens	*Corambe obscura*	*Pagurus longicarpus*	McDermott, 2001

These relationships consist primarily of a symbiont with its hypersymbiont, the hermit crab and its shell being the third party in the relationship. All hypersymbionts, except as indicated below are predators of the primary symbiont.

[a] Commensal.

[b] Hypersymbiont of hermit crab associates but not yet documented from hermit crabs.

[c] Either the polyclad or slipper shell could be primary symbiont.

[d] Parasite.

Brown and Olivares (1996) suggested males of *Crepidula coquimbensis* colonize new shells during host clustering.

4.6. Associates—negative effects from hermit crabs

4.6.1. Kleptoparasitism/predation

Cerrano et al. (1998) found that under laboratory conditions, *D. pugilator* would steal *Artemia* nauplii from the polyps of *P. exigua* located near the shell aperture. Other hermit crabs can steal the food from hydroids or feed directly on them (see benefits to hermit crabs from associates, Section 4.4.3).

4.7. Hypersymbioses and interactions between associates

It is not surprising that a variety of epibionts such as sponges, hydroids, bryozoans and tunicates are found attached to shells of hermit crabs, and they, in turn, attract specific predators. Nudibranch molluscs are good examples of such predators and it is well known that their veliger larvae find and metamorphose on species that may eventually be used as food for the developing adults (Thompson, 1976; Yonge and Thompson, 1976). These gastropods often deposit their eggs on or near prey. We refer to such associations as hypersymbiotic relationships, which, in turn, may be the beginning of a symbiotic web (Rees, 1967) involving the hermit crab (Table 4). Christensen (1977) has argued that this is a typical prey–predator relationship and not a symbiotic one because nudibranchs must find more food than may be attached to shells, thus leaving the hermit crab complex. His study involved the *P. peachi–H. echinata–P. bernhardus* association in the eastern

Atlantic. However, such nudibranchs probably metamorphose on the prey and it is unlikely that they can easily or safely leave to find other hosts.

The nudibranch *C. obscura* feeds on encrusting bryozoans (Cory, 1967; Franz, 1967; Perron and Turner, 1977) (Table 4). However, the nudibranch is attracted to *A. albescens* living on the shells of *P. longicarpus* from New Jersey where it has been shown to be >75 times more abundant on shells with this bryozoan than shells lacking *A. albescens* (McDermott, 2001). *C. nana* is found on shells with *P. acadianus* and presumably *P. arcuatus* encrusted with *Hydractinia polyclina* in New England waters, where the nudibranch metamorphoses and feeds on this symbiotic hydroid (Harris et al., 1975). The same nudibranch species from the eastern Atlantic apparently feeds on *H. echinata* attached to *P. bernhardus* shells (Christensen, 1977). Christensen (1977) also showed that *P. peachi* veligers are induced to metamorphose in the presence of *H. echinata.* Another cuthonid nudibranch, *Tergipes despectus*, is a predator of *Hydractinia*, but is rarely found on hermit crab shells from Long Island Sound, CT (Buss and Yund, 1988).

Sandford (1994) found the nudibranch *D. verrucosa* feeding on the sponge *P. suberitoides*. Additional predators of sponges on hermit crab shells include the copepods *Asterocheres simulans* and *A. suberitis* (Ivanenko, 1997; Mariani and Uriz, 2001). The copepods can reach high numbers (>3000) on sponges (Ivanenko, 1997).

Certain pycnogonids are predators of hydroids (McDermott, 2001). Harris et al. (1975) noted that *P. femoratum* was found on free-living *Hydractinia* colonies in Maine and presumably on colonies encrusting shells with *P. acadianus*, but they gave no evidence that the sea spider preyed on the hydroid. In New Jersey, *Anoplodactylus* sp. was found on four shells of *P. longicarpus* encrusted with *H. symbiolongicarpus*, but feeding was not documented (McDermott, 2001). Not all examples of hypersymbioses are based on predator–prey relationships (Table 4). For example, two species of the copepod genus *Mesnilia* are obligate commensals of polydorid worms that bore in mollusc shells. An undescribed species of *Mesnilia* has been found in the burrows of *Dipolydora* cf. *socialis* from hermit crab shells in Hong Kong (Williams, personal observation). Other hypersymbionts of polydorid worms include peritrichous ciliates that attach to the setae of these worms (Williams and Radashevsky, 1999; Bick, 2001; Williams, 2001b).

The porcelain crab *P. sayana* may be found free-living but is usually associated with a variety of hermit crabs (Table 1), and may harbor a branchial parasite *Aporobopyrus curtatus* (Richardson, 1904) (Markham, 1975, 1988). This is the only bopyrid isopod known from *P. sayana*. Two pinnotherid crabs are involved in hypersymbiotic associations. *Fabia granti* resides in the mantle cavity of *Crepidula* cf. *nivea*, itself a internal epibiont of *P. californiensis* (Glassell, 1936), and *Tumidotheres maculatus* may be found in the mantle cavity of *Anomia simplex*, an external epibiont of *P. pollicaris* (McDermott, unpublished data). Two other species, a porcellanid crab and a polynoid polychaete, are part of the symbiotic web with *P. californiensis*.

Other hypersymbiotic relationships represent incidental associations. For example, Sandford (1994) indicated that the sponge, *P. suberitoides*, might contain barnacles, brittlestars, crabs, isopods, amphipods, and polychaetes. Similarly, a variety of organisms may live on or within crevices created by encrusting bryozoans found on hermit crab shells (Kirkpatrick and Metzelaar, 1922; Morris et al., 1989; Taylor, 1991). Taylor (1991)

observed feeding of tanaids and spionids associated with *D. gordoni* and suggested cleaning symbioses might exist between these hypersymbionts and the host bryozoan.

5. Conclusion

The fossil record indicates that hermit crab associations probably first arose in the Jurassic, and multi-species assemblages may have been established by the Cretaceous. In all major phyla examined, symbiotic relationships with hermit crabs have evolved multiple times. It appears that most associations arose initially as a function of hermit crab shells providing a substrate for attachment or for boring. These associations were reinforced by enhanced feeding and protection from predators of the symbionts through the activity of hosts. Shell availability and use is a critical aspect in the life history of hermit crabs and many populations appear to be controlled by this factor (Hazlett, 1981; but see Barnes, 1999). For this reason shells remain in circulation within hermit crab populations because of ontogenetic shell exchanges, and few shells remain empty among such populations. The impacts of associates on the shell utilization patterns of hermit crabs could be significant and need to be examined (Fig. 9).

Hermit crabs have generally gained less from their relationships with symbionts than their associates but in many regions they must inhabit shells with these associates because of a limited supply of empty shells. However, encrusting organisms such as cnidarians and bryozoans may provide extension of shell apertures and thereby reduce or remove the need for hosts to find new shells, a benefit with clear fitness consequences. Among cnidarians there are also examples of mutualism whereby anemones and hydractinians provide protection from predators (e.g., crabs, octopus, and fish) to host hermit crabs. Alternatively, among four phyla (Cnidaria, Platyhelminthes, Annelida, and Arthropoda) there are examples of species previously described as commensals that feed on the eggs of hosts, indicating that their relationships with hermit crabs need to be reexamined. Additional phyla contain species that exhibit temporal changes in the symbiotic nature of their relationships with hosts, changing from commensalistic or mutualistic to parasitic interactions depending on environmental and biological factors (e.g., anemones may provide protection in the presence of predators but in the absence of predators are an energy burden to hosts). In this way a complex variety of interactions and symbiotic relationships have evolved in the community established by hermit crabs through their use of gastropod shells. As indicated above, many of these symbiotic relationships do not fit clearly into one category; thus the symbioses are better thought of as continuums where the benefits and costs to hosts and associates can change depending on conditions (Bush et al., 2001).

In spite of the difficulty in defining the symbiotic relationships between some hermit crabs and their associates, it is clear that hermit crabs are allogenic ecosystem engineers in a wide range of habitats from terrestrial to deep-sea regions. In addition, their use of gastropod shells can extend the distribution and diversity of associated species and thus provide an example of facilitation (Bruno et al., 2003). In terms of the facilitation model, the realized niches of these associates are larger than predicted by their fundamental niches. The situation is similar to the impacts of *Spartina alterniflora* expanding the range
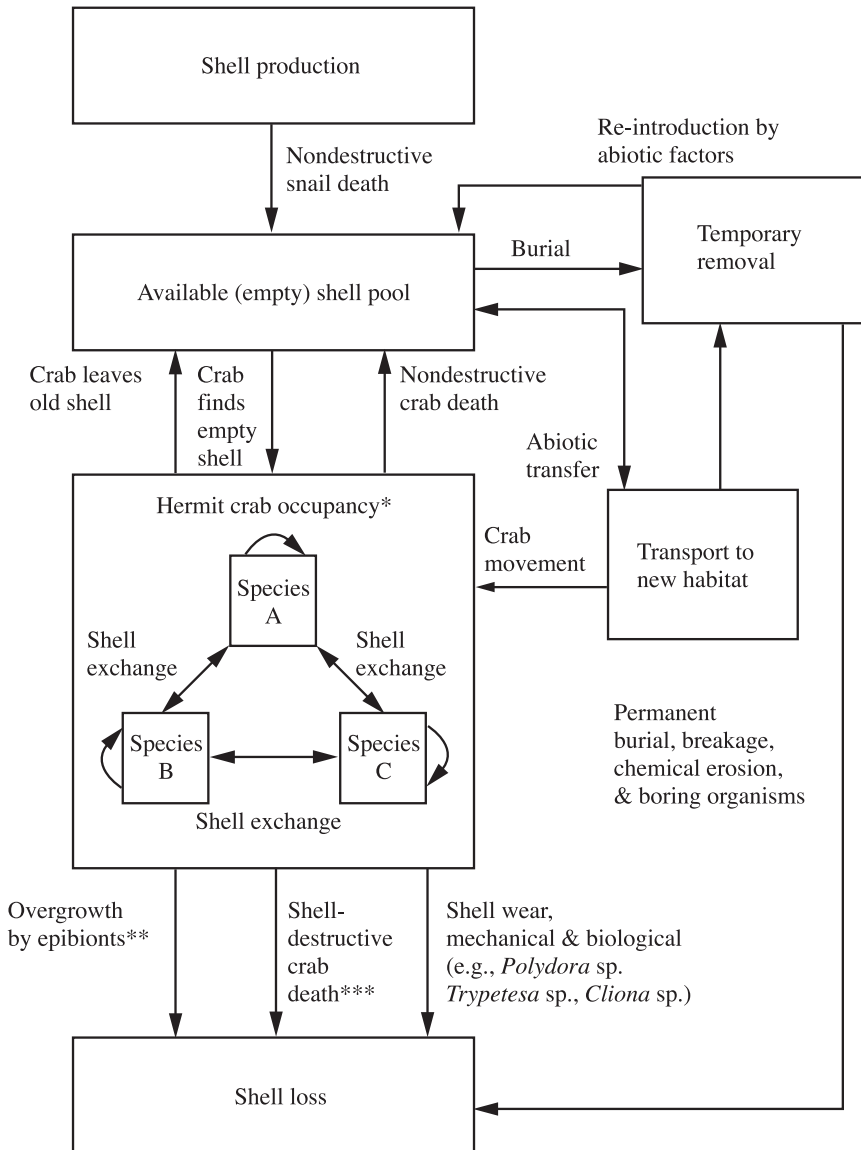
Fig. 9. Flowchart showing shell movement in hermit crab populations with impacts of symbionts noted (modified from Lancaster, 1988, Fig. 7). *Shell exchanges can be influenced, negatively (shell abandonment) or positively (shell adoption), by symbionts. **Overgrowth can lead to shell loss but can also alleviate the need for occupancy of new shells through growth with hermit crabs (e.g., sponges, cnidarians, and bryozoans). ***Shell boring associates can increase the success rates of hermit crab predators.

of a whole community of fauna and flora (Bruno et al., 2003) and oyster beds that provide refuge for a diverse assemblage of species (Wells, 1961). Reiss et al. (2003) have shown that in deep, soft-bottom habitats of the North Sea hermit crab shells occupied by *P. bernhardus* are important in providing solid substrates for the association of epifauna normally restricted to hard-bottom habitats. Some hermit crab associates may also extend the range of hosts. For example, by providing protection from predation, cnidarians allow hermit crabs to survive in areas where predators are abundant or in deep-sea regions where shells may be limited. Research on the possible impacts of hermit crab parasites on the structure of communities, as has been investigated in communities associated with cockles (Thomas et al., 1998; Lafferty et al., 2000; Mouritsen and Poulin, 2003) should be completed. Continued study of hermit crab biocoenoses will enable us to further assess the importance of hermit crabs as marine ecosystem engineers (e.g., possible within the framework established for the ghost shrimp, *Callianassa filholi* H. Milne-Edwards 1878; Berkenbusch and Rowden, 2003) and provide a model for including facilitation into ecological theory.

Factors influencing the diversity of communities associated with hermit crabs and interactions within these communities remain poorly studied. The distribution of hermit crab hosts may influence diversity patterns. For example, Reiss et al. (2003) found significant differences in assemblages of species associated with *P. bernhardus* from northern and southern regions of the North Sea, most likely due to differences in the physical conditions (currents and temperatures) between these regions. However, differences in number of taxa associated with hermit crabs within and between geographic regions in the present review (Fig. 2) most likely represents disparities in sampling efforts of the hermit crab biocoenoses rather than real differences in diversity patterns. For example, while some temperate species (e.g., *P. bernhardus*) are associated with over 110 invertebrates, most Indo-West Pacific species have been found with only a few associates; these findings run counter to expectations based on biodiversity of the regions and are probably biased due to the efforts of researchers focusing on particular regions (Fig. 2). We hypothesize that with additional studies, the communities of invertebrates associated with hermit crabs will more closely approximate global biodiversity patterns found among free-living species (e.g., Roy et al., 1998; Briggs, 1999). Specifically, it is predicted that diversity will be highest in the Indo-West Pacific and less in the Atlantic, with diversity decreasing with increasing latitude.

Hermit crabs and the communities of species they support could act as excellent models to examine diversity patterns among geographic regions at a variety of scales. Barnes (2003) investigated the organismal trends of shell use among hermit crabs and provided evidence for discernable global trends in shell resource utilization, similar to studies that have been completed on live gastropods (Wahl and Sönnichsen, 1992; Voight and Walker, 1995). Researchers could complete such investigations on whole communities of species associated with hermit crabs from a wide range of geographic regions as well as habitats. This review can act as a baseline for such studies but the time has come for more quantitative analyses of hermit crabs assemblages.

It is our hope that this review provides a springboard for future experimental studies on the multitude of questions regarding the natural history, ecology, and symbiotic relations of hermit crabs and their associates. Deep-sea hermits potentially have a variety of associates many of which may be new species (particularly actinians; Ates, 2003) but

studies of such communities have been meager or inadequate. Similarly, although land hermit crabs have been studied in terms of behavior, few researchers have examined their associates and virtually nothing is known of interactions between these symbionts and hosts. Investigations of the physical and biological factors related to the establishment of the symbioses, as well as hypersymbioses and predator–prey relationships, in these communities would provide rewarding research for many theses.

Acknowledgements

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